

Research article

Species differences in exhibit use by antelope, addax *Addax nasomaculatus*, and sable *Hippotragus niger*

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Abstract

Some conservation breeding centres provide semi-natural conditions for hoofstock herds, to achieve the goal of maintaining genetic and behavioural resilience suitable for eventual reintroduction of conservation-reliant species. Little is known about mixed-species grazing by allopatric herbivores outside their native ranges (ex situ), although species and breed differences have been documented for domestic livestock as well as for sympatric wildlife species. The grazing and resting activities of two species of horse antelope (Hippotraginae) were examined in a central Texas ecoregion characterised by wooded and open grass patches. Theoretically, the mesic-adapted sable antelope *Hippotragus niger*, would prefer high productivity patches more than the desert-adapted addax *Addax nasomaculatus*. At three times of the day, behavioural activity and locations of sable (n=28) and addax (n=37) relative to three types of vegetation patches were recorded. It was predicted that sable would more likely (1) forage in locations with higher biomass and (2) rest in shade during midday. Ranked by decreasing forage biomass, the vegetation patch types included introduced exotic grass species (improved), forbs and grasses (native), and woody shrubs or trees (juniper). Shade was greatest in the juniper patches, and temperature was highest during midday. Sable were more likely to be in improved patches (overall and while foraging) and addax were more likely located in native patches. Both species rested in shady juniper patches, primarily during morning and midday. Based on hierarchical analyses using logistic regression models, individual use of patch types was a complex interaction of species, time of day and activity. Use of patches changed significantly during the day, species used patches differently, and foraging behaviour differed among the patches. Better understanding of species differences in use of an ex-situ landscape can contribute to maintaining herd health and behavioural resilience, as needed to meet goals of in-situ population restoration.

Introduction

Understanding how animals use habitat is essential for enhancing the success of reintroductions (Stamps and Swaisgood 2007; Berger-Tal et al. 2011; Berger-Tal and Saltz 2014). For management of ungulate species at risk of extinction in their native habitat, ex-situ mixed-species grazing systems are a viable option to augment population size and maintain behavioural diversity (Sawyer 2012; Packard et al. 2014). Managing large herds in semi-natural pasture conditions contributes to achieving ex-situ conservation goals; however,

little is known about landscape use by allopatric ungulate species outside their native ranges.

Scimitar-horned oryx *Oryx dammah* are an example of an ungulate species that has benefitted from ex-situ conservation efforts (Woodfine and Gilbert 2016; Chuyen et al. 2018). Previously declared extinct in the wild, captive populations have contributed to recent introductions in Chad (Chuyen et al. 2018). Multiple institutions have collaborated to achieve the goal of maintaining genetic diversity and behavioural resilience in a healthy self-sustaining population suitable for further reintroduction programmes throughout the Sahelo-Saharan

region (Chuyen et al. 2018). Lessons learned will contribute to restoration of other rare species in the region (Durant et al. 2014; Newby et al. 2016), most notably the value of herd cohesion for individuals to learn about suitable sites for foraging and resting behaviour.

The extent to which genetic propensities for foraging are modified by social learning is still an open question. Evidence for differential use of habitat patches within the same landscape emerged from comparisons of different livestock species (Ferreira et al. 2013; Falú et al. 2014; Bremm et al. 2016), different breeds within a species (Peinetti et al. 2011; Bear et al. 2012; Dolev et al. 2014), and domestic versus wildlife species (Pruvot et al. 2014; Schroeder et al. 2014; Nagarajan et al. 2016; Schieltz and Rubenstein 2016). Intrinsic factors potentially influencing foraging patterns may include body size, ranging behaviour (i.e. locomotion) and use of shaded sites (i.e. thermoregulation).

Extrinsic factors influencing differential use of a landscape by sympatric herbivores include density of woody vegetation (i.e. thickets), access to water, presence of green leafy vegetation (Macandza et al. 2012), burn patches (Venter et al. 2014), aversion to roads (Jiang et al. 2010) or other species (Johnson et al. 2000) and movement between foraging arenas (Owen-Smith et al. 2015; Owen-Smith and Martin 2015). Foraging arenas are the locations where foraging activities are concentrated for one period (e.g. weeks to months) before a herd moves on to another location of concentrated foraging activity within its home range. Added complications in determining resource use may be competitive displacement of one species by the other (Macandza et al. 2012) and facilitation of plant growth by grazing (Arsenault and Owen-Smith 2002). Competition and facilitation between cattle and wild ungulates varies with location, species and season (Schieltz and Rubenstein 2016).

Habitat use by two allopatric species (*Addax nasomaculatus* and *Hippotragus niger*) was examined in a multiple-species mixed-grazing system located in the Cross Timbers ecoregion of central Texas, a mosaic of wooded and grassy vegetation patches. The objectives were to determine: (1) how species differed in use of feeding arenas within a landscape, (2) how use of patches was associated with temperature, time of day and animal activity states, and (3) how well the complex interactions among internal and external factors predicted use of shaded and open vegetation patches.

Methods

Study species and site

Subjects were two species of Hippotraginae (African horse antelope) adapted to distinctly different ecoregions: wooded savanna (sable) and desert (addax). Sable are characterised as an edge species in eastern and southern Africa, moving seasonally between woodland and grassland patches to forage on green vegetation (Estes 1991; IUCN SSC Antelope Specialist Group 2017). Overall, the dietary tolerance of sable allows them to use areas of poor soil where they are less vulnerable to predation risk (Owen-Smith et al. 2013). During dry seasons, sable select a diet that includes green growing leafy vegetation in stands of tall grasses on the uplands near floodplains (Hensman et al. 2014) or regrowth on burn patches (Magome et al. 2008; Parrini and Owen-Smith 2010; Hensman et al. 2012; Asner et al. 2015). In contrast, addax are adapted to the Sahelo-Saharan region, moving long distances between patches of grasses that emerge in response to sporadic rainfall and obtaining most water from vegetation (Estes 1991; Durant et al. 2014). Since addax are virtually extinct in the wild, very little is known about free-ranging foraging behaviour (Krausman and Casey 2007; IUCN SSC Antelope Specialist Group 2016; Newby et al. 2016).

Both species are the focus of ex-situ conservation breeding programmes designed to maintain sustainable populations for species recovery (Sawyer et al. 2011; Sawyer 2012). Addax are listed as Critically Endangered (IUCN SSC Antelope Specialist Group 2016) and efforts are underway for reintroduction (Woodfine et al. 2004; Durant et al. 2014). Intensive recovery efforts have yielded tools for reproductive and genetic management of the ex-situ addax population (Morrow et al. 2009; Heim et al. 2012). Reproductive behaviour of addax has been studied ex situ (Spevak et al. 1993; Packard et al. 2014). Although some sable populations have been in decline (Asner et al. 2015; Crossmary et al. 2015), overall the species is listed as of Least Concern (IUCN SSC Antelope Specialist Group 2017).

Ideally, large herds of both species would be maintained for captive breeding (Sawyer 2012). Social cohesion differs between addax and sable. Female groups of five to 20 sable typically occupy the territory of one male (Estes 1991). In contrast, addax switch between mixed-sex groups during migratory periods and male territoriality during sedentary periods (Krausman and Casey 2007; Spevak et al. 1993).

The study site (Fossil Rim Wildlife Center, Texas, USA) was a conservation breeding centre accredited by the Association of Zoos and Aquariums (AZA). The Fossil Rim Wildlife Center study site was similar to wooded savannah in Africa, the site was located (32.180556, -97.796389) in the Limestone Cut Plain of the Cross Timbers ecoregion (Griffith et al. 2007). Vegetation has been described in detail for the site (White 2015) and region (Dyksterhuis 1946; Correll and Johnson 1970; McGregor et al. 1986). The landscape included native patches of open grassy meadows. Productivity of selected patches on moisture retaining soils had been improved by introduction of Bermuda grass, an exotic of mid-eastern origin. Patches of wooded thickets were dominated by Pinchot juniper *Juniperus pinchotii* and Ashe juniper *J. ashei*, with drainages including blackjack oak *Quercus marilandica*, post-oak *Q. stellate* and diverse shrubs. Unpalatable plant species included common horehound *Marrubium vulgare*.

In addition to the addax (n=37) and sable (n=28), this mixed grazing system included white tailed deer *Odocoileus virginianus*, axis deer *Axis axis*, fallow deer *Dama dama*, gemsbok *Oryx gazella*, and waterbuck *Kobus ellipsiprymnus*. The area (182 ha) was fenced to exclude predators (Figure 1). Vegetation patches within the visible area from the survey route were categorised based on dominant species composition: (1) native patches had forbs and grasses with less than 50% Bermuda grass (434 m², 41%), (2) improved patches had a species composition of over 50% Bermuda grass (390 m², 33%), and (3) juniper patches were wooded with over 80% canopy cover (346 m², 26%) and negligible forage. The quantity and quality of forage was higher in improved patches compared to native (White 2015). Juniper patches provided the most shade. Water was available ad libitum in a creek, several ponds and watering troughs. Supplemental feed pellets (17% protein) were provided on a daily basis: (1) spread by staff along specified sections of the survey route in the morning and (2) tossed by visitors from vehicles traveling on the tour route from 0900 to 1700.

Data collection

The sampling design was balanced, with 10 repetitions of a standardised survey within each of three time periods: morning (0600–0900), midday (1200–1500), and evening (1800–2100). Temperature was recorded on site at the beginning of each survey. All surveys were conducted during July 2014, a dry season in this region. The predefined survey route (Figure 1) was driven until the first encounter of either species. Upon encounter, location of the vehicle was recorded using a Global Positioning System. Individual animals were categorised to species, sex, age (adult, yearling,

Table 1. Distribution of sightings by species (addax and sable), patch type (improved, juniper and native) and time period (morning 0600–0900, midday 1200–1500 and evening 1800–2100).

Species	Patch type	Sightings (% per patch type)	Time period (% per time period within patch)		
			Morning	Midday	Evening
Addax	Improved	100 (22%)	19 (19%)	39 (39%)	42 (42%)
	Juniper	167 (37%)	67 (40%)	76 (46%)	24 (14%)
	Native	183 (41%)	65 (36%)	17 (9%)	101 (55%)
Totals		450	151 (34%)	132 (29%)	167 (37%)
Sable	Improved	335 (64%)	84 (25%)	94 (28%)	157 (47%)
	Juniper	152 (29%)	79 (52%)	69 (45%)	4 (3%)
	Native	38 (7%)	4 (11%)	6 (16%)	28 (74%)
Totals		525	167 (32%)	169 (32%)	189 (36%)

calf), patch type (native, improved, juniper) and behavioural activity state (alert, feeding, locomote, rest, social; as defined in Packard et al. 2014). For each individual, a compass bearing was recorded from the vehicle to the animal as well as the distance in metres (obtained by rangefinder).

All data collected were recorded into a real-time event programme Mysticetus Observation System (Entiat River Technologies, Preston, WA, USA <http://mysticetus.com>). This programme used the vehicle location coordinates, compass bearing and distance to calculate a proximate position of each individual sighting and to plot the data in real time. To improve accuracy, locations were viewed on the map window displayed by the Mysticetus programme and remeasured if the visual location was inconsistent with the mapped location.

Data analysis

To visualise overall distribution of the two species relative to habitat patches, density isoclines were mapped using the “heatmap” function of Quantum GIS with a radius of 30 m (QGIS Development Team, 2014). Sightings included in the analysis (addax, $n=450$; sable, $n=525$) met the predetermined criteria for spatial accuracy (estimated at 10–100 m). Observations that were outside the boundaries of defined habitat patches were coded as missing data due to technical error. Inaccurate locations were primarily due to oblique angles measured from the vehicle to the animal.

A hierarchical approach to data analysis was used, examining first single effects, then pairwise interactive effects (described below). The response variable was the number of sightings in each patch type. Finally, separate logistic regressions were used to determine the best combination of variables predicting sightings in (1) each type of forage (native, improved), and (2) shaded (juniper) compared to open vegetation (native and improved).

To test the independent association of each species (addax, sable) with patch type (native, improved, juniper), the X^2 goodness of fit test was used (Bakeman and Gottman 1986). The expected values for each patch type were based on the area visible from the survey route: native (41%), improved (23%), juniper (36%). Each specific patch type was delineated as a polygon. Size was

calculated for each polygon and summed within each category of patch type. Values for all polygons in a given category were summed to estimate the availability of that patch type. This analysis was repeated separately for each species (addax, sable). The null hypothesis was no difference between patch use and availability.

To test for pairwise interactive effects among variables, the G-squared log likelihood test (G^2) and binomial z-score were used (Bakeman and Gottman 1986). Given that a sighting of a given species occurred in a given patch type, the likelihood of a given activity to be different than expected by chance was analysed. The same logic was used to examine the association between time of day and patch type. Finally, the G^2 was used to test whether the species differed in the likelihood of foraging in each patch type. The data set was partitioned by activity and only the sightings classified as foraging were examined, to determine the interaction between species and patch type.

To determine the relative importance of predictive variables in forage and resting behaviours of addax and sable, two logistic regressions were conducted in JMP® Version 11.2 (SAS Institute Inc., 2015) with four covariates (temperature, time period, species and activity) and six interactions among covariates. The first logistic model reflects a larger scale where the effects of predictive variables on the probability that sightings were in grass versus wooded patches (open/shade) were examined. Then, at a finer scale, the use of grass patches was analysed to see which variables best predicted the use of native versus improved vegetation.

Results

Patch types

Use of vegetation patch types differed significantly for sable ($X^2=3923.74$, $df=2$, $P<0.001$) and for addax ($X^2=3345.93$, $df=2$, $P<0.001$). Sable were more likely to be sighted in improved than native grassy patches, in contrast to addax, for which this pattern was reversed (Table 1). Wooded juniper patches were used by both addax (37% of sightings) and sable (29%).

The sable herd was more cohesive than the addax herd (Figure 1), using a smaller foraging arena that overlapped only partially

with the larger foraging arena of the addax herd. Often all the sable sightings could be recorded from one vehicle location, whereas the addax sightings were spread among multiple vehicle locations. Addax were distributed more widely, with low densities of sightings in locations that were hotspots for sable (Figure 1). Sable were more likely to be sighted in the eastern portion of the pasture, where improved patches were located and supplemental feed pellets were distributed on the tour route (Figure 1).

Time of day

Both sable and addax were equally likely to be sighted at all times of day (Table 1). However, there was a significant interaction between use of patch type and time of day for both sable ($G^2=143.83$, $df=4$, $P<0.001$) and addax ($G^2=104.63$, $df=4$, $P<0.001$).

The differential use of improved and native patches occurred primarily in the evening (PM), when sable were more likely in improved ($z=4.14$) or native patches ($z=4.84$) and addax were primarily in native patches ($z=5.06$). Use of juniper by both species was less than expected by chance in the evening (addax, $z=-6.08$; sable, $z=-8.57$).

In the morning, sable were more likely in juniper ($z=5.34$) and less likely in improved ($z=-2.65$) or native patches ($z=-2.82$). Morning sightings of addax were least likely to be in improved ($z=-3.08$) and no different than chance in juniper or native patches ($z=1.80$).

By midday, sable remained in shady juniper patches ($z=3.48$) and sightings were no different than chance in native or improved patches ($z=-1.62$). Relatively more addax had moved into the juniper ($z=4.59$) and improved patches ($z=2.12$) by midday, when temperatures were highest.

Activity

For both species, feeding was the most likely activity (sable 45%, $n=233$; addax 52%, $n=232$), while the least likely activities were social (sable 2%, $n=8$; addax 2%, $n=8$) and alert (sable 6%, $n=33$; addax 4%, $n=18$). Both rest and locomotion activities differed between species. Sable were more likely to rest (sable 40%, $n=209$; addax 24%, $n=109$) and addax were more likely to locomote (sable 8%, $n=40$; addax 18%, $n=83$).

For each species separately, activity was compared in relation to vegetation patch type (Figure 2). The activities of sable and addax differed significantly between patch types (sable $G^2=27.24$; addax $G^2=49.68$; $df=8$, $P<0.001$). Feeding by sable was more likely in improved patches ($z=2.70$), in contrast to addax more likely to feed in native patches ($z=3.16$). In juniper, both species were more likely to rest (sable $z=2.00$; addax $z=4.67$), and unlikely to feed (sable, $z=-3.31$; addax, $z=-3.95$). Addax were unlikely to rest in native patches ($z=-3.96$). Alert activity was more likely in juniper (sable $z=2.90$; addax $z=2.11$). Sable were least likely to be alert in improved patches ($z=-2.95$).

The type of activity was controlled for to compare patch use for each species (Figure 3). Given that individuals were feeding, the species differed significantly in their use of patch types ($G^2=136.81$, $df=2$, $P<0.05$). Compared to addax, sable were more likely to feed in improved ($z=7.42$) and less likely in native patches ($z=-8.37$). Foraging addax showed the opposite pattern, more likely to be in native ($z=8.37$) and unlikely in improved patches ($z=-7.42$).

Logistic regression models

The variation in use of woody versus grassy patches was better explained by species, activity and time period than by temperature (Table 2 and 3). Considering the overall combination of single effects and interactions of variables in the logistic model, animals used woody shade patches significantly differently than open grassy patches ($X^2=201.51$, $df=10$, $P<0.0001$). Three single effects (species, activity, and time period) were significant ($P<0.0001$),

indicating the use of woody patches was different between species, activity differed in woody and grassy patches, and use of woody patches changed over time. Temperature alone had no effect in the use of open or shade patches ($P=0.1443$). Species interactions with time period, activity and temperature were not significant ($P=0.0531$, 0.1494 and 0.5922). Interactions of activity with time period and temperature were both significant ($P=0.0085$ and 0.0020), likely related to the significant interaction between time period and temperature ($P=0.0009$). Therefore, variation in use of shade was best explained by the separate effects of species and activity relative to time of day.

When animals were located in grassy vegetation, the overall logistic model predicting use of native versus improved patches was significant ($X^2=221.0492$, $df=10$, $P<0.0001$). Two single effects (species, time period) were significant ($P<0.0001$) and two were not (activity, 0.3803 ; temperature, $P=0.4920$). Significant

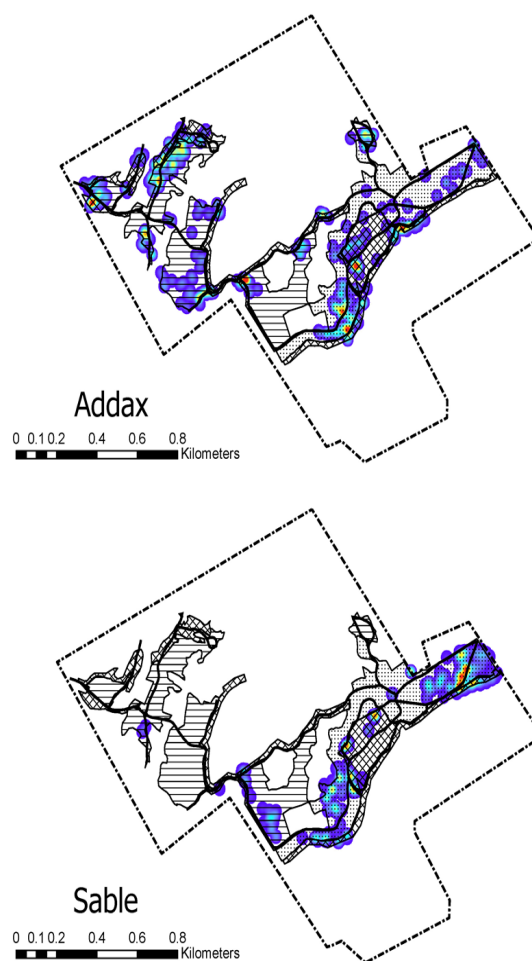


Figure 1. Density heatmaps at 30-m resolution of all addax (top) and sable (bottom) locations within habitat patches (native=checked, improved=dots, and juniper=horizontal lines). Red shows the highest density while blue represents low density. The survey route is shown by a thick black line.

Table 2. Logistic regression result of the effect likelihood ratio test for open/shade. Asterisks (*) denote significant P-values.

	χ^2	Probability> χ^2
Temperature	2.1311	0.1443
Time period	70.8788	<0.0001*
Species	17.1670	<0.0001*
Activity	24.8759	<0.0001*
Temperature × Time period	11.0413	0.0009*
Time Period × Species	3.7416	0.0531
Species × Activity	2.0787	0.1494
Temperature × Species	0.2869	0.5922
Time period × Activity	6.9241	0.0085*
Temperature × Activity	9.5950	0.0020*

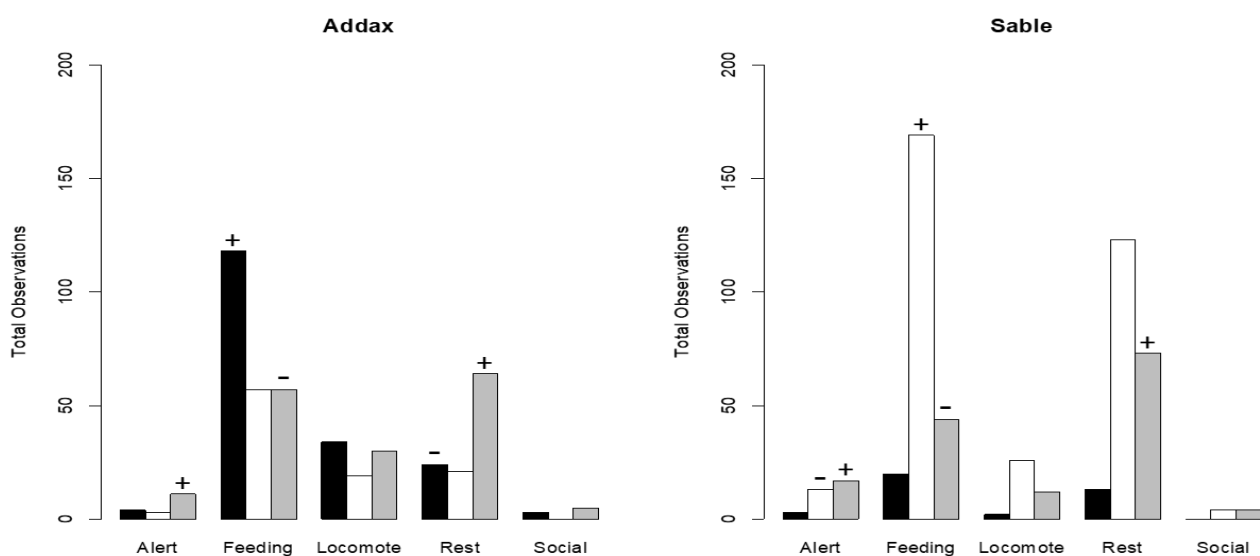
Table 3. Logistic regression results of the effect likelihood ratio test for native/improved. Asterisks (*) denote significant P-values.

	χ^2	Probability> χ^2
Temperature	0.4721	0.4920
Time period	17.7822	<0.0001*
Species	131.8486	<0.0001*
Activity	0.7697	0.3844
Temperature × Time period	27.1979	<0.0001*
Time period × Species	9.7581	0.0028*
Species × Activity	0.7603	0.3869
Temperature × Species	10.2150	0.0018*
Time period × Activity	5.7783	0.0178*
Temperature × Activity	12.7568	0.0005*

interactions occurred between species and time period ($P=0.0018$) as well as species and temperature ($P=0.0014$), likely related to the significant interaction between time period and temperature ($P<0.0001$). The interaction between species and activity was not significant ($P=0.3832$). The insignificant single effect of activity was complicated by significant interactions with time period ($P=0.0162$) and temperature ($P=0.0004$). In summary, the variables predicting use of grassy patches (improved, native) included both species and time of day, but the interaction indicated that species did not use these patches in the same way at different times of day.

Discussion

This study is the first comparison of two allopatric African species observed simultaneously in the same mixed-species grazing system, documenting incomplete overlap in foraging arenas during a snapshot in time (10 days). Given the same choices in this new-world wooded prairie landscape, sable were more likely to use green grassy patches with stands of more productive exotic grass species, compared to addax. Both species rested in shady juniper patches during midday, although addax also moved into improved patches in midday.

**Figure 2.** Activities of addax and sable within each habitat (native=black, improved=white, and juniper=gray). A plus (+) represents that the activity was more likely to occur than expected while a minus (-) represents that the activity was less likely to occur than expected.

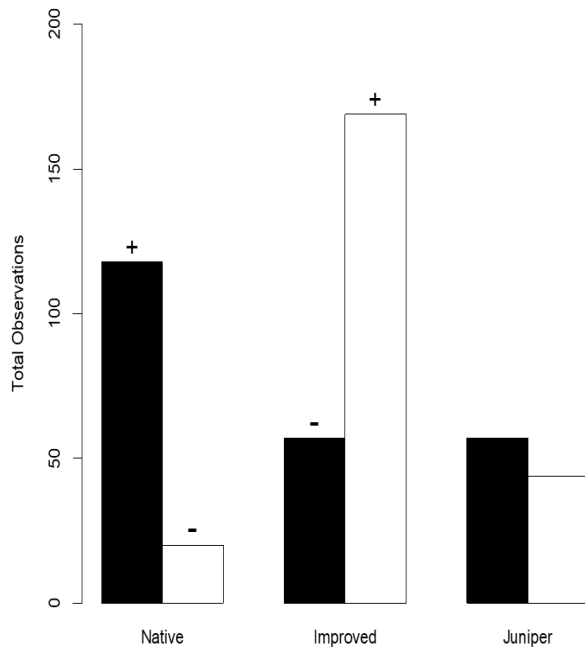


Figure 3. Feeding activity of addax (black) and sable (white) in each patch type. Symbols indicate feeding was more likely to occur than expected (+) or less likely to occur than expected (-) based on binomial z-scores.

The complex interaction among variables associated with patch choice, leads to the suggestion that both internal and external factors were involved. Below is a discussion of the implications for manipulating external factors to meet vegetation management goals for comparable mixed-species grazing systems, with the caveat that each species is likely to respond differently when internal factors differ due to divergent evolutionary adaptations. Additionally, external factors are likely to change with ecological cycles (e.g., seasonal and climatic oscillations).

Internal factors

If there is a genetic basis to species-specific differences in foraging patterns, it needs to be tested by comparing individuals of different species reared in the same environment (Rook et al. 2004). This study found that these two species differed in their use of the same pasture in the present study, despite the same rearing environment. Although diets of addax and sable are similarly categorised as variable grazers (60–90% monocots), the mass of sable is twice that of addax (Gagnon and Chew 2000). Consistent with their different physiological adaptations, sable in the present study were more likely to use grassy patches with moderately productive exotic species, in contrast to the desert-adapted addax that also used the patches of sparse native grasses.

Use of sparse vegetation by addax is consistent with their adaptations to arid conditions and nomadic lifestyle in their native range within the Sahelo-Saharan region (Krausman and Casey 2007; Durant et al. 2014). Fluids and food particles are retained

in the gut for a relatively long time, providing for efficient use of water and enhanced digestibility of low quality forage (Hummel et al. 2008). Addax can go long periods without drinking (Dolan 1966), possibly gaining most of their water from plants, such as grasses, forbs and leaves of shrubs (Krausman and Casey 2007).

Due to their physiological adaptations to a more mesic environment than addax, sable require a diet with higher protein content, associated with higher water demand. In southern Africa, sable selected burned areas with green growing grass relatively high in protein content (Magome et al. 2008), remained longer in green patches and moved less between patches (Parrini and Owen-Smith 2010). Where grasses did not remain green, sable appeared vulnerable to protein deficiency during periods of low rainfall (Macandza et al. 2014). Intervals between sable visits to water sources varied from 1–5 days, with shorter intervals (2–3 days) more likely later in the dry season (Cain et al. 2012). Variation between herds was related to the distance between foraging arenas and water sources, as well as rainfall (Cain et al. 2012; Owen-Smith et al. 2013).

Different species-specific adaptations to nutrient and water requirements may also influence movement patterns (Cain et al. 2012). This study found locomotion activity was more likely in addax and resting more likely in sable. Seasonally nomadic addax migrated long distances from north to south in desert regions, following vegetation green-up with the rains (Krausman and Casey 2007). Relatively sedentary sable herds moved an average of 9–16 km roundtrip between foraging arenas and point water sources (Cain et al. 2012). On the other end of the grazer spectrum, zebra *Equus quagga* herds sympatric with sable in Kruger National Park, travelled half the distance and drank twice as frequently (Cain et al. 2012). Travelling longer distances allowed sable to use feeding arenas not used by zebra in Kruger. In the present study, roles were reversed in that addax travelled more and used patches of native vegetation not used as much by sable.

External factors

Multiple species respond in a similar manner to thermal cycles, resting in the midday heat in Kruger National Park (Owen-Smith and Goodall 2014). Although it was expected for sable to be less sun-tolerant than addax, both species used shady wooded patches during midday. In desert regions, addax reportedly rested in the shade of trees or cliffs (Dolan 1966). However, there was more variation among individual addax in the use of shady Juniper patches at midday. Sable remained in a tight cohesive herd, whereas addax spread out across a larger space and many moved into the improved patches during midday.

A midday peak in visitor traffic and provisioning of food pellets by visitors may have contributed to the variation in addax response to thermal cycles. The visitors drove a tour route adjacent to improved patches and tossed high protein pellets from the car windows to attract animals. Addax were observed feeding from cars more often than sable. Ungulate response to human activity includes both avoidance (McLoughlin et al. 2011; Ndaimani et al. 2014) and attraction (van Beest et al. 2010). Possibly addax showed more individual variation than sable in the relative salience of repellent and attractive cues associated with midday visitor traffic.

Competitive interference may also influence how species use resources in a landscape, although the effect is difficult to demonstrate without experimental manipulations (Maitz and Dickman 2001). Since there were no measures of resource depletion for the present study, competition could not be addressed, nor could one species be removed to examine the effects on distribution of the other species. No overt displacement interactions among any of the species in the enclosure were observed during surveys. Displacement interactions were only

observed opportunistically outside surveys, in the context of supplemental feed pellets distributed daily by staff along the tour route adjacent to improved patches. Staff routinely observed each species and noted any problems with individuals during supplemental feeding lasting 30–45 minutes. Order of access to pellets was highly predictable: sable, gemsbock, deer, addax, waterbuck. The feed was distributed in a manner that all individuals obtained access to the supplemental nutrition. Potential effects of competition and supplemental food delivery could not be assessed in the present study, given the complex interactions among external factors.

Management implications

In conservation breeding centres, such as Fossil Rim Wildlife Center, individual animals are carefully monitored for diseases and parasites, thereby minimising concerns that may be more applicable to multi-species grazing systems on other private lands with less veterinary oversight and with more extensively managed herds. Nevertheless, managers should be proactive in identifying shaded resting sites used by multiple species vulnerable to parasites and arthropod vectors. Shared resting sites, as identified in the present study, would be high priority locations for control of ticks as the need arises.

Wherever multiple species use the same resting sites in woody vegetation patches, ectoparasites such as ticks may serve as vectors of pathogens (Busch et al. 2014). More information is known about tick-borne diseases of sable than that of addax. Sable have been affected by and/or exposed to the following tick-borne diseases: babesiosis (McInnes et al. 1991; Hove et al. 1998), theileriosis (Nijhof et al. 2005), anaplasmosis (Kuttler 1984), heartwater (Burrige et al. 2002) and Lyme disease (Sirmarová et al. 2014).

Parasite transmission of roundworms (Nematoda) and tapeworms (Cestoda) may also present a risk where ungulates feed in locations infected with eggs, proglottids or larvae hatched from feces, which rest on vegetation (Kearney et al. 2016). Both sable and addax are hosts to abomasal roundworms (Craig 1993; Grobler 1981), namely *Trichostrongylidae* (e.g. *Haemonchus* spp.) and *Longistrongylus curvispiculum*, as well as whipworms *Trichuris* spp. (Mikolon et al. 1994). Tapeworms within the genus *Echinococcus* and *Taenia* are known to infest addax in captivity in Tunisia (*E. granulosus*) and sable in Texas (*T. hydatigena*) and Africa (*T. multiceps*) (Grobler 1981; Boufana et al. 2017).

Superficially, broader use of native vegetation by addax, compared to sable, might suggest addax would be less vulnerable to reinfection if some individuals avoid the infected improved pasture favored by sable. However, the toolbox required for effective management of parasite infestations is complex, requiring site-specific treatment strategies (Kearney et al. 2016). Although mixed-species grazing systems (e.g. sheep, goat, cattle) offer potential for reducing reinfection, rotation of pastures is usually required (Kearney et al. 2016). The shifting foraging arenas reported for free ranging sable (Owen-Smith and Martin 2015) would function to reduce parasite reinfection in situ, an ideal that might be difficult to replicate at ex-situ conservation breeding centres.

In the native range of sable, management options for maintaining biodiversity and productivity within mixed-species grazing systems include fire (Burkpile et al. 2016) and wetland protection (Fynn et al. 2015). Although controlled burns and access to seasonally flooded meadows have limited direct applicability at previously established sites such as Fossil Rim Wildlife Center, the underlying principles have been integrated into management practices. Invasion of woody and weedy species has been controlled by mechanical removal, judiciously

combined with limited burns and selective localised application of herbicides. Mimicking seasonal flooding, ungulates are excluded from food plots with green growing vegetation planted in soil patches with high moisture retaining capacity. Gates to food plots are opened when standing biomass exceeds pasture forage, thereby reducing grazing pressure on native vegetation during dry months. In design of future multi-species grazing systems to meet conservation goals, this study recommends integration of fire and wetland management within larger landscapes.

Conclusion

In this ex-situ mixed-species grazing system, sable differed from addax in their use of vegetation patches. As predicted based on their evolutionary adaptation to wetter environments, sable were more likely to use grassy patches that had been improved with stands of productive exotic species likely stimulated by grazing. Addax also foraged in less-productive patches with native grass and herbs, illustrating a larger foraging arena with incomplete overlap between the two species. Consistent with their in-situ migratory patterns in the Sahelo-Saharan region addax were more likely to locomote and less likely to rest compared to sable. This differential activity and use of the landscape occurred despite a similar rearing environment for both species and similar classification as mixed grazers (60–90% monocots).

Both species rested in shaded patches dominated by woody vegetation (juniper), more so during midday heat. However, the differential use of vegetation patches was a complex interaction of species, time of day and activity. Internal factors potentially influencing this variation included: body size, gut physiology and locomotion activity. Potential external factors included human activity, supplemental feed and seasonality.

It is recommended that managers of mixed-species grazing systems consider species differences in response to resources that can be manipulated to meet the dual goals of productivity and biodiversity conservation. Similarities, such as shared shaded resting sites, should be monitored to reduce the likelihood of pathogen transmission through vectors.

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