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Uppsala 2014

Husdjursvetenskap

Foto: Pieter Habets

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ABSTRACT

Prey species make behavioral decisions to reduce the perceived risk of predation and the time spent vulnerable to predation. Behavioral responses to predators are for example selection of specific habitat types and the presence of predators influence individual vigilance. Furthermore, there is a variation in feeding niches with different herbivores focusing their foraging effort on different vegetation types which is also expected to affect the choice of habitat. Behavioral data on anti-predation and foraging behavior at on waterhole is collected from Thomson's and Grant's gazelles at Ol Pejeta Conservancy (0°00'N, 36°56'E) located in semiarid bushed grassland in Laikipia district of central Kenya. The main predators at the waterhole are lions, black-backed jackals, spotted hyenas, cheetahs and African wild dogs. Direct observations were carried out from a car 250 meters from the waterhole. Observations were carried out daytime by scan sampling from sunrise to sunset in February 2014. The aim of this study was to design and test a study that investigates how Thomson's and Grant's gazelles differ in foraging and anti-predation behavior during daytime close to a waterhole. The results show that the number and visiting frequency of Thomson's gazelles was higher at the study area than Grant's gazelles and the number of Thomson's gazelles was higher in the morning than in the afternoon. Because of low amount of Grant's gazelles, no further analysis on this species was made. Based on results or when not possible by literature, Thomson's and Grant's gazelles seem to differ in anti-predation and foraging behavior by differences in habitat preferences, water dependency, group size and physical characteristics.

SAMMANFATTNING

Bytesdjur gör beteendemässiga beslut för att minska risken för predation och tiden sårbara för predation. Beteendemässiga reaktioner till rovdjur är till exempel val av specifika vegetationstyper och närvaro av rovdjur påverkar individens vaksamhet. Dessutom finns det en variation i betesnischer. Olika herbivorer skiljer sig i sitt födosöksbeteende på olika vegetationstyper, vilket också förväntas påverka valet av habitat. Insamling av data för antipredation och födosöksbeteende vid ett vattenhål från Thomsons och Grants gaseller genomfördes på Ol Pejeta Conservancy (0 ° 00 'N, 36 ° 56'E) som ligger i Laikipia-distriktet i centrala Kenya. De främsta rovdjuren vid vattenhålet är lejon, schakaler, fläckiga hyenor, geparder och afrikanska vildhundar. Direkta observationer genomfördes från en bil 250 meter från vattenhålet. Observationer genomfördes dagtid med genom att skanna individer från soluppgång till solnedgång under februari 2014. Syftet med denna studie var att utforma och testa en studie som undersöker hur Thomsons och Grants gaseller skiljer sig i antipredations- och födosöksbeteende under dagtid, nära ett vattenhål. Resultaten visar att antalet och besöksfrekvensen på Thomsons gaseller var högre i studieområdet än Grants gaseller och antalet Thomsons gaseller var högre på morgonen än på eftermiddagen. På grund av det låga antalet Grants gaseller genomfördes ingen ytterligare analys på denna art. Baserat på resultaten och litteraturen, verkar Thomson och Grants gaseller skilja sig i antipredation- och födosöksbeteende genom skillnader i habitatpreferenser, behov av vatten, gruppstorlek och fysiska egenskaper.

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1 INTRODUCTION

Background

Thomson's and Grant's gazelles possess similar social structures composed by three sub-groups during stationary periods; territorial herds, herds of females and bachelor herds (Estes 1967; Walther 1969). They are more likely to alter diet selection under different environmental conditions than larger grazers such as Oryx (*Oryx beisa*) and wildebeest (*Conochaetes taurinus*) (Maloiy *et al*. 2008; Jarman 1974) and are able to change feeding strategy (i.e. switching from browsing to grazing) according to season or overgrazing (Hofmann 1989). Both Thomson's and Grant's gazelles are well adapted to withstanding periodic heat stress (Maloiy *et al*. 2008). Grant's gazelle use more extensive habitat than Thomson's gazelles, but are more likely seen in smaller groups than Thomson's gazelles (Walther 1972).

Thomson's gazelles

Thomson's gazelles are relatively small, 15-25 kg, (Hofmann 1989) water dependent intermediate feeders (Hofmann, 1989) that prefer grazing (Estes 1967) of high quality short grass (Maloiy *et al*. 2008; Wilmshurst *et al*. 1999) low in fiber (Demment and Van Soest 1985) to maximize digestibility (van der Merwe and Marshal 2004). They are mostly found in dry vegetation on open plains in the vicinity of water (Estes 1967; Walther 1973). Also during wet season they tend to chose more dry vegetation with intermediate annual rainfall on open plains (Maddock 1979). Herd size of Thomson's gazelles varies from 2 up to over 1000 individuals and the groups are larger in short-grass areas than in tall-grass areas (FitzGibbon and Lazarus 1995).

Grant's gazelles

Grant's gazelles are larger than Thomson's gazelles with a mean weight of 40-70 kg (Hofmann, 1989) and are more independent of water (Cain *et al*. 2006; Walther 1972), but have similar alarm signals (Estes 1967). They are adapted to a variety of habitats ranging from desert regions to tall grassland and light bush (Estes 1967; Walther 1972). The Grant's gazelle is also, unlike the Thomson's gazelle, mostly a browser (Estes 1967; Jarman 1974; Walther 1972). Moreover, the males of Grant's gazelles tend to defend larger territories than Thomson's gazelle males (Estes 1967).

Anti-predator strategies

Predation contributes to the natural selection and influence evolution of animal behavior by selection. Prey species make behavioral decisions to reduce the perceived risk of predation and the time being vulnerable to predation (Valeix *et al.* 2009a), for example during night when predators are more active (Fischhoff *et al.* 2007). Weather and temperature could also influence the vulnerability due to energetic stress (Lima 1988). The main predators for Thomson's and Grant's gazelles are cheetah (*Acinonyx jubatus*) (FitzGibbon 1989; Fitzgibbon 1993; FitzGibbon and Lazarus 1995), Asiatic and black-backed jackal (*Canis aureus* and *C. mesomelas*) (Estes 1967; FitzGibbon and Lazarus 1995) spotted hyena (*Crocuta crocuta*), wilddog (*Lycaon pictus*), leopard (*Panthera pardus*) and in some cases lion (Estes 1967; FitzGibbon and Lazarus 1995; Fitzgibbon 1993). There may be seasonal variation of predators due to migration of preferred prey (Estes 1967). The anti-predation strategies within a species differ between age, sex and reproductive status (FitzGibbon 1993). Two of the most studied behavioral effects are group formation and vigilance (Valeix *et al.* 2009a). Other behavioral responses of predators are for example selection of specific habitat types (Valeix *et al.* 2009a) and stotting (Walther 1969). Herbivores are dependent on waterholes and are thereby influenced of the distribution of waterholes (Valeix *et al.* 2009b), but many kills by predators occur close to waterholes (Valeix *et al.* 2009a).

Group formation

Individuals in group are considered to be less vigilant to predators than solitary animals within the same species as group formation increases the probability to detect predators and group formation decreases the probability of each animal to be detected by predators (Delm 1990). Thomson's and Grant's gazelles also tend to join each other in mixed-species groups and as a result further increase the group size (FitzGibbon 1990a). This has advantages for Thomson's gazelles compared with remaining on its own since they are less vulnerable to cheetahs due to the many-eyes effect, lower success rate for cheetahs and also because cheetahs tend to avoid hunting larger group (ibid. 1990a). On the other hand, since cheetahs prefer the smaller Thomson's gazelles it's beneficial for Grant's gazelles to form mixed-species (ibid. 1990a).

Vigilance

The most common way for gazelles to avoid the approach of a predator is vigilance by at least one individual at a time which is looking around (Walther 1969). If a gazelle recognizes a threat it puts ears forward, erects its neck and sometimes stamps with a front leg (ibid. 1969). According to FitzGibbon (1990a) Grant's gazelles spend more time vigilant than Thomson's gazelles. Furthermore, predators such as cheetahs tend to select individuals of gazelles that are less vigilant than the ones scanning at higher rates (FitzGibbon 1993) and gazelles in smaller groups tend to be vigilant at higher rates than in larger groups (FitzGibbon 1990a).

Habitat choice

The major part of their habitat selection is that the animals select the vegetation type that will satisfy the feeding requirements (Jarman 1974). However, the risk of predation may affect the choice of habitat: e.g. do gazelles in high vegetation spend more time vigilant (FitzGibbon 1993). The group size of ungulates also tends to be larger in open habitats than in areas with dense vegetation (FitzGibbon 1993).

Stotting

Thomson's gazelles communicate by stotting when alarmed which can be described as series of high jumps with the head held high and the legs stiff (Estes 1967). Stotting can be described as a signal directed to the predator; according to FitzGibbon (1993) gazelles that are stotting at lower rates are more likely to be selected by predators and those gazelles which are stotting for longer duration are more likely to outrun the predator (ibid. 1993). In addition, sex and seasonal factors affect the stotting rate (FitzGibbon 1993). The individual differences in body condition give rise to variation in the rate of stotting and predators use this variation when selecting their prey (ibid. 1993). Moreover, stotting rate decreases when in larger groups and when distance to distance to predator increases (FitzGibbon and Lazarius 1995).

Foraging behavior

There is a variation in feeding strategies (e.g. concentrate selectors, grass and roughage eaters and intermediate feeders) with different herbivores focusing their foraging effort on different vegetation types (Hofmann 1989) which is also expected to affect the choice of habitat. Thomson's and Grant's gazelles are intermediate feeders (Cerling *et al.* 2003; Hofmann 1989; Tieszen *et al.* 1979; Jarman 1974) which mean that they are intermediates between concentrate selectors and grass/roughage eaters and chose a mixed diet (Hofmann 1989). Both Thomson's and Grant's gazelles feed on grasses and browse rather selectively within a fairy wide home area (Jarman 1974). However, Thomson's gazelles prefer grazing while Grant's gazelles prefer browsing (Hofmann 1989). Grasses are rich in cell wall materials whereas browse is rich in cell contents (ibid. 1989). The cell walls consist of neutral-detergent fiber (NDF) and the contents increase with maturity and thereby decrease digestibility (McDonald *et al.* 2010). High digestibility and high rate of digestion promote high intake and the content of NDF (cell wall material) is the primary chemical component determining the rate of digestion (ibid. 2010). The cell contents, as in browse, are rich in for example soluble carbohydrates and protein (ibid. 2010).

Food preferences

Intermediate feeders

Intermediate feeders such as the gazelles have a short retention and rapid flow through rumenoreticulum (i.e. high fermentation rate) compared to grazers and requires more buffer to protect them against pH depression (Hofmann 1989). Also the concentration of cellulolytic microbes varies between browsers and grazers: in animals adapted to a browse diet, such as the Grant's gazelle, the level of cellulolytic activity in the rumen is lower (ibid. 1989). Small ruminants have a high metabolic rate compared to non-ruminants such as zebras and larger ruminants and require higher protein contents (Maddock 1979) and high digestibility (Jarman 1974). Additionally, intermediate feeders have larger salivary glands than grazers, which supplies them with more diluting liquid and a higher proportion of serous saliva to carry away much of the soluble plant cell contents from dicots (Hofmann 1989).

Thomson's gazelles

Thomson's gazelles are intermediate feeders that prefer grazing: dicotydelons (such as Acacia and Barleria) compose not more than 20% of the diet of a Thomson's gazelle (Tieszen *et al.* 1979). Up to 80% of their rumen content is shown to consist of grasses: mainly *Cynodon* and *Themeda* (ibid. 1979). Foraging behavior and grazing rate of Thomson's gazelle are also shown to vary between short and tall swards: the short swards were shown to consist of widely spaced clumps of grass, whereas tall swards had more homogenous spatial distribution (Bradbury *et al.* 1996).

Grant's gazelles

Grant's gazelles prefer dicots (Tieszen *et al.* 1979) and are more tolerant for dry conditions than Thomson's gazelles (Taylor 1970). Grant's gazelles browse most of the time and according to Estes (1967) they select legumes and low, thorny shrubs such as *Indigofera* spp. In Tieszen *et al.* (1979), Grant's gazelles were shown to feed on 24% grasses and 68% browse. The browse consisted of mainly *Acacia* spp., but also *Barleria* spp. (ibid. 1979).

Seasonal variations

Their diet and preference for vegetation types changes seasonally (Jarman 1974). They adapt anatomically to changes in forage quality and they switch to browsing when the plants are lignified which in turn leads to reduced metabolism and food intake (Hofmann 1989). During drought gazelles are shown to rather choose such as Acacia spp. that contain anti-nutritional factors such as condensed tannins (ibid. 1989) and 4-*N*-acetyl-2,4-diaminobutyric acid (ADAB) (McKie *et al*. 2004) than sundried lignified grass which they cannot digest (Hofmann 1989). The presence of tannins in food decreases fermentation rate and the predicted digestibility of the food (Gordon and Illius 1996; McDonald *et al.* 2010).

Physiological and behavioral responses to heat stress and limited access to water

Both domestic and wild animals suffer under dry conditions from water shortage and poor pasture, but also external heat stress due to high air temperatures and strong solar radiation (Taylor 1970). Internal heat production such as maintenance metabolism, food intake, muscular activity, growth and lactation also contributes as sources of heat (Kay 1997). The maintenance metabolism, for example, includes visceral activity, muscular contractions needed for basal body functions, ionic exchange across membranes and the synthesis and breakdown of chemical constituents (ibid. 1997). This conflicts with water losses mainly through faeces containing 60-70% water, but also water losses from urine, evaporation and by inclusion of growing tissues (ibid. 1997). Moreover, water is required to replace losses of fluids from the body by excretion and evaporation (ibid. 1997). Water loss through faeces increases the potassium intake since most of the potassium in the diet is excreted in the faeces (ibid. 1997). Gazelles rely on panting to keep cool in hot conditions (Taylor 1970). Panting can be described as a controlled increase in respiratory frequency to elevate evaporative heat loss by increasing the ventilation of the upper respiratory tract and preserve alveolar ventilation (Robertshaw 2006). The advantages of panting instead of sweating are that salt is not lost, deep tissues are cooled directly and the evaporative surfaces are ventilated by the animal rather than depending on the wind (Kay 1997). However, there is a risk of alkalosis by excessive respiration through loss of carbon dioxide and it requires muscular activity which generates some heat (ibid. 1997).

Water sources

Water sources include drinking water, food water and metabolic water (Kay 1997; Willmer et al. 2000). A smaller proportion of water comes from metabolic water (ibid. 1997). The production of metabolic water refers to the oxidation of hydrogen in the cells (Sjaastad *et al.* 2010) when organic nutrients are catabolized to carbon dioxide and water in the body (Kay 1997). Forage of moderate digestibility yields about 550 g of metabolic water per kg dry matter digested (300 g per kg of fresh weight eaten) and this contributes to 10-20% of the water requirements under cool conditions when the water requirements are low (ibid. 1997). During hot conditions when the water requirements are higher and will hence only contribute to 5-10% of the water requirements (ibid. 1997).

Heat stress

Heat stress during a prolonged time leads to reduced activity, loss of appetite and decreased metabolic rate (Kay 1997; Silanikove 1991). Both Thomson's and Grant's gazelles are shown to decrease their food intake during dehydration in an environment of 22°C (Maloiy *et al.* 2008). However, Grant's gazelles showed no further reduction in food intake when the effects of heat stress were added to the effects of dehydration whereas Thomson's gazelles reduced their food intake during exposure to intermittent heat load for 12 h at 40°C (ibid. 2008). This can partly be described by a decrease in metabolic rate (Kay 1997) which could be an

adaptation to conserve water in consequence of the reduced generation of heat under warm conditions (Maloiy *et al.* 2008). The decrease in metabolism may in turn decrease the maintenance requirements during limited food supply (Silanikove 2000), but as a consequence of the nutrient deficiency also the digestibility of foods may be reduced (McDonald *et al.* 2010).

Physiological responses to dehydration

When dehydration occurs effects are mediated through an increase of plasma osmolarity (Silanikove 1991) and a decline in blood volume (Sjaastad *et al.* 2010). The increased osmolarity in intracellular and extracellular fluids induce an increased secretion of antidiuretic hormone (ADH) which in turn increases the reabsorption of water by osmosis and increases the permeability of the distal tubules and collecting ducts in the kidneys due to aquaporins, water pores regulated by ADH (ibid. 2010). ADH is synthesized by hypothalamic neuroendocrine cells connected to osmosensors which are sensitive to changes in the osmolarity of the extracellular fluid and is stored and secreted by the posterior pituitary (ibid. 2010). This results in excretion of more concentrated urine and conservation of body water (ibid. 2010). The greatest concentration is found in desert animals and is over 3000 mOsm in many desert antelopes (Kay 1997). Moreover, urea contributes to more concentrated urine (Sjaastad *et al.* 2010) and is the main metabolic product excreted in the urine (Kay 1997). Urea formed in the liver partly diffuses from the blood into the forestomachs where it can be used for production of microbial protein if sufficient fermentable carbohydrates are provided (Kay 1997). This in turn reduces excretion of urea in the urine and urea is reabsorbed to maintain nitrogen balance during dehydration (ibid. 1997) and also enabling ruminants to thrive on a low protein diet (Sjaastad *et al.* 2010). When dehydrated in the heat, the gazelles are panting in lower rates and the body temperature is higher – especially regarding the Grant's gazelle (Taylor 1970). The body temperature of Grant's gazelle exceeds the air temperature of 45°C whereas the body temperature of Thomson's gazelles does not exceed 45°C even if the air temperature is 45°C and the onset of panting occurs in higher air and body temperatures during dehydration to minimize heat gain from the environment and reduce the loss of water (ibid. 1970) and the requirement of both water and energy (Kay 1997). They will also reabsorb more water from their faeces (ibid. 1997).

Aim and questions

The aim of this study was to design and test a study that investigates how Thomson's and Grant's gazelles differ in foraging and anti-predation behavior during daytime close to a waterhole. The interactions between vigilance and group size are also investigated. The following questions will be answered either by own data or when not possible by literature only:

1. Are there differences in foraging behavior between Thomson's and Grant's gazelles?
2. Are there differences in frequency spent drinking between Thomson's and Grant's gazelles?
3. Are there differences of using the waterhole area between Thomson's and Grant's gazelles?

2 MATERIAL AND METHODS

Study site

The study was conducted in Ol Pejeta Conservancy (0°00'N, 36°56'E) located in a semiarid bushed grassland in Laikipia district of central Kenya. Thomson's and Grant's gazelles were observed at one waterhole to investigate differences in anti-predation and foraging behavior. The population size of Thomson's and Grant's gazelles are estimated to 1029 and 686 respectively (Ol Pejeta Conservancy, unpublished data). The main predators at the waterhole are lions, black-backed jackals, spotted hyenas, cheetahs and African wild dogs. The conservancy covers 380 km^2. The area consists of tree savannah; visibility depends partly on grass height and on the presence of tree and shrubs.

Recording methods

Direct observations were carried out from a car 250 meters from the waterhole during daytime from sunrise to sunset in February 2014 using binoculars. For each observation the date, time of day, weather and behavior of all mammals and large birds at the study area were recorded. Total duration of direct observations was ten days. A group of animals were defined as a herd of individuals with no more than 50 m separating any two group members. As the individuals are unmarked and the number of animals varied it is likely that the same individuals were monitored more than once during the study period.

Behavioral observations

During the instantaneous recordings seven different behavioral events were observed in 10 min intervals: standing, lying, walking, running, drinking, foraging and other behaviors. Continuous recordings were made on one hour intervals on drinking, vigilance and sprinting. Foraging behavior for prey and predators were distinguished. Foraging behavior for herbivores occurred during grazing with its head down below horizontal plane or eating on a bush. Vigilance took place when more than 50 percent) of a group of at least three individuals was detecting potential danger with the heads turned to the same direction.

Table 1: Ethogram of recorded behavior of Thomson's and Grant's gazelles

Behavior	Definition
Standing	Standing still (not grazing, social etc.)
Lying	Belly, side or back touching the ground
Walking	Moving forward without running or sprinting
Running	Any running expect sprint
Foraging	
- **herbivores**	Head down or eating on a bush
- **predators**	Walking zigzag, stalking, sneaking, hunting, eating
Social	Body contact, chasing, playing
Drinking	Head down to the water
Vigilance	Majority of group detecting potential danger, head turned to the same direction
Jumping	Jumping straight up in the air
Sprinting	Fast run away from potential predators
Group of animals	Herd of at least three individuals with no more than 50 m separating any two group members

Measurements

Foraging behavior

To investigate the frequency and number of individuals visiting accessing waterhole instantaneous and continuous recordings were made by scan sampling. Furthermore, the proportion of time spent foraging and drinking at the study area was investigated. The area around the waterhole was more open than other parts of the conservancy, probably due to the frequent visits of herbivores. Hence, the waterhole area does not only provide water but also grass of high quality, at least in the rainy season. Therefore we recorded the behavior of animals not only when drinking but also when grazing close to the waterholes.

Avoidance of waterholes during high risk of predation

Observations are made to test if Thomson's and Grant's gazelles are avoiding using waterholes by temporal variations (i.e. hours of high predation risk at dusk/dawn). The choice of habitat is compared to investigate possible differences of using the waterholes between the two species.

Data analysis

The data were sorted by using Microsoft Excel 2000 and analyzed by one-way ANOVA by using Minitab software in order to assess the significance of differences in foraging and drinking behavior at the waterhole between Thomson's and Grant's gazelles.

3 RESULTS

The number and visiting frequency of Thomson's gazelles was higher at the study area than Grant's gazelles ($F_{(12, 50)}$; $P = 0.002$, fig. 1). Because of low amount of Grant's gazelles, no further analysis on this species was made. Number of Thomson's gazelles was lower in the morning (07.00-12:00) than in the afternoon (15.00-18.00), ($F_{(56, 29)}$; $P < 0.001$, fig. 2). There were no significant relations between behavior and weather.
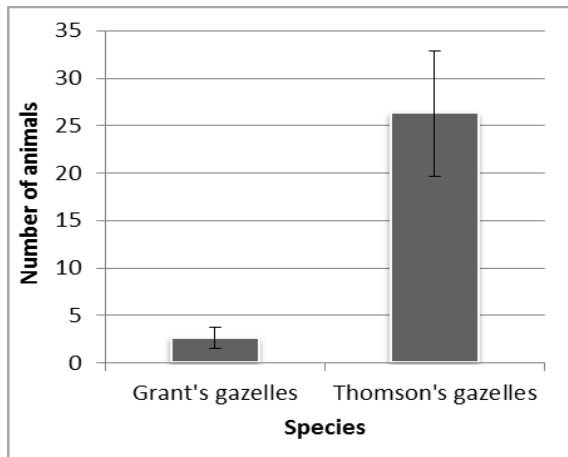

Figure 1. Number of animals as mean $\pm$ SE at the study area
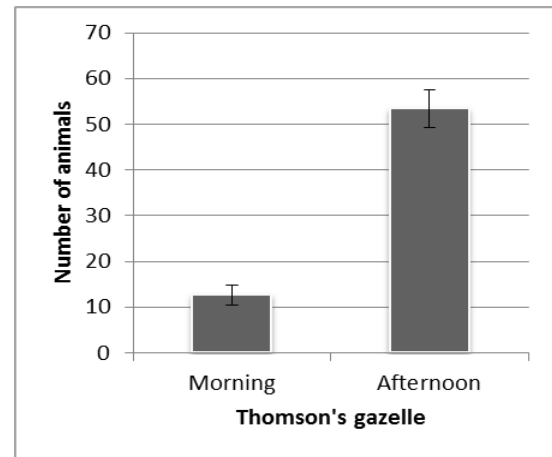

Figure 2. Number of Thomson's gazelles as mean $\pm$ SE during morning and afternoon

Thomson's gazelles tended to spend more time foraging during the morning ($F_{(3, 50)}$; $P = 0,070$) and spent more time lying during the afternoon ($F_{(5, 24)}$; $P = 0,028$). For the other recorded behaviors I did not find any significant differences between morning and afternoon. Thomson's and Grant's gazelles did only drink on the afternoon when groups of Thomson's gazelles drank ten times and groups of Grant's gazelles drank three times during the study period. However, because of this low amount of data, no statistical analysis was made.
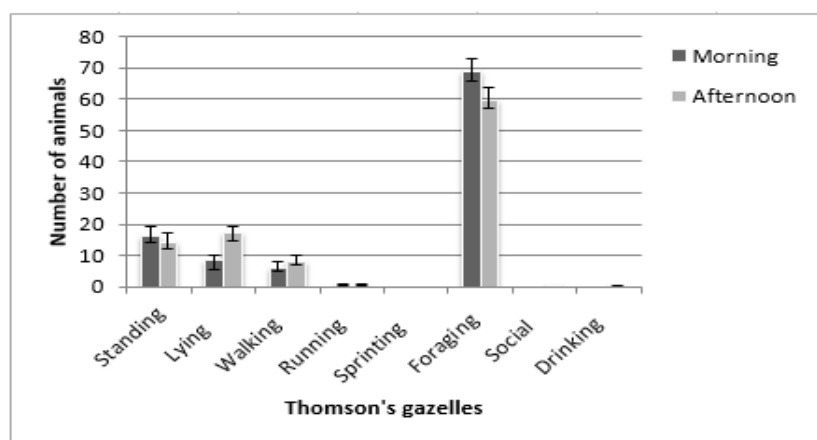

Figure 3. Behavior of Thomson's gazelles in percent of observations as mean $\pm$ SE at the study area.

4 DISCUSSION

This study was conducted in a homogeneous habitat of open grassland surrounded by bush land. Due to the distribution of the waterholes in the conservancy, the gazelles have no choice but to use or at least walk through these open habitats at the waterholes when drinking. The waterholes are therefore corresponded to areas of high long-term predation risk (FitzGibbon 1993). On the contrary, benefits may arise by having several escape routes due to increased visibility. Thomson's and Grant's gazelles seem to share the same predators (Estes 1967; FitzGibbon and Lazarus 1995; Fitzgibbon 1993; FitzGibbon 1989) but the risk of predation may vary between the two species. For example it may be seasonal variation due to habitat preferences and differences in anti-predator strategies such as vigilance, group size and flight responses between the two species. The preference of prey by predators would also be expected to influence the risk of predation. For example cheetahs are shown to prefer Thomson's gazelles (FitzGibbon 1990a). The study was conducted in the end of the dry season and the beginning of the rainy season when the animals are expected to be in poorer condition due to the scarcity of water and poor quality of food, especially regarding Thomson's gazelles considering their water dependency and their preference of grazing. During dry season the short grass stop growing and they may have to graze longer, lignified grass which makes it more difficult for grazers to select high-protein parts (Bell 1971). Grasses mature rapidly in warm climate which increases the fiber content whereas their content of protein and phosphorus fall to low levels (McDonald *et al.* 2010). If the cell-wall content in the grass is too high they will fail to utilize enough protein to meet the maintenance requirements (Bell 1971; McDonald 2010). Nonetheless, their diet changes seasonally (Jarman 1974) and during drought gazelles are shown to rather choose such as Acacia spp. that contain anti-nutritional factors such as condensed tannins than sundried lignified grass which they cannot digest (Hofmann 1989). The presence of tannins in food decreases fermentation rate and the predicted digestibility of the food (Gordon and Illius 1996; McDonald *et al.* 2010). This leads to a decreased microbial biomass in the rumen and an increased food intake (Gordon and Illius 1996). However, more recent studies have shown that both Thomson's and Grant's gazelles are likely to possess detoxification and metabolism capacity to deal with Acacia species since they have microbes that are able to degrade ADAB in Acacia species such as *Acacia angusitissima* (McKie *et al.* 2004). Nonetheless, condensed tannins in moderate levels are shown to be beneficial for ruminants by for example protecting proteins from hydrolysis in the rumen and thereby increasing the absorption of amino acids from the small intestines (McDonald *et al.* 2010).

The moisture content in grass is greatly influenced by weather conditions: the water content in grass ranges from 10% during dry season to 80% in rainy season (Kay 1997). Likewise the water content of fresh browse ranges from 30-70% (ibid. 1997). During rainy seasons when the moisture content is high in grass and browse the animals will get a larger proportion of water by food water and less from drinking water, which suggests that the Thomson's gazelle would not use the area as water source to the same extent. A further

comparison on the use of the waterhole between dry and rainy seasons could give more information of habitat choice depending on food quality and access to water. Nonetheless, Grant's gazelles are more tolerant to dehydration and heat (Maloiy *et al.* 2008). But poor quality food may also have consequences for the Grant's gazelle since the cellulolytic activity is suggested to be lower in browsing animals (Hofmann 1989; Gordon and Illius 1996) which in turn could lead to poor condition and increase the vulnerability. However, it is difficult to determine whether the choice of habitat depends on food preferences or anti-predation behavior.

Thomson's gazelles dominated at the study area whereas the number and visiting frequency of Grant's gazelles was low in comparison. This can be explained by the fact that the study area represents the preferred habitat of Thomson's gazelles: short grass plains in the vicinity of water (Estes 1967; Walther 1973) whereas Grant's gazelles prefer brows (Estes 1967) and are more independent of water (Cain *et al.* 2006; Walther 1972). Thomson's gazelles tended to spend more time foraging in the morning and spent significantly more time lying during the afternoon. Small ruminants have a high metabolic rate compared to non-ruminants and require higher protein contents (Maddock 1979). The food value of the plants for small ruminants such as the gazelles therefore depends upon its having a high protein and digestible carbohydrate content (Jarman 1974) and low fiber content (Demment and Van Soest 1985). A low content of water-soluble carbohydrates would to an increased uptake of ammonia and depressed urea synthesis because of a reduced microbial protein synthesis in the rumen (McDonald *et al.* 2010). The possible preference of foraging on the morning could therefore be due to young, high quality forage with high protein content and digestibility due to the heavy rain during the study period. In the beginning of rainy season the early stage growth the plants consist of growing tissues with thin cell walls (Bell 1971). Moreover, the protein content is highest in young plants and lowest in mature and lignified foliage (Jarman 1974) and the crude protein content may range from 30 g/kg DM in mature grass to 300 g/kg DM in young herbage (McDonald *et al.* 2010). In mature grass most of the protein may be indigestible because it is bound to fiber such as acid-detergent insoluble nitrogen, ADIN (ibid. 2010). But the preference of foraging in the morning can also be due to dew on the grass which increases the daily water intake (own observation). This could also be an explaining factor why both Thomson's and Grant's gazelles were only drinking on the afternoon. During the afternoon the temperature is generally higher which increases the requirement of drinking water. Furthermore, large grazers are shown to be beneficial for gazelles by grazing older grass and making the herbs more available and stimulate grass growth (Bell 1971) which may also affect the preference of this area since the waterhole is used by both cows and wild grazers. However, the large amount of animals visiting the area and dense populations would also be expected to lead to an increased parasitic pressure (Altizer *et al.* 2003).

Individuals in groups are also considered to be less vigilant to predators than solitary animals within the same species since group formation increases the probability to detect predators and group formation decreases the probability of a single animal to be detected

by predators (Delm 1990). Accordingly an individual can spend more time feeding and less to vigilance. The number of Thomson's gazelles was higher in the afternoon than in the morning and the group size of ungulates tends to be larger in open habitats than in areas with dense vegetation (FitzGibbon 1993). This may be caused by the differences in the distribution of food items (Jarman 1974) or restricted visibility in bushland which makes it difficult to maintain contact with other group members (Lagory 1986). Thereby, the increased time spent lying on the afternoon may arise from the increased number of conspecifics during afternoon, compared to the low number of animals in the morning, which may result in less time spent vigilant and possibly more time for rumination. Furthermore, heavy rain has been shown to lead to an increase in lying followed by a decline in grazing (Walther 1972), but this has not been analyzed by the present data. The preference of grass of Thomson's gazelle (Hofmann 1989) would also be expected to prolong the retention time (i.e. rumination) compared to Grant's gazelles. Grasses are rich in cell wall material (McDonald *et al.* 2010) and hence available for cellulolysis in the rumen and fermentation should thus be more important in Thomson's gazelle. Grant's gazelles are also well adapted to areas with scarcity of water which are not suitable for livestock such as cattle, since they are more selective

According to Lima (1988), weather and heat influence the vulnerability due to energetic stress. But weather conditions such as heat may prolong the time spent lying during the afternoon and the predators are less active during daytime (Fischhoff *et al.* 2007) which decreases the long-term predation risk. This in turn may decrease the time spent vigilant and more time spent lying. Furthermore, not all individuals are equally vulnerable to predators since predators tend to choose prey that differs from other group members (Landeau and Terborgh 1986). As an example do cheetahs tend to choose individuals on the edge of small groups of gazelles (FitzGibbon 1990b). Since the level of vigilance may also differ between individuals due to physical characteristics such as condition and morphology (FitzGibbon 1999; FitzGibbon 1993) it would be expected that there is seasonal variations in level of vigilance and vulnerability. For example less vigilant gazelles are preferred by cheetahs because they are easier to catch due to slower reaction and a poorer physical condition than a more vigilant individual (Fitzgibbon 1989). Animals would then be expected to be in poorer condition during dry seasons (because of scarcity of water and poor quality food) than during rainy seasons, especially regarding Thomson's gazelles since they are dependent of water. But it could also have consequences of Grant's gazelle since the cellulolytic activity is suggested to be lower in animals adapted to a browse diet (Hofmann 1989; Gordon and Illius 1996) when switching from browse to low quality grass. This has a major effect on the energy obtained from the diet to meet the metabolic requirements (Gordon and Illius 1996). Accordingly, the diet selection is important as the microbial adaptation would cause browsers to suffer a penalty on switching from browse to grass (ibid. 1996) which in turn could lead to poor condition and increase the vulnerability. The vulnerability and vigilance may also differ between individuals due to sex, age and reproductive state (e.g. females with young) (FitzGibbon 1993). For example, ungulates are most vulnerable during the first few weeks of life

(FitzGibbon 1993) and male gazelles are stotting less rapidly than females and gazelles are shown to stot at a higher rate during wet season when they are in good condition, than in the dry season (FitzGibbon and Fanshawe 1988) which may increase the vulnerability. According to FitzGibbon (1993) male gazelles also spend more time on their own, spend less time vigilant and are generally in poorer condition than females which may increase the risk of predation.

One explanation why Thomson's gazelles prefer short grass plains could be that by foraging on swards of low-to-intermediate biomass (either very short or very tall tillers) and the digestibility remains high, the gazelles can maximize their energy intake (Wilmshurst et al. 1999). Another could be to decrease the risk of predation. The restricted visibility in bushes makes it difficult to maintain contact with other group members (Lagory 1986) and the gazelles spend more time vigilant in high vegetation (FitzGibbon 1993). The groups are also shown to be larger on short-grass areas than in tall-grass areas (FitzGibbon and Lazarus 1995) which then would decrease the level of vigilance. In short grass plains they can therefore spend less time vigilant and more to foraging. Since Grant's gazelles are more water independent (Cain et al. 2006; Walther 1972) and seem to be more tolerant to heat and dehydration (Maloiy et al. 2008) it would be expected that they can remain on plain habitat absent from water longer than the Thomson's gazelles. During the dry season the Thomson's gazelles are able to select high-protein food and gazelles (mainly Grant's gazelle) can utilize pasture that is poor for grazers, as intermediate feeders have larger salivary glands than grazers, which supplies them with more diluting liquid (which in turn reduces the retention time) and a higher proportion of serous saliva to carry away much of the soluble plant cell contents from dicots (Hofmann 1989). The moisture content in grass is greatly influenced by weather conditions: the water content in grass ranges from 10% during dry season to 80% in rainy season (Kay 1997). Likewise the water content of fresh browse ranges from 30-70% (ibid. 1997). During rainy seasons when the moisture content is high in grass and browse the animals will get a larger proportion of water by food water and less from drinking water, which suggests that the Thomson's gazelle would not use the area as water source to the same extent. A further comparison on the use of the waterhole between dry and rainy seasons could give more information of habitat choice depending on food quality and access to water. However, the differences in digestive physiology which would affect diet selection and thus time spent foraging are still unclear. More investigations of comparative physiology of wild herbivores to increase knowledge of the selection of habitat could also improve the understanding of the relationship between the domestic herbivores and wild herbivores, and thus the management of land and the domestic animals in the conservancy.

Sources of error

The number of observers (four) contributes to a source of error during observations due to different interpretations. It is also sometimes difficult to differ between Thomson's and Grant's gazelles, especially when they are lying down. The gazelles are usually moving

forward while grazing and in this study walking occurred only when gazelles did not graze/browse. Hence, grazing could occur while moving. Improved observing methods for the different behaviors could give more data. For example short behaviors such as being social and drinking may not be representative by instantaneous recordings. The observations may not be representative due to the heavy rain during the dry season which affects the access to water. This study was conducted only by observations during daytime from sunrise to sunset which restricts the amount of data because of the lack of data during night. During the scanning of animals it is also a risk of miscounts, mixing of individuals, missed behaviors, missing animals (for example when they are lying down), incorrect estimations of distances between individuals and also the human factor. Furthermore, there was a 'blind' area behind the waterhole where animals could not be detected from the car. Shorter intervals would have given more data for analysis. Different binoculars were used throughout the study, which also may contribute to a source of error. The size of the study area contributes to possible error margins and it can be difficult to estimate the boarders of the study area. Observations of present predators and for example number of killings would give data of the immediate predation risk. However, the short period of the study makes the data unreliable. Further information of plant and grass species at the study area and analysis of faeces would have given more data regarding the choice of habitat and food preferences.

5 CONCLUSIONS

Anti-predation strategies conflicts with foraging: prey must balance the risk of predation with nutritional needs. Thomson's gazelles spent more time foraging in the morning and more time drinking on the afternoon. Thomson's and Grant's gazelles seem to differ in anti-predation and foraging behavior by differences in habitat preferences, water dependency, group size and physical characteristics.

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