Habitat use by mountain nyala *Tragelaphus buxtoni* determined using stem bite diameters at point of browse, bite rates, and time budgets in the Bale Mountains National Park, Ethiopia

Solomon A. TADESSE*, Burt P. KOTLER
Mitriani Department for Desert Ecology, Blaustein Institutes for Desert Research, Ben-Gurion University of the Negev, Midreshet Ben-Gurion 84990, Israel

**Abstract** We studied the habitat use of mountain nyala *Tragelaphus buxtoni* in the northern edge of the Bale Mountains National Park, Ethiopia. Two major types of habitat (i.e. grassland versus woodland) are used by mountain nyala. Generally, grasslands provide the mountain nyala with several advantages over the woodlands, including offering lower foraging costs, greater safety, and more time for foraging. The study advocates how behavioural indicators and natural GUDs are used to examine the habitat use of the endangered mountain nyala through applying non-invasive techniques. We conclude that the resulting measures are helpful for guiding conservation and management efforts and could be applicable to a number of endangered wildlife species including the mountain nyala [Current Zoology 59 (6): 707–717, 2013].

**Keywords** Behavioural indicators, Bite rates, Mountain nyala, Natural giving-up densities, Non-invasive techniques, Stem bite diameters, Vigilance.

Food preferences and foraging efficiencies of animals can be quantified through measurement of patch use and giving-up densities. Stem bite diameters at point of browse (dpb) can be used to quantify patch use and the amount of food consumed by herbivores (Wilson and Kerley, 2003; Morris, 2005). For example, the approach of measuring stem dpb was successfully applied to domestic goats and other wild ungulates (Haschik and Kerley, 1997a, b; Wilson and Kerley, 2003). Morris (2005) also quantified stem dpb to address the patch use behaviour of snowshoe hare *Lepus americanus*. Stem dpb provides a measure of natural giving-up densities (GUDs) (Brown, 1988, 1992; Morris, 2005) by providing a physical record of the amount of fibrous, indigestible materials that the forager is willing to process. Here, the larger the stem dpb, the less fibrous should be the bite. Consequently, the shorter will be the processing time, and the higher will be the digestible content and the ingestion rate of energy (i.e. lower GUDs and higher harvest rates). In contrast, the smaller the stem dpb, the higher fibrous should be the bite, the longer will be the processing time, and the lower will be the digestible content (i.e. less food removed and consumed), corresponding to higher GUDs and lower harvest rates.

We studied the habitat use of mountain nyala *Tragelaphus buxtoni* in the northern edge of the Bale Mountains National Park, Ethiopia. Two major types of habitat (i.e. grassland versus woodland) are used by mountain nyala. The woodland is richer in abundance, diver-
feeding. Previous studies noted that reproductive state of mountain nyala is more favored toward the grassland than the woodland. In line with this, we hypothesized that the habitat use of mountain nyala is determined by foraging costs and efficiencies (e.g. Brown, 1988, 1992; Kotler et al., 1994; Tadesse and Kotler, 2012). So, we expect that our hypothesis is more supported by the predation-sensitive foraging (Sinclair and Arscie, 1995; Banks, 2001) and/or the predation risk hypothesis “tradeoff between food acquisition and safety” (e.g. Stephens and Krebs, 1986; Lima and Dill, 1990; Brown and Kotler, 2004) than by the forage maturation hypothesis “selection of high quality forage” (e.g. Fryxell et al., 1988; Albon and Langvatn, 1992; Hebblewhite et al., 2008).

Behavioural indicators based on foraging theory can be used to assess the habitat use of mountain nyala (Druce, 2005; Hochman and Kotler, 2006a; Morris et al., 2009). We measured and quantified stem dbh in two major habitats (grassland versus woodland), (2) quantify the bite rates (number of bites per minute) and activity time budgets of mountain nyala as functions of habitat type and sex-age category.

1 Materials and Methods

1.1 Study species

Mountain nyala Tragelaphus buxtoni is an endemic flagship species to Ethiopia (Brown, 1969; Evangelista et al., 2007). Listed as endangered (IUCN, 2012), mountain nyala is only found in a few locations in the Ethiopian highlands (Evangelista et al., 2008). It is a sexually dimorphic antelope in which adult males are much larger than females (Refera and Bekele, 2004). Mountain nyala are social animals with females congregating in family units of three to eight individuals and males forming small bachelor groups outside the mating season (Hillman, 1985; Mamo, 2007). They are found in a variety of high-elevation habitat types requiring access to seasonal forage and cover from predation risk (Hillman and Hillman, 1987; Evangelista et al., 2007). Potential predators of mountain nyala include leopard Panthera pardus, spotted hyena Crocuta crocuta, and African lion Panthera leo (Brown, 1969).

1.2 Study area

The study was conducted in the Bale Mountains National Park. The park is located between 6°29′ North latitude, and 39°28′ and 39°58′ East longitude (Hillman, 1986) in the Oromiya administrative regional state some 400 km southeast of the capital Addis Ababa, Ethiopia. The altitude of the park extends from 1,500 meters at the southern edge to 4,377 meters above sea level at the summit of Mount Tulu Dimtu in the central peaks (Yalden and Largen, 1992). The annual and the daily temperatures in the park largely vary with altitude (Williams, 2002). The rainfall in the park is characterized by one long rainy season from March through October with the greatest bulk of the rains falling in April and then August through October. The mean annual rainfall differs with altitude, with lower altitudes receiving between 600 mm and 1000 mm of annual rainfall and higher altitudes receiving up to 1200 mm (Hillman, 1986; Williams, 2002).

The Bale Mountains National Park harbors unique and diverse faunal and floral resources in Ethiopia. The park was primarily established to protect mountain nyala, Ethiopian wolf Canis simensis, and other endemic species found in the Bale Mountains (Waltermire, 1975). Vegetation communities in the park are spatially...
situat ed within four altitudinal zones: the Afro-alpine (> 3,700 m), sub-alpine and ericaceous (3,200 m to 3,700 m), upper Afro-montane forests (2,300 m to 3,200 m), and lower Afro-montane woodlands (1,500 m to 2,300 m) (Hillman, 1986; Bekele-Tesemma et al., 1993; Williams, 2002; Evangelista et al., 2007). The floristic composition and diversity associated with the four altitudinal zones have been well documented (e.g. Weinert and Mazurek, 1984; Bussman, 1997; Wesche et al., 2000). The importance of each zone to the mountain nyala has been also well described by Brown (1969) and Evangelista et al. (2007).

The northern edge of the park was selected to be the specific site for this study (see Fig. 1), because it harbors the largest herd of mountain nyala in the world (Refera and Bekele, 2004; Evangelista et al., 2007; Mamo, 2007). Two major habitat types are found: woodland and grassland. The woodland comprised three isolated habitat patches, the Dinsho Sanctuary, the Adele Ridge, and the Boditi Ridge. The Dinsho Sanctuary is characterized by dominant plant species such as Juniperus procera, Hagenia abyssinica, Hypericum revolutum, Solanum marginatum, Rosa abyssinica, Cardus nyassanus, and Achyranthes aspera. However, the invasive and unpalatable Euphorbia dumalis is becoming a dominant plant species there. The Adele and the Boditi Ridges are characterized by dominant tree species such as J. procera, H. abyssinica, H. revolutum, and Rapanea simensis. The understory is dominated by S. marginatum, Artemisia afr a, Senecio ragazzi, Nepeta azurea, Cineraria abyssinica, C. nyassanus, A. aspera, Helichrysum spp. and R. abyssinica. The mountain nyala mostly use the woodland habitat as a source of forage, cover, and shelter from risk of predation and extreme weather (Hillman and Hillman, 1987; Evangelista et al., 2007; Mamo, 2007).

The grassland habitat in the Gaysay Valley is characterized by dominant plant species such as N. azurea, A. afr a, Helichrysum spp., Alchemilla spp., R. abyssinica, and S. marginatum. Shrubby H. revolutum is also found at the edge of the grassland. The mountain nyala mostly use the grassland habitat as a source of forage (Refera and Bekele, 2004; Evangelista et al., 2007; Mamo, 2007).

Previous studies noted that the mountain nyala in the northern edge of the park occupied a very small geographic area (about 10 km²) that is densely populated by mountain nyala (probably more than 900 individuals) (Refera and Bekele, 2004; Evangelista et al., 2007; Mamo, 2007). The area is heavily impacted by human and livestock encroachments such as deforestation, agricultural land expansions, hidden illegal hunting, illegal settlement, and free-range livestock grazing (e.g. Woldegebriel, 1996; Stephens et al., 2001; Refera and Bekele, 2004; Malcolm and Evangelista, 2005; Evangelista et al., 2007; Mamo, 2007). All these factors likely negatively influence forage availability, habitat use, patch selection, and behaviours of mountain nyala.

1.3 Data collection

There are no physical barriers between the woodland and the grassland habitats in the study site. The altitude of the landscape is more or less similar and allows the mountain nyala to move between the two habitats. So, movement of mountain nyala between the two adjacent habitat types was common, with some individuals being

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1 Malcolm J, Evangelista P, 2005. The range and status of the mountain nyala. A report to the Ethiopian Wildlife Conservation Department, Addis Ababa, Ethiopia. 43 pp.
observed to forage in patches from each of the two habitats on different occasions. Along the altitudinal gradient, we randomly aligned a total of three transects through the three isolated woodland habitat patches (i.e., one transect through each habitat patch). Three more transects were randomly aligned through the grassland habitat in north-south direction. Transects varied in length from 0.7 km to 1 km, i.e. the length of each transect varied with the size of each habitat patch. All the fieldwork in this study was conducted in January and February 2011 between 6:00 and 9:00 in the morning and 16:00 and 18:30 late in the afternoon when mountain nyala are actively foraging in their natural habitat patches.

**Stem bite diameter measurements:** Measuring and quantifying the natural food items consumed by wild herbivores is crucial for habitat and species management. Along each transect, mountain nyala were regularly followed and observed in the field with the aid of binoculars (7 × 35). Field observations were carried out to identify plants freshly browsed by mountain nyala. By measuring the stem dpb, we obtained habitat-based stem diameters of bites for common but important natural browse plant species cropped by mountain nyala.

Following Wilson and Kerley (2003), for each individual animal that foraged during the field observations, we measured with the aid of a Vernier caliper the diameter of the stem twigs in the bites cropped from each browsed plant species using the stem dpb. All stem bites on a single branch were measured; observations were repeated until enough numbers of bites were measured per plant species per habitat type. We did not include grass species in our stem dpb measurements data in both habitats because it is hard to quantify the stem dpb. Measuring stem bite diameters of browsers comes with logistical and experimental challenges that can limit the precision of assigning data to particular individuals, and their age and sex classes. This happens when a group of mountain nyala containing different sex-age classes all forage from the branches of a single plant. Consequently, stem bite diameter measurements were combined together across sex and age classes for each habitat type and browse species.

**Bite rate quantification:** Bite rate method was adopted from Owen-Smith (1994) in the study of kudos *Tragelaphus strepsiceros*. Focal individual observations were carried out along each of the six transects to quantify the bite rates (number of bites per minute) of foraging mountain nyala. Focal individual is arbitrarily defined as an individual animal where all occurrences of specified actions (e.g. number of bites per minute, etc.) are recorded during a predetermined sample period (Altmann, 1974). To do so, each focal individual (i.e. adult male, adult female, sub-adult, or juvenile) was observed with binoculars at an average sighting distance of approximately 50 meters while the animals were foraging in their natural food patches. We identified sex-age class of the focal individuals as follows. Adult males are easily distinguished by their long twisting horns, large body size, and dark brown / grey color (Brown, 1969). Sub-adult males are identified by their straight spiked horns (but not twisted), medium body size, and brownish color (Mamo, 2007). Adult females are differentiated by their absence of horns, red-brown appearance, and smaller body size than adult males (Woldegebriel, 1996). Sub-adult females are differentiated from adult females by their smaller body size and reddish color (Refera and Bekele, 2004). However, previous studies revealed that sub-adult males and sub-adult females more or less exhibit similar activity behaviours (Brown, 1969; Hillman, 1985; Hillman and Hillman, 1987). Thus, we merged sub-adult males and sub-adult females together for this study. Juveniles are defined by their small body size and absence of horns.

If the foraging group contained a mix of ages and genders, stratified random sampling according to age and gender was employed to select focal individuals. The stratification was based on sex-age category while random sampling was achieved through use of random numbers in selection of the focal animal. As sex-age category of mountain nyala includes four classes (i.e. adult male, adult female, sub-adult, or juvenile), card numbers representing each class (i.e. 1 = adult male; 2 = adult female, 3 = sub-adult; 4 = juvenile) were prepared and randomly drawn when a group of mountain nyala was observed before starting the focal animal observations. For example, if a card with ‘2’ is randomly drawn, then, this implies that the first focal animal in the group to be considered is adult female. If this age or sex class is not found in the group, another card with different number will be randomly drawn to select the category of the focal animal from the group. Then we took focal observations of animals representing each category of sex and age. Each focal individual was observed for three minutes (timed with a stop watch) when it was actively foraging in its natural food patch. Then, the number of bites taken, sex-age class of the focal animal, habitat type, transects number, and date was recorded for each session. A total of 259 focal individual moun-
tain nyala were observed.

We took care to sample mountain nyala on different days, locations, and habitat types within our study site to reduce the chance of sampling the same individual twice. In addition, we tried to collect bite rate data from only a single focal individual of each age and sex class from a group. This spread observations out across habitats, time, location, sex and age classes as much as was possible for this population.

**Focal animal observations to quantify time budgets:** We used this method to quantify the time budgets allocated by wild animals to the different activities of vigilance, feeding, moving, and/or resting (Hochman and Kotler, 2006b; Tadesse and Kotler, 2011). Following the focal animal observation method proposed by Altmann (1974) and Martin and Bateson (1993), we took field observation on focal individual mountain nyala encountered while we walked along each of the six transects. To minimize any effect caused by the observer’s presence, we waited for a minimum of 10 minutes before collecting information allowing time for the animals to become acclimated and resume feeding (Hochman and Kotler, 2006b; Tadesse and Kotler, 2011). We classified observed individuals according to sex and age class (i.e., adult males, adult females, sub-adults, or juveniles) in each group as defined above. Individuals were considered to be in the same group if the separation distance was less than approximately 50 meters from the edge individual (Hillman and Hillman, 1987; Refera and Bekele, 2004). Solitary individuals father than 50 meters its closest mountain nyala were considered groups of one. Following Brown (1969) and Refera and Bekele (2004), we divided observations according to sex-age category (i.e. adult male, adult female, sub-adult or juvenile) of the focal individual.

We classified the behavioural activities of each observed focal mountain nyala into four types: vigilance, feeding, moving, and resting (Altman, 1974; Martin and Bateson, 1993). The activity types were defined as follows. Vigilance referred when the animal had its head up, neck erect, ears oriented forward and eyes wide open for watching, and appeared alert. Here we are only interested in quantifying the induced vigilance (Blanchard and Fritz, 2007), because animals may often need to perform more active vigilance in response to external stimuli, notably when risk is high. This induced vigilance necessitates the interruption of chewing and the disruption of the ingestion process (Blanchard and Fritz, 2007). Feeding was defined as the entire process of food searching, locating, biting, chewing, and ingestion as characterized by slight movements with the head down or foraging with head in a bush and/or shrub. Moving was defined as when the animal showed steady movement with the head held horizontally or was running. Resting referred to when the animal was lying down or sleeping, standing in the shade, standing still with head held horizontally and ears drooping, but not appearing alert. For each focal animal observation session, we noted the type of activity in which the mountain nyala was engaged at the start of the observation period and recorded the length of time spent in different activities using a stopwatch. We also recorded habitat type, transect number, group size, and date for each focal observation session. We carried out the observations for 10 minute sessions for each focal individual. We took a total of 106 focal observations of individual mountain nyala.

### 1.4 Data analyses

**Stem dpb analyses:** We used two-way ANOVA to analyze the effects of habitat type (i.e. woodland versus grassland), natural forage plant species, and the interaction of habitat type and natural browse plant species on the stem dpb by mountain nyala. A post-hoc Tukey’s HSD was used to test for the multiple comparisons across natural browse plant species.

**Bite rates analyses:** Numbers of bites per minute data were log transformed to ensure normality and better meet the assumption of ANOVA (Zar, 1999). Then, two-way ANOVA was used to analyze the effect of habitat type, sex-age category, and the interaction of habitat type and sex-age category on bite rates. We used a post-hoc Tukey’s HSD test for the multiple comparisons across sex-age categories.

**Focal animal time budgets analyses:** The proportion of time spent in each activity type (i.e. vigilance, feeding, moving, or resting) was calculated from the focal animal observations. To analyze the general activity time budget patterns of mountain nyala, we pooled together data for time allocation by all the four animal categories (i.e., adult males, adult females, sub-adults, and juveniles). Since the proportion of time spent on each activity varies between 0 and 1, it would be more appropriate to use a statistical approach that guarantees this requirement is satisfied. Thus, we used logit transformation to ensure normality (Zar, 1999) and to better meet the assumption of ANOVA. Then one-way ANOVA was used to analyze the data. Furthermore, Generalized Linear Model (GLM) with MANOVA (Multivariate Analysis of Variance) along with univariate statistics was used to analyze and interpret the effect.
of habitat type, sex-age category of the focal animal, and the interaction of habitat type and sex-age category on the activity time budgets of mountain nyala. For all analyses, we defined the alpha value to be 0.05. The analyses were performed by *STATISTICA* version 10.

2 Results

2.1 Stem bite diameters

To quantify stem dpb (natural GUDs), we measured a total of 9,366 stem bites from 15 natural browse plant species cropped by mountain nyala (Table 1). This included stem bite diameters of 15 browse species from woodland, and six species from grassland habitat (Table 1). The six grassland browse species also occurred in the woodland habitat and allowed cross-habitat comparisons. The 15 browsed plant species, their growth forms, occurrence of habitat type, and parts of the plant cropped by mountain nyala were also shown in Table S1. Habitat type and natural browse species interacted to affect the stem dpb ($F_{5, 6469} = 23.73; P < 0.001$), with mountain nyala showing higher stem dpb in the grassland for only half of the browse species (Fig. 2). Habitat type also affected stem dpb ($F_{1, 6469} = 9.79; P = 0.002$) for the six common browse species cropped by mountain nyala. Independent of browse species, mountain nyala cropped browse plants to larger stem dpb in the grassland (mean = 3.32 mm; SD = 0.06 mm) than in the woodland (mean = 3.21 mm; SD = 0.05 mm). Furthermore, mountain nyala browsed the six plant species common to both grasslands and woodlands to different stem dpb ($F_{5, 6469} = 61.42; P < 0.001$), leaving *S. marginatum* (mean = 6.12 mm) at the largest stem dpb. A post-hoc Tukey’s HSD test for multiple comparisons across browse species showed a significant difference in stem dpb between *S. marginatum* versus *R. abyssinica*, *R. abyssinica* versus *A. afra*, and *H. revolutum* versus *N. azurea*.

### Table 1  Mean stem bite diameters and standard deviations of twigs (stems) cropped and consumed by mountain nyala in the northern edge of the Bale Mountains National Park

| Scientific names               | Habitat type | n   | Mean stem diameter (mm) | Standard deviation |
|-------------------------------|--------------|-----|-------------------------|--------------------|
| Achyranthes aspera            | Woodland     | 459 | 2.54                    | 0.87               |
| Artemisia afra                | Woodland     | 283 | 2.48                    | 1.02               |
| Asparagus abyssinicus         | Woodland     | 113 | 2.00                    | 1.22               |
| Carduus nyassanus             | Woodland     | 533 | 3.94                    | 1.48               |
| Cineraria abyssinica          | Grassland    | -   | -                       | -                  |
| Cupressus usitatana           | Grassland    | -   | -                       | -                  |
| Helichrysum splendidum        | Woodland     | 308 | 2.25                    | 0.87               |
| Hypericum revolutum           | Grassland    | 972 | 3.02                    | 1.28               |
| Junipers procera              | Grassland    | 456 | 2.95                    | 0.98               |
| Maytenus spp.                 | Grassland    | 278 | 2.93                    | 0.98               |
| Nepeta azurea                 | Grassland    | 362 | 2.20                    | 0.88               |
| Rapanea simensis              | Woodland     | 522 | 6.95                    | 1.69               |
| Rosa abyssinica               | Grassland    | 476 | 3.65                    | 1.73               |
| Senecio ragazzi               | Woodland     | 134 | 3.00                    | 1.24               |
| Solanum marginatum            | Grassland    | 745 | 5.97                    | 1.41               |
| *n* = number of twigs measured.

**Fig. 2** The effect of habitat type and natural browse plant species on the diameters at point of browsing by mountain nyala in the northern edge of the Bale Mountains National Park

Diameters at point of browsing of common natural forage plant species cropped by mountain nyala in each habitat type were included in these analyses. The error bars represent +1SD. Bars labeled with different letters significantly differed.
2.2 Bite rates

Habitat type and sex-age class interacted to affect the bite rates of mountain nyala ($F_{3,251}=3.11; P = 0.027$), with greater differences among classes occurring in the grassland and the differences between grassland and woodland being greater for adults than for sub-adults and juveniles (Fig. 3). Habitat type also affected ($F_{1,251} = 98.26; P < 0.001$) the bite rates for mountain nyala, with higher bite rates in the grassland (mean = 17.72 bites per minute) than in the woodland (mean = 13.86 bites per minute). Furthermore, bite rates differed according to sex-age classes ($F_{3,251} = 83.31; P < 0.001$), with adult females taking the most bites per minute (mean = 19.03 bites per minute), followed by juveniles (mean = 17.14 bites per minute), sub-adults (mean = 15.16 bites per minute), and adult males (mean = 13.11 bites per minute). A post-hoc Tukey's HSD test for multiple comparisons across sex-age classes showed a significant difference in bite rates between adult females versus sub-adults, adult females versus adult males, and juveniles versus adult males.

Fig. 3  The effect of habitat type and sex-age category on the bite rates of mountain nyala in the northern edge of the Bale Mountains National Park

The number of focal individual mountain nyala considered for these analyses was 21 adult males, 38 adult females, 41 sub-adults, and 28 juveniles for the grassland; and 31 adult males, 34 adult females, 35 sub-adults, and 31 juveniles for the woodland. The error bars represent +1 SD. Bars labeled with different letters significantly differed.

2.3 Focal animal time budgets

To quantify the general activity time budget patterns of mountain nyala, we assessed a total of 106 focal indviduality. Mountain nyala differed in the proportion of time they devoted to different activities ($F_{3,620} = 27.69; P < 0.0001$). Mountain nyala devoted most of their time moving (39.55 ± 29.76%), followed by feeding (30.15 ± 37.2%), vigilance (22.28 ± 27.28%), and resting (8.02 ± 22.54%). A post-hoc Tukey's HSD test for multiple comparisons across activity types showed a significant difference in time budgets between moving versus resting, moving versus vigilance, and feeding versus resting.

Habitat type affected most behaviours of mountain nyala (MANOVA: Pillai's Trace value = 0.103; $F_{3,96} = 3.68; P = 0.015$), including the proportion of time being vigilant (ANOVA: $F_{1,98} = 8.12; P = 0.005$) and feeding (ANOVA: $F_{1,98} = 8.21; P = 0.005$). Mountain nyala were more vigilant in the woodland (mean = 0.28; $SD = 0.06$) than in the grassland (mean = 0.14; $SD = 0.04$) (Fig. 4). In contrast, mountain nyala more fed in the grassland (mean = 0.43; $SD = 0.08$) than in the woodland (mean = 0.27; $SD = 0.05$) (Fig. 4). Neither sex-age categories of the focal animals nor the interaction of habitat type and sex-age categories affected any behaviour of mountain nyala.

Fig. 4  The effect of habitat type and sex-age category on the activity time budgets of mountain nyala in the northern edge of the Bale Mountains National Park

The number of focal individual mountain nyala considered for these analyses was 10 adult males, 20 adult females, 8 sub-adults, and 9 juveniles for the grassland; and 15 adult males, 25 adult females, 9 sub-adults, and 10 juveniles for the woodland. The error bars represent +1 SD. Bars labeled with different letters significantly differed.

3 Discussion

Habitat quality and characteristics influence activity time budgets, foraging, and anti-predator behaviours of animals (e.g. Brown and Alkon, 1990; Rosenzweig, 1981; Cresswell, 1994; Kotler et al., 1994; Druce, 2005). Habitat use by an individual, group or population is strongly influenced by habitat essentials, such as food, cover, and escape access (Stephens and Krebs, 1986; Kotler et al., 1994; Shrader et al., 2008; Tadesse and Kotler, 2010). The study revealed that mountain nyala forage on a wide range of natural browse species to meet their nutrient and energy requirements, especially in the woodland habitat (Table 1). However, lower natural GUDs revealed by higher stem dpb, higher bite rates, higher proportion of time feeding, and lower induced vigilance level in the grassland make it the more used habitat by mountain nyala, probably due to its safety. In a recent study, Mamo (2007) also noted that
the grassland is more suitable habitat than the woodland for the foraging mountain nyala in the Bale Mountains National Park. However, we note that the woodland habitat provides the mountain nyala with cover from predators that may affect encounter rates especially when the mountain nyala are resting during the mid-day and overnight. It may also shelter from extreme weather (Evangelista et al., 2007; Mamo, 2007). For example, mountain nyala were frequently observed while moving into the woodland habitat to get shelter (shade) from the strong sun radiation during the mid-day. Nonetheless, mountain nyala while foraging prefer the grasslands. As predicted, our results are supported by the predation-sensitive foraging and/or the predation risk hypothesis that proposes that animals tradeoff between safety and food acquisition. In contrast, our results opposed the forage maturation hypothesis that proposes that ungulates’ habitat preference is driven by selection for high quality forage. In this way, behavioural indicators can be used to assess habitat quality and patch use by animals in their natural environment even when invasive or experimental techniques are not available to researchers.

Generally, stem bite diameters of common natural browse species cropped by mountain nyala were higher in the grassland than in the woodland. In particular, stem dpb by mountain nyala for A. afra, H. revolutum, and S. marginatum were all higher in the grassland than in the woodland habitat (Fig. 2). This suggests that foraging costs may differ between the two habitats, and the differences are most likely due to risk of predation. Evangelista et al. (2007) noted that mountain nyala use open sightlines to detect and locate approaching predators. So, the openness of the Gaysay grassland may favor the foraging mountain nyala by allowing them to more easily locate predators, leading to lower foraging costs arising from the risk of predation and higher harvest rates, resulting in larger overall stem dpb. Other studies also support our findings. For example, Risenhoover and Baily (1985) reported that bighorn sheep Ovis canadensis prefer to feed and harvest more food in open areas where they can more easily detect approaching predators. In another instance, Kotler et al. (1994) and Hochman and Kotler (2006b) noted that Nubian ibex Capra nubiana mostly prefer to feed in open areas which are situated on the cliff or near the cliff. Furthermore, experimentally blocking sightlines cause Nubian ibex to increase their GUDs and alter their induced vigilance level (Iribarren and Kotler, 2012). However, habitat selection and the associated foraging behaviour of animals depend on density (Morris, 2005). Refera and Bekele (2004) and Evangelista et al. (2007) noted that group size and density of mountain nyala is usually higher in the grassland than in the woodland. Although it is beyond the scope of this study, group size and spatial variation in density may have a role to affect the foraging metrics and stem dpb by mountain nyala. In addition, plant diversity, abundance, and composition differ between the two habitats in the study site (Evangelista et al., 2007; Mamo, 2007), and hence this may also affect the stem dpb by mountain nyala.

Browse species affected the stem dpb by mountain nyala (Fig. 2). The difference in stem dpb among the different browse species may have resulted from differences in nutritional content, energetic value, woodiness, digestibility, and morphology of the plant species; however, it is beyond the scope of this study. We compared the stem dpb of six browse species which were commonly cropped by mountain nyala in the woodland versus grassland habitats, namely S.marginatum, A. afra, H. splendidum, H. revolutum, N. azurea, and R. abyssinica (Fig. 2). The greatest mean stem dpb was for S. marginatum. Mountain nyala commonly forage on fruits and young shoots of S. marginatum. Assefa (2003) noted that mountain nyala is the main seed dispersal agent for S. marginatum in the Bale Mountains National Park, suggesting that there is a strong association between mountain nyala and S. marginatum where the former is the main browser and the latter is a good browse species.

Food resources in the natural environments are distributed in patches of variable size and shape with fluctuating quality, quantity, and safety (e.g. Houle et al., 2007). Another plant species frequently browsed by mountain nyala is H. revolutum (Table 1). This shrubby species is especially found in the ecotone between woodland and grassland where it is heavily exploited by mountain nyala (Brown, 1969; Mamo, 2007). This helps to make the ecotone especially attractive to mountain nyala. We observed in many instances when mountain nyala foraged on flowers, twigs, and leaves of H. revolutum. This suggests that vegetation type also influences the habitat and patch use behaviour of mountain nyala. In places where H. revolutum is not available, we mostly observed mountain nyala to forage on S. marginatum, A. afra, H. splendidum, N. azurea, R. abyssinica, and other palatable browse species (see also Table 1).

Bite rates (number of bites per minute) by mountain nyala differed between habitats (Fig. 3). Regardless of sex-age category, bite rates were higher in the grassland
than in the woodland habitat. A possible explanation is that due to the open sightlines vigilance may be especially effective, and therefore animals may require a little for safety (Brown, 1999), leaving more time for foraging. Indeed, the mountain nyala there devote more of their time for feeding and less to induced vigilance (Blanchard and Fritz, 2007), resulting in higher overall bite rates. At the same time, mountain nyala in the woodland spent more time vigilant and less time feeding than in the grassland habitat (Fig. 4). Fortin et al. (2004) also found that induced vigilance decreased the overall bite rates for bison Bison bison and elk Cervus canadensis.

Sex-age category of mountain nyala affected bite rates (Fig. 3). Adult females had the highest number of bites per minute compared with adult males, sub-adults, and juveniles. The high nutritional demand of reproductive and lactation may be reflected in the bite rates of adult females. Hillman (1985) noted that mountain nyala exhibit peak calving period in the months of August and September, but lactation continues several months after birth. Reid (2005) also reported that adult female springbok Antidorcas marsupialis in Augrabies National Park spent a greater proportion of their time feeding than adult male or other age groups. It is well-documented that reproductive state has a significant effect on nutritional requirements, with reproductive individuals having higher nutritional needs than non-reproductive males (e.g. Beier, 1987; Young and Isbell, 1991; Ginnett and Demment, 1997). Neuhaus and Ruckstuhl (2002), in their field study on the foraging behaviour of plains zebra Equus burchelli, also reported that adult females take more bites per minute when foraging than the non-reproducing adult males. Another possible explanation is that adult males are more concerned with mating (also known as “the male investment hypothesis”) than feeding during the reproductive season so that they should have lower bite rates than do adult females or other age groups. The body size of mountain nyala may also have played a role in determining bite rates. Adult male mountain nyala have longer mouths and should have correspondingly greater bite mass than do adult females. Consequently, adult females need to have a greater number of bites than do adult males to achieve the same food intake rate. Ginnett and Demment (1997), in their field study on the foraging behaviour of free-ranging giraffes in Tanzania, reported that males took larger bites than females, but females cropped bites more quickly and chewed faster. Males had longer per-bite handling times than females so that males had lower bite rates than females (Ginnett and Demment, 1997).

Regardless of habitat type, mountain nyala allocated the largest portion of their time budget to moving behaviour. Large time allocation to movement by mountain nyala could be due to the shortage of quality forage during the dry season in the study site. Previous studies noted that mountain nyala in the park face a shortage of preferred foods during the dry season due to the prevalence of intensive competition for limited forage resources with livestock (e.g. Refera and Bekele, 2004; Malcolm and Evangelista, 2005; Evangelista et al., 2007; Mamo, 2007). This should lead to high roaming behaviour in mountain nyala in quest for food and nutrients. Stephen et al. (2001) also stated that free-range livestock grazing is one of the common problems affecting the habitat use and behaviours of mountain nyala in the Bale Mountains National Park. To obtain sufficient foods, greater movement by mountain nyala during the dry season makes their home range size to be larger than that in the wet season (e.g. Ethiopian Wildlife Conservation Authority, unpublished data).

In conclusion, behavioural indicators can provide reliable metrics of patch and habitat use (Morris et al., 2009; Gaillard et al., 2010; Tadesse and Kotler, 2012). The combined results obtained from stem dpb, bite rates, and activity time budgets could help to assess the habitat quality for mountain nyala. Unlike population density, animal behaviours reveal much about habitat quality because animal behaviours instantaneously change with the changing environment. Thus, the resulting measures are leading indicators of habitat quality (Hochman and Kotler, 2006a; Olsson and Molokwu, 2007). For example, changes in the behaviours of individuals can indicate a change in environmental conditions that may later influence fitness (Morris et al., 2009). Knowledge on adaptive habitat use behaviours helps wildlife managers to develop proper conservation strategy and management plans (Morris et al., 2009). For example, quantifying stem dpb may help to compare food preferences, habitat use, impact of risk of predation, and track changes in range quality. Such measures are especially important in that they provide a measure of range quality as perceived by the foragers. Such field information can also direct habitat conservation priorities to the habitats that require greater levels of protection from human and livestock use. In this way, adaptive habitat use behaviours can guide conservation and management efforts for a number of endangered wildlife species including the mountain nyala.
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