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Habitat Quality Assessed with a Habitat Suitability Model and Habitat Selection Revealed by Isodar Analysis for the Mountain Nyala (*Tragelaphus buxtoni*) in Munessa, Ethiopia

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ABSTRACT---- ***Knowledge of habitat quality and adaptive habitat selection behavior of endangered species such as the mountain nyala (Tragelaphus buxtoni) can be invaluable for conservation and management, but quantitative information is lacking. The objectives of this study were to: (1) investigate the environmental variables that determine the suitable habitats for the mountain nyala, and (2) apply the isodar technique to look for density-dependent habitat selection behavior in mountain nyala. Following transects aligned through three major habitat types, environmental variables and activity densities of mountain nyala were estimated. The fieldwork was carried out in the wet and dry season in Munessa, Ethiopia. In addition, with the help of a spotlight, night-time mountain nyala censusing was carried out during the dry season. The result revealed that mountain nyala didn't show density-dependent habitat selection behavior in the wet season. However, during the dry season, the natural forest was the most suitable habitat for the mountain nyala, when crown diameter of trees and abundance of shrubs affected the habitat suitability. Significant isodars were obtained only across season and dry season comparisons between natural forest versus plantation and natural forest versus cleared vegetation habitats. The regression analyses revealed that the natural forest was qualitatively, but not quantitatively, more suitable than both the plantation and the cleared vegetation habitats. The isodars suggested that the strength of density-dependence was lower in the natural forest than either in the plantation or the cleared vegetation habitat. Spotlight censusing revealed that mountain nyala selected the cleared vegetation habitat during the night-time. The study demonstrated that habitat suitability models are important tools to evaluate the habitat quality for mountain nyala. Isodar analyses support the habitat suitability models by increasing our understanding on the qualitative and quantitative differences in density-dependent habitat selection by mountain nyala and thereby to enhance their conservation and management.***

Keywords ---- activity density; habitat suitability models; isodars; mountain nyala; Munessa

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1. INTRODUCTION

Theories of habitat selection can be applied in various ways to create a set of relatively simple behavioral assays that provide leading indicators of habitat quality, use and change[1,2]. Habitat selection and use can be inferred by directly observing and counting the number of individuals of the study species along transects across major habitat type[3,4,5]. However, to maximize the usefulness of activity density as an indicator of habitat quality of a particular species, the field data should be collected over a range of seasons and environmental conditions[5,6,7]. Information on habitat selection and use can be summarized in various types of model that simulate the relation between an animal population and its habitats[3,8,9,10]. These include models of habitat suitability that identify features of the environment that correlate with individuals activity density, and models of habitat selection (i.e. isodars) that identify salient features of the environment that determine how individuals choose to distribute themselves in space and time[1,3, 11,12,13].

Habitat suitability index (HSI) models are intended to be general indicators of suitability that are easily and repeatably applied under field conditions[14]. HSI models can be constructed from environmental variables and relative animal activity densities [5,15]. The models assume that habitat is an important factor in determining the presence and relative abundance of the species in question[16]. The selection of appropriate environmental variables largely depends not only on the species studied, but also on the costs of collecting the variables and the purpose of use of the empirical data[7]. Minimizing the number of variables in the HSI model serves two purposes: the model becomes more easily applied and the likelihood of model over-fitting is reduced[17]. However, to maximize the usefulness of the habitat suitability models, it is important that they should be constructed using as much prior information as possible[18].

Isodars are graphical lines in a state space of population densities in which fitnesses are equal across two adjacent habitats[1,19,20]. Empirically, an isodar is obtained by regressing the activity density of the study species in one habitat against the activity density in the other adjacent habitat. The slope of the isodar and its intercept reveal basic information on the underlying mechanisms of density-dependent habitat selection behaviors[19,20]. If the slope is significantly different from 1, then the two adjacent habitats differ qualitatively[1,19,20]. Qualitative differences often reflect differences in the strength of density-dependence. If the Y-intercept is significantly greater than zero, then the two habitats differ quantitatively[19,20]. Quantitative differences usually refer to differences in resource availability or productivity relative to the foraging species.

We applied habitat suitability models to evaluate the habitat quality and isodar analyses to understand the adaptive habitat selection behaviors of the endangered mountain nyala in Munessa, Ethiopia. We hypothesized that the habitat selection behavior of the mountain nyala should differ among habitats depending on the seasonal availability and quality of forages. In the wet season, grass and herbs are more available (i.e. both in quantity and quality) in the cleared vegetation than in any other existing habitats (i.e. plantation and natural forest habitats) in Munessa. In the wet season, thus, we predicted that the activity density of the mountain nyala should be higher in the cleared vegetation than in the plantation or natural forest habitat. However, during the dry season, we predicted that the activity density of the mountain nyala is higher in the natural forest than in the plantation or cleared vegetation habitat. This is because, in the dry season, the natural forest habitat provides the mountain nyala with a wide opportunity for availability of quality forages (i.e. due to high diversity and availability of palatable shrubs there), good refuge and escape routes from predators, and critical cover for thermal regulation[9,21,22,23].

When habitats demonstrate regular seasonal variation in both qualitative and quantitative components, it is modest to expect predictable seasonal differences in isodar slope and/or intercept[24,25]. In line with the above activity density predictions, we expected that the cleared vegetation is qualitatively and/or quantitatively better than the plantation and/or the natural forest habitats during the wet season. In contrast, during the dry season, we expected that the natural forest is qualitatively and/or quantitatively better than the plantation and/or the cleared vegetation habitats. The objectives of this study were to: (1) investigate the environmental variables that determine the suitable habitats for the mountain nyala, and (2) apply the isodar technique to look for density-dependent habitat selection behavior in mountain nyala.

2. MATERIALS AND METHODS

2.1 Study Species

The mountain nyala *Tragelaphus buxtoni* is an endemic species to Ethiopia[21]. Listed as endangered[26], mountain nyala is only found in a few locations in the highlands of Ethiopia[10]. It is a sexually dimorphic antelope in which adult males are much larger than adult females. The mountain nyala is a social animal with females congregating in family units of three to eight individuals and males forming small bachelor groups outside the mating season[22]. They are found in a variety of high-elevation habitats requiring access to seasonal forage and cover from risk of predation[27]. The mountain nyala mostly forages on grass and herbs during the wet season[9,22,23,28]. However, they rely on shrubs as their typical sources of forage during the dry season when grass and herbs become less available and poor in their nutritional status[9,21,22,29]. This suggests that the mountain nyala are able to modify their habitat selection behavior depending on the quality and quantity of food resources between seasons in a given habitat.

2.2 Study Area

The study was conducted in Munessa which is situated in Oromiya Administrative Regional State, Ethiopia. Its geographical location is at 7°13′ N, 38°37′ E (see Fig. 1). The altitude range extends from 2100 to 2700 m asl. The mean annual rainfall is about 1250 mm. The mean annual temperature varies between 15 °C and 20 °C. The vegetation is composed of natural and plantation forests where the main forest blocks are found on the escarpment and associated plateau lying between the Rift Valley lakes and the eastern edge of the Rift Valley[30,31]. Munessa has an area of 111 km^2 of natural and plantation forests[22]. The natural forests approximately cover 85 km^2 while the remaining 26 km^2 are plantation forests[22]. Both natural and plantation forests are potentially good habitats for a variety of wild animal species including the mountain nyala. Population size of the mountain nyala in Munessa is estimated to be around 200 individuals[22]. The mountain nyala in the area are subject to managed trophy hunting and unregulated poaching. We identified three major types of habitat over the study area: natural forest, plantation and clear vegetation habitats.

The natural forest habitat: The natural forest habitat is situated on undulating terrain providing the mountain nyala with good refuge and escape routes from predators and people. It also serves as valuable cover for thermal regulation and provides a good source of palatable forages especially in the dry season when the mountain nyala rely on shrubs as their typical sources of food. Characteristic indigenous tree species of the natural forests include *Afrocarpus falcatus*, *Syzygium guineense*, *Prunus africana*, *Bersama abyssinica*, *Aningeria adolfi-friederici*, *Hagenia abyssinica*, *Celtis africana*, *Millettia ferruginea* and *Croton macrostachyus*. However, there are various human- and livestock-induced impacts on the natural forests. For example, some natural forests have been totally cleared and converted into agricultural fields, while others suffered from heavy grazing and selective logging of economically important tree species[22,30,31].

The plantation habitat: The plantation habitat is mainly composed of exotic tree species, such as *Eucalyptus globulus*, *Eucalyptus grandis*, *Cupressus lusitanica*, *Pinus patula*, *Pinus radiata* and *Grevillea robusta*. Although the plantations offer a sparse herbaceous understory, they provide a very important habitat by offering escape refuge from risk of predation, valuable cover for thermal regulation and travel corridors especially in areas where the natural forest is extremely disturbed and/or limited[21]. However, illegal tree-cutting activities by local people for fuel-wood and construction materials, unrestricted livestock grazing and browsing are common threats to the plantation habitat especially in the crop-growing rainy season[32].

The cleared-vegetation habitat: The cleared vegetation habitat is characterized by relatively freely draining areas that are rich in grass and other palatable herbs. So, it serves as good feeding habitat for the mountain nyala especially in the rainy season. There are also some salt licks that attract the mountain nyala at night in the rainy season when people and livestock are not present. Lack of cover could allow the mountain nyala to detect approaching potential predators at greater distances, for example, by providing less stalking cover for leopard (*Panthera pardus*). In addition, the leopard is absent in the cleared vegetation habitat so that the mountain nyala can safely access forage there during the night-time. However, due to lack of cover, risks of human- and livestock-induced disturbances are highest in the cleared vegetation during the daytime[31]. As most of the cleared vegetation habitat is surrounded by natural forests and plantations, it is fairly easy for the mountain nyala to escape from human and livestock disturbances. Previous studies also noted that dense vegetation provides the mountain nyala with good cover from such disturbances[9,22,32].

2.3 Data Collection

To collect mountain nyala habitat selection and use data from all existing habitats across the landscape, we set out permanent walking transects with the aid of a GARMIN 75 GPS device, with each transect sampling a major existing habitat type within the study site. We established a total of 12 transects i.e. four transects in each habitat type. Along each transect, we quantified the viewable area of each habitat by walking perpendicularly from a given line transect until the unevenness of the topography or the thickness of the vegetation cover no longer allowed us to view that transect[3,5]. The GPS locations on both sides of all the viewable parts of each habitat type were then taken. This activity is important in determining the sample area of each habitat type along each transect walk. The GPS locations which were taken on both sides of the visible points for each transect were transformed into the Ethiopian coordinate system and imported into Arc GIS, and overlaid on the map of the study area. We then digitized the GPS coordinates of all the visible points for each transect walk using lines to make a polygon along all the transect walks. This gave us the areas of all the habitats sampled in each transect as shown in Table A1. Following the minimum sample area proposed by previous work, the sampling protocols covered 2-5% of the total area of the study site[33]. Transects varied in length from 0.8 km to 2.3 km, i.e. the length of each transect varied with the size of each habitat patch. The total area of our study site is about 111 km^2. So, we took transect samples whose total area is 3.83 km^2, which is 3.45% of the study site.

Daytime mountain nyala censusing: Movement of mountain nyala among the three habitat types was common, with some individuals being observed to forage in patches from each of the three habitats on different occasions. To measure activity density of the mountain nyala along transects, we conducted regular population censusing by walking along each transect. During each field censusing, we recorded the habitat type of each observed mountain nyala along with its sex-age class and group size. The season at the time of field observation was also recorded. Counts were carried out early in the morning from 06:00 to 09:00 local time when the mountain nyala are most active. We conducted the censusing in the wet and dry season. Each transect was assessed six times for the wet season, and seven times for the dry season.

Night-time mountain nyala censusing using a spotlight: Due to intensive human and livestock disturbances during the dry season in the study site, the mountain nyala became active during the night-time when people and livestock were absent in the area[32]. We found that spotlighting complemented the daylight field data on the activity density of the mountain nyala. The spotlighting was carried out at night from 20:30 to 24:00 local time. Each of the three habitats (i.e. cleared vegetation, plantation and natural forest) in the study site was assessed ten times either by car or on foot for times when the area is inaccessible for driving.

Measurement of habitat variables: We quantified environmental variables that were thought to affect the habitat selection behavior of the mountain nyala in each habitat patch along each transect used for estimating the activity densities of the mountain nyala. The environmental variables include abundance of trees, crown diameter of trees, abundance of shrubs, percent cover of herbs and grass, percent cover of bare soil, altitude and slope. This then allowed us to correlate activity densities with the various environmental variables to construct habitat suitability models.

A systematic sampling design was employed to lay plots and collect microhabitat and environmental data. The first plot within each habitat patch on each transect was randomly located; then successive plots were systematically added at 100-m intervals along each transect. The total number and distribution of sample plots for each habitat type varied with the total size of each habitat patch. A total of 109 plots were assessed (i.e. 31 plots in the cleared vegetation, 41 plots in the plantation and 37 plots in the natural forest). We first laid out a circular sample plot with a radius of 5 m on each line transect. All trees (a tree is arbitrarily defined as any woody plant species with a height of ≥ 3 m) within the 5-m-radius circular plot were identified and counted, and crown diameter for each tree in the plot was measured with a metre tape. Then a circular nested plot with a radius of 2 m was laid out within the larger circular plot and all shrubs (a shrub is defined as any woody plant species with a height of < 3 m) within this nested plot were identified and counted. Within each nested plot, another sub-nested plot with a radius of 0.5 m was laid out, and per cent plant cover (grass and herbs) and bare soil were estimated with a square grid (10 x 10 cm). The square grid was just used in order to precisely estimate the per cent plant cover (grass and herbs) and bare soil in the sub-nested circular plot. In addition, at the centre of each circular sample plot, slope (using declinometer) and altitude (using altimeter) were measured.

2.4 Data Analyses

Activity densities: We incorporated the sample area information (Appendix - Table A1) with population census data obtained through transect walk counting during the wet and the dry season. That enabled us to estimate the activity densities of the mountain nyala in each habitat type for the wet and the dry season as shown in Table 1. As the data were composed of both categorical and continuous variables, we used ANOVA to check whether the mountain nyala were exhibiting seasonal habitat selection behavior. To do so, we included habitat type, season, and the interaction of habitat type and season as predictors, with activity density of the mountain nyala as the dependent variable.

Habitat suitability models: We developed the habitat suitability models with the assumption that all sex-age classes of the mountain nyala have equal access to all prevailing habitat type in the study area. We correlated environmental variables to the activity densities of the mountain nyala in order to obtain models of habitat suitability. For environmental parameters, we incorporated abundance of trees, crown diameter of trees, abundance of shrubs, per cent cover of herbs and grass, altitude and slope. We then combined them with the activity density estimates generated in the previous section. Given the number of environmental parameters under consideration, we used only the simplified response curves for those environmental parameters included in this study. We converted the range of activity densities of the mountain nyala into a 0 to 1 scale, with 0 representing poor habitats and 1 representing optimal habitats for the mountain nyala[34]. In that way, we transformed the samples into a suitability index scaled from 0 to 1.

Taking the typically non-linear nature of the relations between environmental variables and the relative activity densities of the mountain nyala into account, we used a polynomial regression by which separate HSI response curves were generated for the wet and dry season[35]. Multiple linear regression analysis is normally applied when activity density data are available[36]. As all the environmental data included in this study were composed of continuous and discrete variables, we used multiple linear regression to determine the coefficients of the HSI variables entered into the models for the wet and the dry season. Since the per cent cover of herbs and grass and the per cent cover of bare soil in each plot are not independent (i.e. they share a degree of freedom), this might have consequences for the multiple linear regression analyses. Previous studies suggested that herbs and grass are valuable sources of food for the mountain nyala especially in the wet season, thus we excluded the per cent cover of bare soil from the multiple linear regression analyses[9,21,22]. So, the independent variables entered into the multiple linear regression analyses included: abundance of trees + crown diameter of trees + abundance of shrubs + per cent cover of grass and herbs + altitude + slope. For the dependent variable, we entered the wet and dry season activity density data separately for each season into the multiple linear regression analyses.

Isodars: Theoretically, it was shown that temporal variation in environmental conditions would produce isodars that differ in slope and/or intercept[37]. Practically, seasonal differences in isodar shape were demonstrated for some species such as eastern grey kangaroo (*Macropus giganteus*) and fat sand rat (*Psammomys obesus*)[24,25]. In the present study, the isodar analyses were restricted to those conditions where both adjacent habitat types were occupied by the mountain nyala since inclusion of zero activity densities can bias the isodar analyses, and hence may not yield a uniquely determined activity density in the alternative habitat[1,19,20]. To determine whether the slopes were above, below or equal to one, and whether the intercepts were above or equal to zero, the 95% confidence intervals around the slopes and intercepts were calculated using activity densities between each pair of habitats. For significant isodars, we calculated and compared the strength of density-dependence using slopes and their respective intercepts. For all analyses, we defined the alpha value to be 0.05 and performed the analyses with *STATISTICA version* 10.

3. RESULTS

3.1 Activity Densities

Mountain nyala activity density estimated from daytime censusing: The mountain nyala did not show density-dependent habitat selection behavior in the wet season ($F_{(2, 69)} = 2.58$; $P = 0.083$) (Fig. 2). In contrast, the activity density of the mountain nyala in the natural forest was different from the other two habitats in the dry season ($F_{(2, 81)} = 24.19$; $P < 0.001$) (Fig. 2). The mountain nyala selected the natural forest in the dry season, being seen there about three quarters of their time (≈75.00%). The mountain nyala had their highest mean activity density (0.31 mountain nyala /ha) and greatest maximum activity density (0.94 mountain nyala /ha) in the natural forest (Table 1). The maximum activity densities varied between 0.28 and 0.94 mountain nyala /ha in the dry season (Table 1). Overall, the activity density of the mountain nyala over the landscape was significantly affected by habitat type ($F_{(2, 150)} = 8.79$; $P < 0.001$) and the interaction of habitat type and season ($F_{(2, 150)} = 13.82$; $P < 0.001$). However, season alone did not affect ($F_{(1, 150)} = 1.33$; $P = 0.249$) the activity density.

Mountain nyala activity density estimated from night-time censusing using a spotlight: In contrast to their activity density during the daytime in the dry season (see also the above section), the mountain nyala changed their habitat selection behavior during the night time. Spotlighting revealed that the activity density of the mountain nyala was greatest in the cleared vegetation habitat during the night-time ($F_{(2, 27)} = 29.12$; $P < 0.001$) (Fig. 3). Consequently, the mountain nyala had the highest mean activity density (0.13 mountain nyala /ha) in the cleared vegetation during the night-time in the dry season (Table 2).

3.2 Habitat Suitability Models

Wet season habitat suitability models: The suitability index slightly increased with an increase in the abundance of trees, but at first increased and then steadily decreased with an increase in crown diameter of trees (Fig. 4). The suitability index was found to be independent of the abundance of shrubs, but steadily increased with an increase in the per cent cover of grass and herbs (Fig. 4). Furthermore, the suitability index was constant up to a certain altitude and then slightly decreased with an increase in altitude, and slightly decreased with an increase in the per cent slope over the landscape (Fig. 4). None of the habitat variables entered into the habitat suitability model had a beta coefficient that is significant at 0.05 alpha value (Table 3). Overall, the six habitat variables explained 15.1% of the variance for the HSI (Table 3).

Dry season habitat suitability models: The suitability index steadily decreased with an increase in the abundance of trees, but significantly increased with an increase in crown diameters of trees and abundance of shrubs (Table 3; Fig. 5). The suitability index was constant over low per cent of cover of grass and herbs, but decreased with high per cent cover of grass and herbs. The suitability index slightly decreased with an increase in altitude, and the per cent slope over the landscape (Fig. 5). Overall, the six habitat variables explained 27.2% of the variance for the HSI (Table 3).

Overall, the suitability index over the landscape was significantly affected by habitat type ($F_{(2, 150)} = 9.489$; $P < 0.001$) and the interaction of habitat type and season ($F_{(2, 150)} = 14.53$; $P < 0.001$). Natural forest was the most suitable habitat for the mountain nyala during the dry season (Fig. 6b). However, season alone did not affect ($F_{(1, 150)} = 0.50$; $P = 0.479$) the habitat suitability.

3.3 Isodars

Significant isodars were obtained only from activity densities of the mountain nyala across seasons and dry season comparisons, between natural forest versus plantation, and natural forest versus cleared vegetation habitats (Table 4). In both cases, the slope of the isodar between the natural forest versus the plantation habitats was significantly different from 1 (Table 4), suggesting that the natural forest was qualitatively better than the plantation habitat. For across season comparison, the isodar revealed that the strength of density-dependence in the natural forest was 1.35 times lower than in the plantation habitat. Similarly, during the dry season, the isodar revealed that the strength of density-dependence in the natural forest was 2.47 times lower than in the plantation habitat. Overall, the strength of density-dependence between the natural forest versus the planation habitat was stronger for the dry season than across seasons. However, in both cases, the Y-intercepts between the natural forest versus the plantation habitats were not different from 0 (Table 4), suggesting that there was no quantitative difference between these two habitats.

Across seasons and dry season comparisons, the slopes of the isodar between the natural forest versus the cleared vegetation habitats were significantly different from 1(Table 4), suggesting that the natural forest is qualitatively better than the cleared vegetation habitat. For across season comparison, the isodar revealed that the strength of density-dependence in the natural forest was 2.07 times lower than in the cleared vegetation habitat. Similarly, the isodar showed that the strength of density-dependence in the natural forest was 2.77 times lower than in the cleared vegetation habitat during the dry season. Overall, the strength of density dependence between the natural forest versus the planation habitats was stronger for the dry season than across season comparison. However, in both cases, there was no quantitative difference between the two habitats (Table 4).

4. DISCUSSION

The mountain nyala did not show significant difference in their activity densities among habitats during the wet season. Rather depending on the availability of food, the mountain nyala were distributed to use mosaic of the three habitats. The mountain nyala were regularly observed in the cleared vegetation, plantation and natural forest habitats where there was quality and abundant grass and herbs. More importantly, a group of mountain nyala was commonly observed around the salt licks in the cleared vegetation during the wet season. This suggested that salt is one of the important nutrients influencing the distribution and habitat use of the mountain nyala especially during the wet season. A recent also noted that the distribution and habitat use of mountain nyala in the Bale Mountains National Park is affected by the availability of salt licks[9]. However, when mountain nyala caught sight of observers in the cleared vegetation, they typically moved straight away into the adjacent plantation and natural forest habitats. This suggested that the cleared vegetation is a risky habitat, but plantation and natural forest habitats provide the mountain nyala with escape refuge and cover from risks of predation[22].

In the dry season, the diurnal activity density of the mountain nyala was significantly greatest in the natural forest which is in line with our prediction. This may be because the natural forest may provide the mountain nyala with diversified food, escape refuge, and good cover from risk of predation as well as shelter from hot weather especially in the dry season[22,23]. However, during the extended dry season, following the high livestock grazing pressures, palatable forages were greatly depleted in all habitats, but most seriously in the cleared vegetation and the plantation habitats[32].

Even the undergrowth status in the natural forest was poor during the extended dry season compared with the wet season (see also Table A2). This inevitably results in a shortage of palatable forage for the mountain nyala due to competition for limited food resources with livestock. Another study also noted that the mountain nyala face a shortage of forage during the dry season when there is high livestock competition for limited food resources in the Bale Mountains National Park[9].

Mountain nyala were observed to adjust their activity density and distribution even on a daily basis in Munessa. For example, during the extended dry season, the presence of foot prints of the mountain nyala in the plantation and cleared vegetation habitats suggest that they become mostly active during the night-time to search for forage[31]. The result obtained from the spotlight censusing during the night time also supported this scenario. Unlike the activity density in the early morning hours (i.e. 06:00 – 09:00 local time) as discussed above, night-time activity density of the mountain nyala during the dry season was greatest in the cleared vegetation habitat. This showed that the mountain nyala alter their activity density even on a daily basis. The possible explanation for this is that the mountain nyala can more easily detect approaching predators and escape in the open than in the natural forest or plantation habitats during the night-time. A recent study also noted that mountain nyala use open sightlines to detect and quickly escape from their potential predators[21]. In some occasions of our spotlight censusing, we encountered leopard both in the plantation and natural forest habitats. Leopard is one of the potential predators of the mountain nyala in Munessa[21,22]. This could be one possible reason that urged the mountain nyala to have highest activity density in the cleared vegetation during the night-time when leopard was actively hunting in the plantation and natural forest habitats. Furthermore, humans and their livestock were absent at night, and the mountain nyala can access the forage in the open more freely. As a result, the per cent of mountain nyala sightings during the transect walk was higher for the spotlight census than the morning daylight hours census in the dry season (Table 1 & 2).

Habitat suitability models are important tools for evaluating habitat quality based on critical environmental factors and relative activity density of animals[3,5,38]. To maximize the usefulness of habitat suitability models, it is important that they should be constructed using habitat variables chosen for *a priori* reasons, and selected using a method that consistently selects models of an appropriate level of complexity[18,39].

The habitat suitability models developed in the present study incorporated six habitat variables considered critical for the mountain nyala. None of the habitat variables significantly correlated with the HSI in the wet season. In contrast, during the dry season, HSI revealed that crown diameter of trees and abundance of shrubs had beta coefficients that significantly affected the habitat suitability for the mountain nyala. Tree crowns may provide the mountain nyala with important shade against hot weather in the day times during the dry season and thereby affect the activity density and the habitat selection behavior of the mountain nyala[22]. In addition, shrubs may provide the mountain nyala with good sources of palatable browse species especially in the dry season when grass and herbs become less abundant and low in their nutritional quality. Previous studies also noted that the mountain nyala rely on shrubs as their typical sources of food in the Bale Mountains National Park during the dry season[9, 29].

In line with our prediction, the habitat suitability model suggested that the natural forest is the most suitable habitat for the mountain nyala in the dry season (Fig. 6). For example, from the habitat suitability models, the components of the dry season habitat suitability for the mountain nyala that importantly reflect those significant differences between the three habitats were the mean crown diameter of trees and the abundance and diversity of shrubs (Table A2, A3), which were higher in the natural forest than in the other two habitats. This implies that the natural forest provides the mountain nyala with valuable cover for thermal regulation against hot weather in the daytime, safe refuge from risk of predation (), and diversified and abundant palatable forages during the dry season[9,22,23,40,41,42,43,44]. This suggests that the mountain nyala are not only aware of the variability of resources in foraging patches from the three habitats, but also they are able to assess the costs and benefits of moving among patches. Other authors also noted that food appears to be one of the limiting factors determining the distribution and the suitable habitats for wild animals during the dry season[5,45,46]. In this way, habitat suitability model can be employed to monitor and evaluate habitat quality and food resource availability for the endangered mountain nyala.

Previous studies demonstrated that isodars reflect quantitative (differences in productivity or availability) and qualitative (differences in density-dependencies) differences in habitats[1,19,20]. In the present study, we analyzed isodars by regressing the activity densities of the mountain nyala in adjacent habitats. Isodars analyses revealed that the mountain nyala showed density-dependent habitat selection behavior only during the dry season and across season comparisons. Some previous studies also obtained seasonal differences in density-dependent habitat selection behaviors for eastern grey kangaroo (*Macropus giganteus*) and fat sand rat (*Psammomys obesus*)[24,25]. The regression analyses in both cases of the isodars suggested that the natural forest was qualitatively, but not quantitatively, more suitable than the plantation or the cleared vegetation habitat. Thus, in both cases, the isodars revealed that the strength of density-dependence in the natural forest was lower than in the plantation or the cleared vegetation habitat. Qualitative differences often arise from differences in risk of predation or efficiency of resource use, suggesting that the natural forest is safer than the other two habitats, especially when population density rises[1,24]. In addition, resource identity and habitat structure may result in qualitative differences between habitats, which could be supported by the availability of higher diversity of shrub species (i.e. source of forage for the mountain nyala during the dry season) and greater multi-layered vegetation strata in the natural forest than either in the plantation or the cleared vegetation habitat[20,47]. Differences in activity density of the mountain nyala in the natural forest may also reflect preferential occupation of habitat that yields the greatest fitness[47].

In conclusion, natural habitats of the mountain nyala are being destroyed or mostly converted to other unsuitable land use types throughout their ranges[10,22]. Understanding the adaptive habitat selection behaviors of the endangered mountain nyala enhances its conservation and management activities. Habitat suitability models and isodar analyses were applied to determine the seasonal habitat quality and evaluate the adaptive habitat selection behaviors of the mountain nyala in Munessa. Habitat suitability models revealed that habitat quality for the mountain nyala varied with the seasonal availability of habitat resources (e.g. food, cover) and extent of predation risk. The isodar analyses also support the habitat suitability models by increasing our understanding on the qualitative and quantitative differences in density-dependent habitat selection behavior of the mountain nyala. For example, the present isodars suggested that the fitness of the mountain nyala in the natural forest was higher than either in the plantation or the cleared vegetation habitat during the dry season and across season comparison. Thus, future management plan for the mountain nyala should give due emphasis toward the conservation and protection of the remnant natural forests. The field information obtained through habitat sampling may also help in designing future monitoring programs to track population size and status of the mountain nyala in Munessa.

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6. CO-AUTHOR CONTRIBUTIONS

S. A. Tadesse and B. P. Kotler developed the concepts and wrote the research proposal for fund requesting. S. A. Tadesse carried out the field data collection, analyzed and interpreted the results. S. A. Tadesse and B. P. Kotler wrote the manuscript of this paper.

7. REFERENCES

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Figure Legends

Figure 1. Location map of the study site.

Figure 2. Seasonal habitat use by the mountain nyala assessed during the daytime. The error bars represent +1 SD.

Figure 3. Dry season habitat use by the mountain nyala assessed with a spotlight censusing during the night-time. The error bars represent +1 SD.

Figure 4. The environmental variables and their response curves included in the mountain nyala habitat suitability model during the wet season.

Figure 5. The environmental variables and their response curves included in the mountain nyala habitat suitability model during the dry season.

Figure 6. Comparison of seasonal habitat suitability index, (a) wet and (b) dry season, for mountain nyala. Suitability index was non-significant among habitats in the wet season; however, it was significant at 95% confidence interval among habitats in the dry season.

Figures

Figure 1

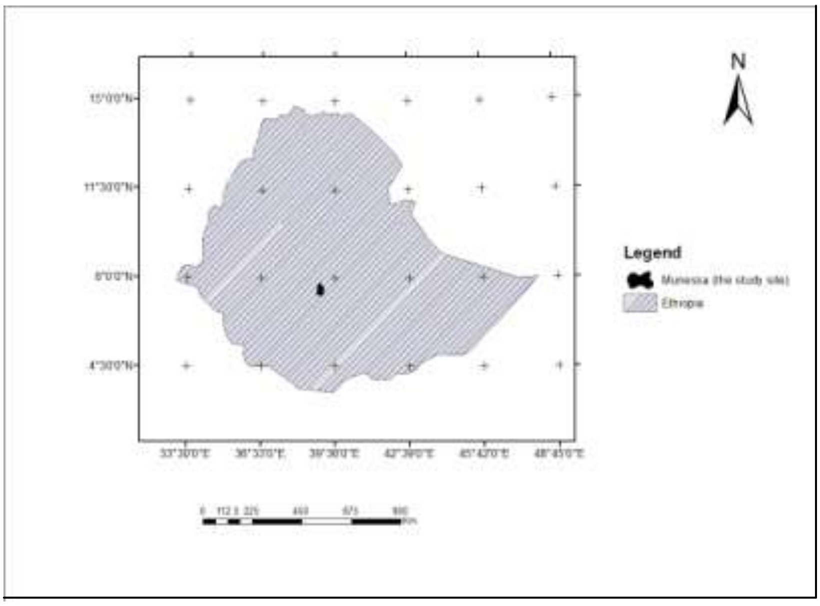


Figure 2

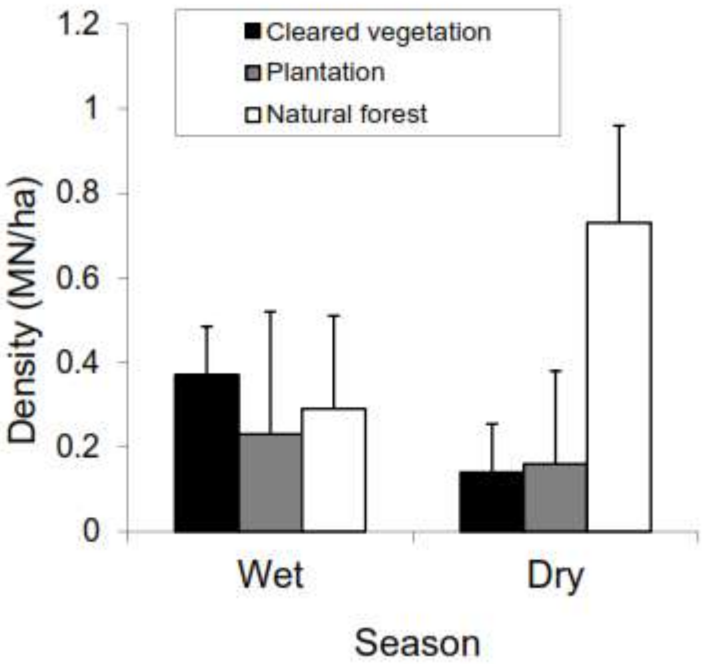


Figure 3

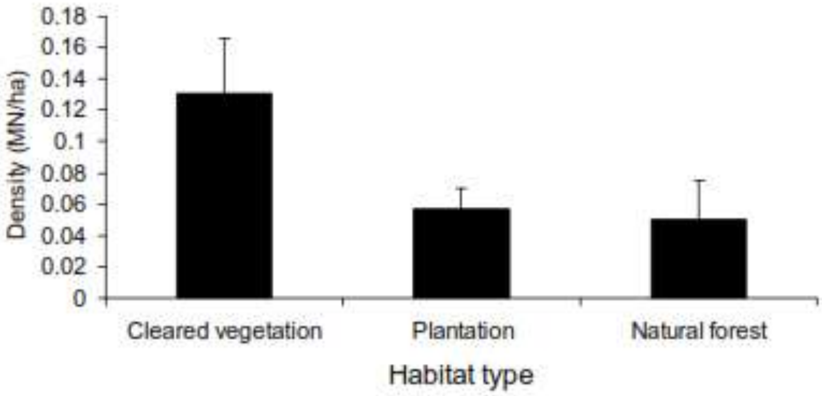


Figure 4

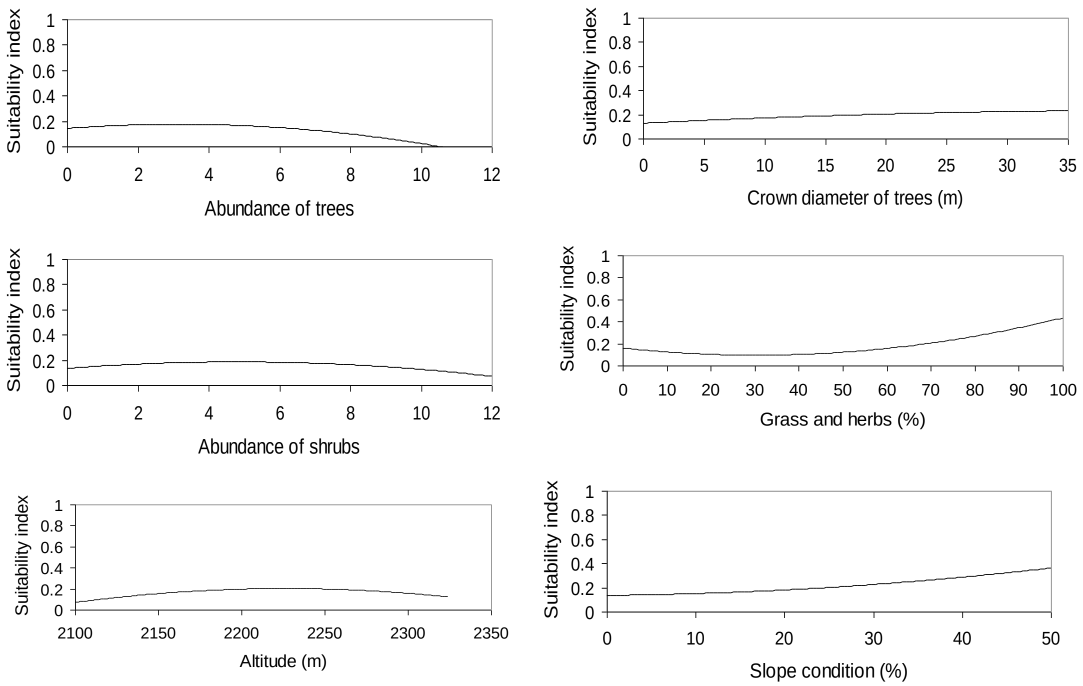


Figure 5

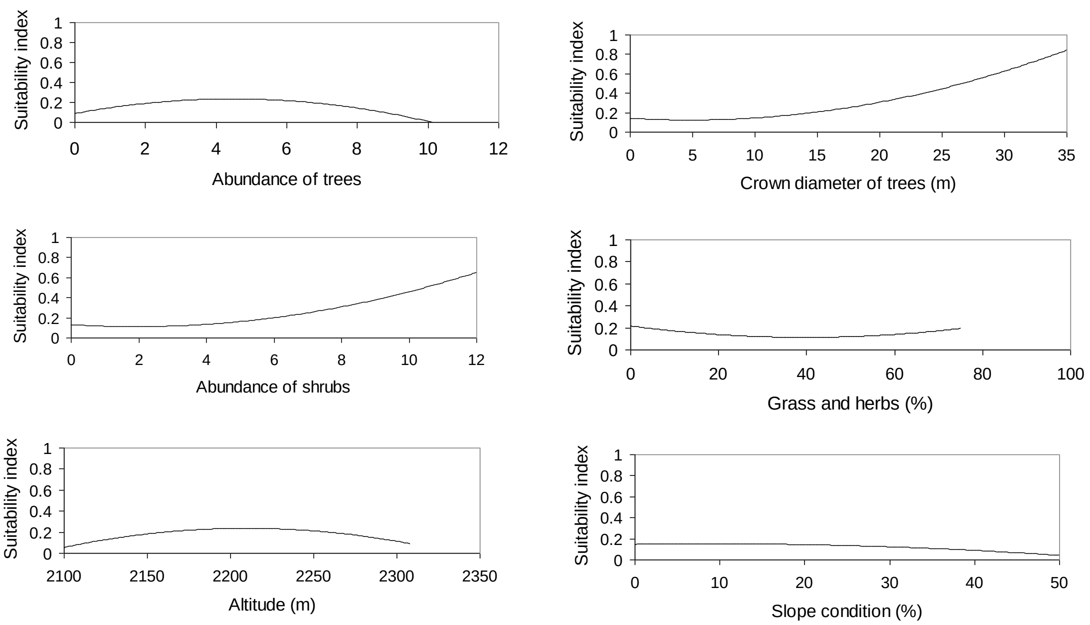
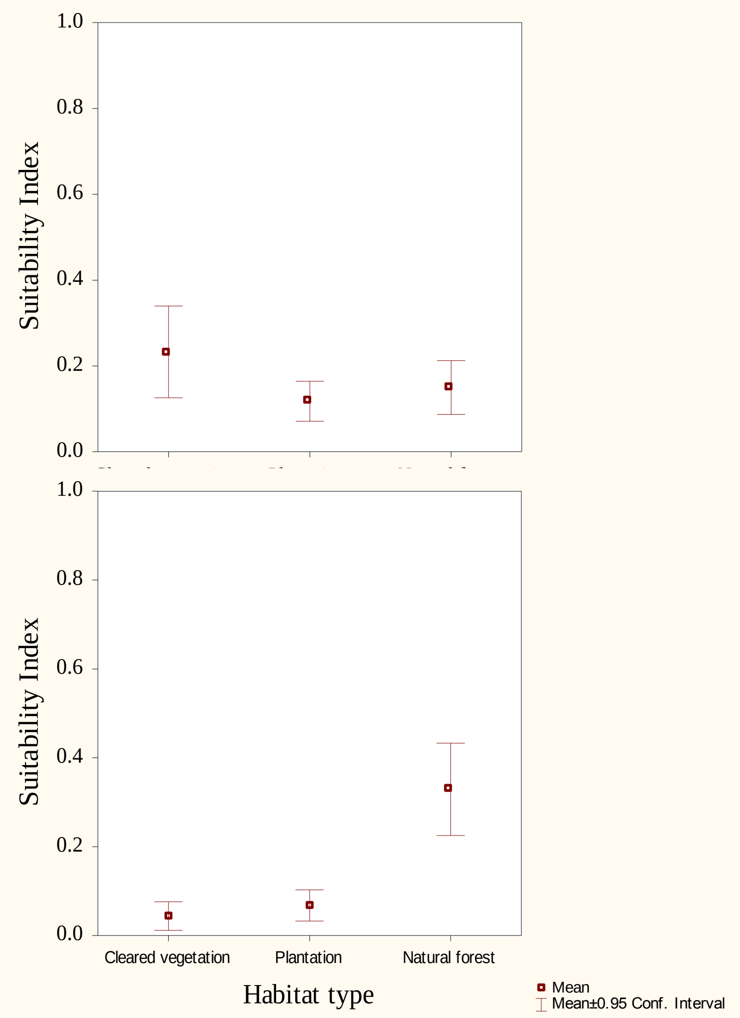


Figure 6

a.

b.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Suitability Index
1.0
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0.0
Suitability Index
Cleared vegetation
Plantation
Natural forest
Habitat type
Mean
Mean±0.95 Conf. Interval

Tables

Table 1. Daytime activity densities of the mountain nyala (MN) in different habitat types during the wet and dry season field survey: mean and maximum activity densities of the MN were shown as the number of times the MN were seen in each habitat type and as a per cent of total number of times that habitat was sampled. The minimum activity densities of the MN in all habitats both in the wet and dry season were zero.

n = number of transects sampled that habitat type.

Season	Habitat type	*n*	Mean density (MN/ha)	Maximum density (MN/ha)	Number of MN sightings	Sightings per transect walk (%)
Wet	Cleared vegetation	24	0.24	1.02	16	66.67
	Plantation	24	0.12	0.31	16	66.67
	Natural forest	24	0.15	0.51	17	70.83
	Total	72	0.51	1.84	49	68.06
Dry	Cleared vegetation	28	0.04	0.28	7	25.00
	Plantation	28	0.06	0.28	13	46.43
	Natural forest	28	0.31	0.94	21	75.00
	Total	84	0.46	1.50	45	53.57

Table 2. Night-time activity densities of the mountain nyala (MN) in different habitats in the dry season with spotlight censusing: minimum, mean, and maximum activity densities of the MN were shown as the number of times the MN were seen in each habitat type and as a per cent of total number of times that habitat was sampled.

Habitat type	*n*	Minimum density (MN/ha)	Mean density (MN/ha)	Maximum density (MN/ha)	Number of MN sightings	Sightings per transect walk (%)
Cleared vegetation	10	0.09	0.13	0.21	10	100.00
Plantation	10	0.04	0.06	0.07	10	100.00
Natural forest	10	0.02	0.05	0.11	10	100.00

n = number of transects sampled that habitat type.

Table 3. Multiple linear regression statistics and constituent variables of the habitat suitability index model for the mountain nyala during the wet and the dry seasons. The incorporated variables are listed in the order in which they were entered into the models. Significant coefficients at 95% confidence level are marked with an asterisk (*).

Season	$F_{(5,69)}$	P	Multiple R^2	Habitat variables	Coefficients	$t_{(69)}$	P
Wet	1.74	0.217	0.151	Intercept (constant)	-0.969	-1.333	-
				Abundance of trees	-0.221	-1.596	0.116
				Crown diameter of trees (m)	0.018	0.121	0.904
				Abundance of shrubs	-0.038	-0.294	0.769
				Per cent cover of grass and herbs	0.157	0.104	0.072
				Altitude (m)	-0.221	-1.673	0. 153
				Slope (%)	0.134	1.448	0. 099
Dry	2.53	0.124	0.272	Intercept (constant)	0.088	0.108	-
				Abundance of trees	-0.011	-1.077	0.939
				Crown diameter of trees (m)	0.334*	5.683	0.020
				Abundance of shrubs	0.269*	4.234	0.041
				Per cent cover of grass and herbs	-0.073	-0.522	0.603
				Altitude (m)	-0.003	-0.024	0.981
				Slope (%)	-0.146	-1.127	0.264

Table 4. Isodars contrasting mountain nyala activity densities in natural forest, plantation and cleared vegetation habitats. Results of linear regression are presented for both seasons and separated into wet and dry season. Significant regressions at 0.05 levels are marked with an asterisk. Slopes which were significantly above or below 1 and y-intercepts significantly greater than zero are also marked with an asterisk.
n = number of data points included in the analysis.

Habitat type	Total visible area in all transects (ha)	Transect No											
		1	2	3	4	5	6	7	8	9	10	11	12
Cleared vegetation	120.9	36.1	0	0	37.3	27.6	19.9	0	0	0	0	0	0
Plantation	142.3	0	37.8	38.6	0	0	0	0	0	0	38.2	0	27.7
Natural forest	119.9	0	0	0	0	0	0	29.8	45.7	18.8	0	25.6	0
Total	383.1	36.1	37.8	38.6	37.3	27.6	19.9	29.8	45.7	18.8	38.2	25.6	27.7

Contrast	Season	R^2	*F*	*n*	Slope	Intercept
Natural forest versus Plantation	Both	0.68	*16.24	23	*0.31 ± 0.16	0.23 ± 0.19
Natural forest versus Cleared vegetation	Both	0.76	*21.78	23	*0.29 ± 0.13	0.14 ± 0.16
Plantation versus Cleared vegetation	Both	0.23	1.37	23	1.12 ± 0.45	0.06 ± 0.29
Natural forest versus Plantation	Wet	0.18	1.41	16	0.92 ± 0.24	0.16 ± 0.37
Natural forest versus Cleared vegetation	Wet	0.24	1.59	16	0.96 ± 0.16	0.12 ± 0.26
Plantation versus Cleared vegetation	Wet	0.14	1.26	16	1.03 ± 0.17	0.17 ± 0.17
Natural forest versus Plantation	Dry	0.81	* 23.89	7	*0.37 ± 0.15	0.15 ± 0.45
Natural forest versus Cleared vegetation	Dry	0.84	* 28.92	7	*0.36 ± 0.14	0.13 ± 0.34
Plantation versus Cleared vegetation	Dry	0.12	1.15	7	0.94 ± 0.32	0.14 ± 0.54

Appendix

Table A1. The twelve sample transects used in the analysis**.** The visible area of each habitat covered by transects is included.

Table A2. A summary of habitat variables measured in the wet and dry season. Mean and standard deviation values are included.

Season	Habitat type	*n*	Parameters	Mean	SD
Wet	Cleared vegetation	31	Altitude (m)	2204.68	90.85
			Slope (%)	10.32	11.11
			% cover of grass and herbs per plot	89.80	15.71
			% cover of bare soil per plot	10.20	15.71
			Number of trees per plot	0.00	0.00
			Number of shrubs per plot	0.80	0.76
			Crown diameter of a tree per plot	0.00	0.00
	Plantation	41	Altitude (m)	2240.93	56.13
			Slope (%)	6.20	5.08
			% cover of grass and herbs per plot	62.39	31.20
			% cover of bare soil per plot	37.61	31.20
			Number of trees per plot	3.98	2.63
			Number of shrubs per plot	1.44	1.47
			Crown diameter of a tree per plot	6.44	2.01
	Natural forest	37	Altitude (m)	2179.70	50.99
			Slope (%)	9.50	8.39
			% cover of grass and herbs per plot	57.38	20.83
			% cover of bare soil per plot	42.62	20.83
			Number of trees per plot	1.97	1.23
			Number of shrubs per plot	3.50	2.71
			Crown diameter of a tree per plot	10.61	6.20
Dry	Cleared vegetation	31	Altitude (m)	2204.68	90.85
			Slope (%)	10.32	11.11
			% cover of grass and herbs per plot	41.40	17.71
			% cover of bare soil per plot	58.60	17.71
			Number of trees per plot	0.00	0.00
			Number of shrubs per plot	0.80	0.76
			Crown diameter of a tree per plot	0.00	0.00
	Plantation	41	Altitude (m)	2240.93	56.13
			Slope (%)	6.20	5.08
			% cover of grass and herbs per plot	17.24	14.24
			% cover of bare soil per plot	82.76	14.24
			Number of trees per plot	3.98	2.63
			Number of shrubs per plot	1.44	1.47
			Crown diameter of a tree per plot	6.44	2.01
	Natural forest	37	Altitude (m)	2179.69	50.99
			Slope (%)	9.50	8.39
			% cover of grass and herbs per plot	16.88	16.30
			% cover of bare soil per plot	83.12	16.30
			Number of trees per plot	1.97	1.23
			Number of shrubs per plot	3.50	2.71
			Crown diameter of a tree per plot	10.61	6.20

n = total number of sampled plots that habitat type.

Table

A3. List of tree and shrub species recorded in plots which were sampled to collect habitat variables data for the mountain nyala

Scientific names	Growth form	Habitat type of occurrence
Acokanthera schimperi	Shrub	Natural forest
Adhatoda schimperiana	Shrub	Natural forest
Afrocarpus falcatus	Tree; Shrub	Natural forest; Plantation; Cleared vegetation
Albizia gummifera	Tree; Shrub	Natural forest; Plantation
Allophylus abyssinicus	Tree; shrub	Natural forest
Aningeria adolfi-friederici	Tree	Natural forest
Arundinaria alpina	Shrub	Natural forest
Bersama abyssinica	Tree; Shrub	Natural forest; Plantation
Buddleja polystachya	Shrub	Natural forest
Calpurnia auria	Shrub	Natural forest; Plantation
Carissa edulis	Shrub	Natural forest
Celtis africana	Tree; Shrub	Natural forest
Combretum spp.	Tree	Natural forest
Croton macrostachyus	Tree; Shrub	Natural forest; Plantation; Cleared vegetation
Cupressus lusitanica	Tree; Shrub	Plantation; Cleared vegetation
Dombeya torrida	Tree; Shrub	Natural forest
Ekebergia capensis	Tree; Shrub	Natural forest
Eucalyptus globulus	Tree	Plantation
Eucalyptus grandis	Tree	Plantation
Grevillea robusta	Tree	Plantation
Hagenia abyssinica	Tree	Natural forest
Millettia ferruginea	Tree; Shrub	Natural forest
Myrtus communis	Tree	Natural forest
Maytenus senegalensis	Tree; Shrub	Natural forest; Cleared vegetation; Plantation
Nuxia congesta	Tree; Shrub	Natural forest
Olea hochstetteri	Tree; Shrub	Natural forest
Phytolacca dodecandra	shrub	Plantation
Pinus patula	Tree; Shrub	Plantation; Cleared vegetation
Polyscias fulva	Tree; Shrub	Natural forest
Prunus africana	Tree	Natural forest
Rhus glutinosa	Shrub	Natural forest
Rosa abyssinica	Climber	Natural forest
Rytigynia neglecta	Shrub	Plantation; Cleared vegetation; Natural forest
Syzygium guineense	Tree; shrub	Natural forest
Teclea nubilis	Shrub	Natural forest