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ORIGINAL ARTICLE

Compared diets of sympatric beira antelopes and domestic goats in the growing season

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Abstract The beira (*Dorcatragus megalotis*) is a threatened antelope of the Horn of Africa, whose feeding habits are poorly documented. Using micro-histological analysis of faeces, we examined its wet season diet in arid hills of the Republic of Djibouti and compared it to that of sympatric domestic goats (*Capra hircus*). As expected, the goat was found to be an intermediate feeder, eating ca. 50 % of grasses. In contrast, the beira was found to be a strict browser, feeding selectively on the leaves of woody plants and forbs. Furthermore, the beira appeared to consume little the forb *Aizoon canariense* and the shrub *Croton somalensis*, two plants that were found to be important food items for the goat, and are known for becoming major components of the flora in the event of overgrazing and subsequent soil degradation. Despite the contrasted diets of the two species, overgrazing by domestic goats may thus constitute a major threat for the long-term survival of the beira.

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Introduction

The only extant species in its genus, the beira (*Dorcatragus megalotis* Menges, 1894) is an antelope endemic to the arid hills and low elevation mountains of the Horn of Africa (northern Somalia, north-east Ethiopia, and southern Djibouti). Its range has regressed and fragmented since the beginning of the 20th century (Künzel and Künzel 1998; Boitani et al. 1999; Laurent et al. 2002; Giotto et al. 2009), and the beira, now common nowhere, is classified as 'vulnerable' on the IUCN Red List of Threatened Species (Heckel et al. 2008).

Whereas certain aspects of the species' behaviour and ecology are now rather well documented (Hammer and Hammer 2005; Giotto and Gerard 2010; Hammer 2011; Giotto et al. 2013), its feeding habits are only known through anecdotal observations (Laurent and Laurent 2002; Giotto et al. 2008). On the basis of its small body size (Hammer 2011) and the Jarman-Bell principle (Bell 1971; Jarman 1974; Geist 1974), the beira can be expected to be a selective browser, feeding mainly on the leaves of woody plants and forbs. However, a quantitative study is required; despite their small body size, certain ruminants such as the oribi (*Ourebia ourebi*) and Chinese water deer (*Hydropotes inermis*) have been reported to feed to a large extent on grasses (Hofmann 1989; Cooke and Farrell 1998; Cerling et al. 2003; Sponheimer et al. 2003).

In the present paper, we compare the wet season diets of sympatric beira and domestic goats (*Capra hircus*), as determined by micro-histological analysis of faeces. In the dry season, the grasses and numerous forbs are unavailable in the habitats occupied by the beira. In contrast, in the growing season, plant diversity and abundance are at their maximum. Moreover, whereas micro-histological analysis of faeces is a non-invasive technique especially useful for investigating the feeding habits of threatened species, it generally gives a distorted image of the diet because digestibility of the consumed items depends on organs and plant species. The technique tends, in particular, to overestimate the proportion of grasses and underestimates the proportion of forbs (Anthony and Smith 1974; Holechek et al. 1982; McInnis et al. 1983). Since the domestic goat is known as an intermediate feeder, consuming grasses as well as forbs and woody plant leaves (Bullock 1985; Hofmann 1989; Sietses et al. 2009), its diet a priori constituted a good reference for positioning that of the beira along the browser-grazer continuum.

Study area and methods

Study area

The study was conducted in the hills of Addaoua Bourale (11° 00′ N; 42° 52′ E), southern Djibouti. The area has a hot, arid climate, with a mean annual temperature around 30 °C, and an average ca. 250 mm rainfall per year (Laurent and Laurent 2002). The months from May to September constitute a hot and dry season, with midday temperatures between 37 and 42 °C, and <25 % of the total annual rainfall. November to March constitute a rather cool and wet season, with midday temperatures between 23 and 33 °C, night dews, and ca. 50 % of the total annual rainfall (Giotto et al. 2013).

With an elevation of 600–850 m above sea level, the study area covered 2 km^2 of 'altitudinal *Acacia etbaica* wooded steppe' (Laurent and Laurent 2002). The vegetation, intensively browsed by domestic goats, was sparse. Trees, mainly *A. etbaica*, were typically less than 2.5 m in height and covered less than 5 % of the total area. Shrubs, subshrubs and herbaceous species covered 20–40 % of the ground during the wet season (Ibrahim 1998). Beira, rock hyrax (*Procavia johnstoni*) and crested porcupine (*Hystrix cristata*) were the only wild herbivores having a body mass >1 kg. In contrast, domestic goats were common (Giotto et al. 2009). Shepherds of the local human community conducted them for foraging in the hills during the day and gathered them in small enclosures in their campsites at the foot of hills for the night.

Faeces collection and vegetation survey

Fieldwork was carried out during 15 days, from late February to early March 2007. At this time, nine adult beira and a young were known for using the study area (Giotto and Gerard 2010), while several tens of goats were present during the daylight hours.

Thirty-nine groups of fresh faecal pellets were collected in beira collective latrines. An equal number of groups of fresh faecal pellets from goats that foraged by day in the study area were collected in their night enclosures. Collected faeces were dried and individually stocked.

Plants' abundance was quantified, counting the number of individuals of each species in 50 circular 10-m^2 plots, located at the nodes of a 200-m grid established on a map of the study area. Plant species were further assigned to six morphological categories, within which their abundance could be considered as an indicator of their relative availability for beira and goats. The six categories were 'trees' (woody species having a single main stem, with mature individuals typically >2 m high), 'shrubs' (woody species with several main stems arising at or near the ground, with mature individuals typically >0.3 m high), 'subshrubs' (dwarf shrubs <0.3 m high), 'Poaceae' (grasses), 'forbs' (other herbaceous species without woody parts above ground) and 'lianas' (species needing support to climb up).

During the vegetation survey, we also collected leaves of each encountered species. These leaves were conditioned in a water solution at 10 % of glycerine, to which 50 % of alcohol and few drops of formalin were added.

Faeces composition

Faeces composition was determined by micro-histological identification of vegetal fragments (Dusi 1949; Croker 1959; Putman 1984). First, in order to constitute a set of reference photographs, we took pictures of the upper and lower cuticles of the collected leaves, using a microscope (Leitz Dialux 20) at ×100 or ×40 magnification and a camera (QImaging MicroPublisher 3.3 RTV). Thereafter, at least eight pellets of each faeces collected were rehydrated, then sieved at 0.2 mm, cleared with bleach (2.6 % sodium hypochlorite) and rinsed with clear water. Two slides were prepared for each faeces then examined under the microscope at ×100 magnification, in such a way that the edge of the microscope field followed successively four spaced straight lines drawn on the lower surface of the slide. For each faeces, the first 200 fragments (be they fragments of epidermal cuticle, or isolated hairs) whose centre entered the microscope field were compared with the reference photographs and classified up to the species level when possible. In this way, we obtained 39 samples of 200 fragments for each of the two animal species.

Conversion of fragment numbers into epidermis areas

Each plant species identified in the faeces was characterised by the number of faecal samples in which it was found in the beira and the goat. Thereafter, we focused on the plants occurring in more than 25 % of the faecal samples of at least one of the two animals and convert the number of their fragments into epidermis area. According to fragment nature (cuticle fragment or isolated hair), conversion coefficients were obtained as follows.

For cuticle fragments, we prepared ten additional slides of faecal samples per animal species. We then measured the surface area of 229 fragments belonging to 16 plant species, using the camera-equipped microscope and the Image-Pro Express software. Thereafter, we fitted three ANOVA models to log-transformed areas: a model only including the plant effect, a model only including the animal effect and a model including both effects and their interaction. Comparison between the models revealed a significant effect of the plant ($F_{29,227} = 4.872$; $P < 0.0001$) but no significant effect of the animal ($F_{15,213} = 1.373$; $P = 0.1632$). As a consequence, mean surface area of cuticle fragments was computed by plant species, pooling the two animal species.

For the isolated hairs, we cut 120 circular samples of 2 mm in diameter out of the collected leaves of 14 plant species and counted the hairs over the upper and lower epidermises of each sample. Epidermis area per hair was then estimated for a species as $a = A/\bar{x}$ where A is the total epidermis area examined per sample (2π mm^2), and $\bar{x}$ is the mean number of hairs counted per sample.

For most of the plant species having pubescent leaves, the remnants found in the faecal samples were either isolated hairs or cuticle fragments carrying hairs. For some, however, both remnant types were present, all or part of the hairs separating from cuticles during digestion or the preparation of faecal samples. In this case, we estimated epidermis area using each fragment type then retained the greater of the two estimates.

Difference between beira and goat in epidermis relative areas

The epidermis areas obtained per plant and animal species were transformed into relative areas (summing to 1) for each of the two animal species. Similarity between the two distributions was then quantified using Schoener's overlap index (Schoener 1970)

$$S = 1-\frac{1}{2}\sum_i |b_i - g_i| = \sum_i \min(b_i, g_i),$$

where b_i and g_i are the relative areas of plant i in the beira and the goat, respectively. This index, which ranges from 0 to 1, increases as the compared distributions converge. However, as other similarity indices, it has an unknown expected distribution under the hypothesis that the differences observed are only random fluctuations due to sampling. The value obtained for Schoener's index was therefore tested by random permutation (Manly 1997). Under the null hypothesis that the faeces of the two animals had the same composition, any random permutation of the labels 'beira' and 'goat' of the faecal samples should give samples as probable as those observed. Accordingly, we performed 9999 such permutations, and for each of them, we recomputed the relative areas of epidermis of the different plant species for the beira and the goat, then the value of Schoener's index. The 9999 values obtained by permutation, and the value observed were ranked together in increasing order, and we finally computed the one-tailed P value (i.e. the probability of obtaining a value lower or equal to that observed under the null hypothesis) as $P = r/10{,}000$, where r is the rank of the observed value.

The random permutations performed for the previous test were further used to test the difference between beira and goat in the relative epidermis area of each plant. Focussing on a given plant, we calculated, for each permutation and the observed samples, the absolute value of the difference between the relative areas of the plant under focus in the two animal species. The 9999 values obtained by permutation and the value observed were ranked together in decreasing order, and we computed the P value as $P = r/10{,}000$, where r is the rank of the observed value. The test (two-tailed in the present case because of the use of the absolute value) was considered as significant when the P value was lower or equal to $\alpha_{\text{corr}} = 0.05/k$, where k is the total number of plants for which the test was performed (Bonferroni's correction).

Difference between plants or plant categories within animal species

Difference between the epidermis areas of two plants (or two plant categories) within the faecal samples of a given animal species was tested, using Wilcoxon's T test for paired samples. The test was considered as significant when the P value was lower or equal to $\alpha_{\text{corr}} = 0.05/k$, where k is the total number of pairwise comparisons that could be performed between plants (or plant categories).

Results

A total of 89 plant species were recorded in the plots, among which ten were trees, 27 shrubs, 15 subshrubs, seven Poaceae, 27 forbs and three lianas (Table 1; supplementary material). Nevertheless, the cuticle fragments of the different Poaceae appeared to be difficult to distinguish. Accordingly, Poaceae were pooled for micro-histological analysis, reducing the number of taxonomic groups potentially distinguishable in the faecal samples to 83.

Fifty-six out of the 83 taxonomic groups were identified in the faeces (Table 1). Twenty-seven (among which no liana) had an occurrence frequency >25 % in the faecal samples of at least one of the two animal species; their fragments made 89.8 % out of the 7800 fragments examined for the beira, and 92.5 % out of the 7800 fragments examined for the goat.

Table 1 Total number of individuals of each plant species found in the 50 ten-m^2 plots, and total number of their fragments found in the faecal samples. Species are ranked in decreasing order of abundance in the plots within each morphological category (trees, shrubs, etc.). Plants known to be favoured by overgrazing are underlined (see Discussion)

Species		Plots	Beira	Goat
Trees				
1.	*Acacia etbaica*	142	556	338
2.	*Boscia coriacea*[a]	45	23	26
3.	*Acacia tortilis*	5	3	0
4.	*Acacia mellifera*[a]	5	4	2
5.	*Commiphora* sp.[a]	3	0	2
6.	*Commiphora myrrha*	2	0	0
7.	*Balanites aegyptiaca*	2	6	2
8.	Undeterminded tree	2	0	0
9.	*Maerua crassifolia*[a]	1	0	0
10.	*Dobera glabra*[a]	1	0	0
Shrubs				
1.	*Iphionopsis rotund*[a]	1525	0	0
2.	*Croton somalensis*[a]	922	137	2253
3.	*Pulicaria somalensis*[a]	629	0	1
4.	*Crossandra* sp.[a]	378	9	0
5.	*Solanum somalense*[a]	350	51	2
6.	*Acalypha fruticosa*[a]	272	0	0
7.	*Cordia* sp.[a]	223	1761	213
8.	*Indigofera articulata*[a]	85	0	2
9.	*Cadaba longifolia*	62	169	10
10.	Malvacea undet. 1[a]	53	948	943
11.	*Cassia senna*[a]	47	8	2
12.	*Acacia oerfota*	24	138	25
13.	*Pupalia lappacea*[a]	23	8	1
14.	Euphorbiacea undet. 1	16	1	4
15.	*Solanum cordatum*	14	0	0
16.	*Hibiscus* sp.[a]	13	268	223
17.	*Dodonaea angustifolia*	12	0	0
18.	*Maerua decumbens*	7	34	1
19.	*Maerua oblongifolia*[a]	7	0	0
20.	Undetermined shrub[a]	6	0	0
21.	*Acacia horrida*[a]	6	7	8
22.	Malvacea undet. 2[a]	3	0	2
23.	*Asparagus asiaticus*	2	0	0
24.	*Blyttia fruticulosum*	2	0	0
25.	Euphorbiacea undet. 2[a]	2	6	5
26.	*Vepris glomerata*[a]	2	3	0
27.	*Premna resinosa*	2	0	0
Subshrubs				
1.	*Seddera latifolia*[a]	3187	94	17
2.	*Barleria* sp. 1[a]	1173	0	0
3.	*Teucrium spicastrum*[a]	963	49	133
4.	*Indigofera arabica*[a]	944	63	5
5.	Lamiacea undet.[a]	541	49	21
10.	*Fagonia schweinfurthii*	96	0	0
11.	*Indigofera* sp. 1[a]	94	9	8
12.	*Seddera arabica*[a]	66	88	10
13.	*Euphorbia* sp. 1	3	0	0
14.	*Indigofera* sp. 2[a]	3	14	0
15.	*Salsola baryosma*[a]	1	0	0
Poaceae (grasses)			17	1566
1.	Poacea undet. 1	1191	–	–
2.	*Tetrapogon* sp.	758	–	–
3.	*Cymbopogon schoenanthus*	325	–	–
4.	*Chrysopogon plumulosus*	180	–	–
5.	*Sporobolus* sp.	85	–	–
6.	*Dactyloctenium* sp.	10	–	–
7.	Poacea undet. 2	5	–	–
Other herbaceous (forbs)				
1.	*Aizoon canariense*[a]	5972	26	580
2.	*Pulicaria* sp.[a]	1809	0	0
3.	*Reseda amblycarpa*	1470	0	1
4.	*Launaea massauensis*	1466	0	0
5.	*Diceratella incana*[a]	973	1383	125
6.	*Euphorbia* sp. 2	550	0	1
7.	*Aerva javanica*[a]	503	10	336
8.	*Heliotropium longiflorum*[a]	463	3	0
9.	Euphorbiacea undet. 3	449	1	0
10.	*Abutilon fruticosum*[a]	382	66	273
11.	*Ruellia patula*[a]	373	5	5
12.	*Chenopodium* sp.[a]	335	2	0
13.	*Solanum adoense*[a]	316	676	27
14.	*Kohautia* sp.[a]	305	2	0
15.	Boraginacea undet. 2[a]	184	0	0
16.	*Psilotrichum gnaphalobr.*	183	0	0
17.	*Campylanthus junceus*[a]	120	116	6
18.	Liliacea undet.	110	0	0
19.	*Ecbolium viride*[a]	110	24	11
20.	*Lotus arabica*[a]	77	0	1
21.	*Helichrysum glumaceum*[a]	55	0	0
22.	*Corchorus trilocularis*[a]	51	1	1
23.	*Rumex vesicarius*	30	0	0
24	*Tribulus* sp.[a]	21	24	11
25.	*Zygophyllum simplex*	2	0	0
26.	*Withania somnifera*[a]	2	0	18
27.	Asteracea undet.[a]	1	2	3
Lianas				
1.	*Euphorbia arabica*	5	0	0

Table 1 (continued)

Species		Plots	Beira	Goat	Species		Plots	Beira	Goat
6.	Boraginacea undet. 1[a]	423	27	9	2.	*Cissus rotundifolia*	5	1	15
7.	Malvacea undet. 3[a]	379	13	13	3.	*Pergularia tomentosa*[a]	1	0	0
8.	*Barleria* sp. 2[a]	302	5	2					
9.	*Echiochilon albidum*[a]	140	211	30	Undetermined fragments		–	679	507

[a] Species with pubescent leaves

Figure 1 shows, for each animal species, the estimated relative area of epidermis of the 27 taxonomic groups, once the number of their fragments had been converted into epidermis area. Schoener's overlap index calculated on these relative areas was much lower than expected under the assumption that the diets did not differ (observed value: 0.279; mean ± SD of the values obtained by permutation 0.903 ± 0.039; permutation test: $P = 0.0001$). In most cases, indeed, the relative areas obtained differed significantly between beira and goat (Fig.1). The greatest difference occurred for the Poaceae (49.7 % for the goat vs 0.9 % for the beira). The second greatest difference involved *A. etbaica*, the dominant tree species in the study area (Table 1); its foliage appeared as a main food item for both animal species, but its relative area was greater for the beira than for the goat (28.9 vs 13.4 %). Among the forbs, the goat fed on the most abundant species,

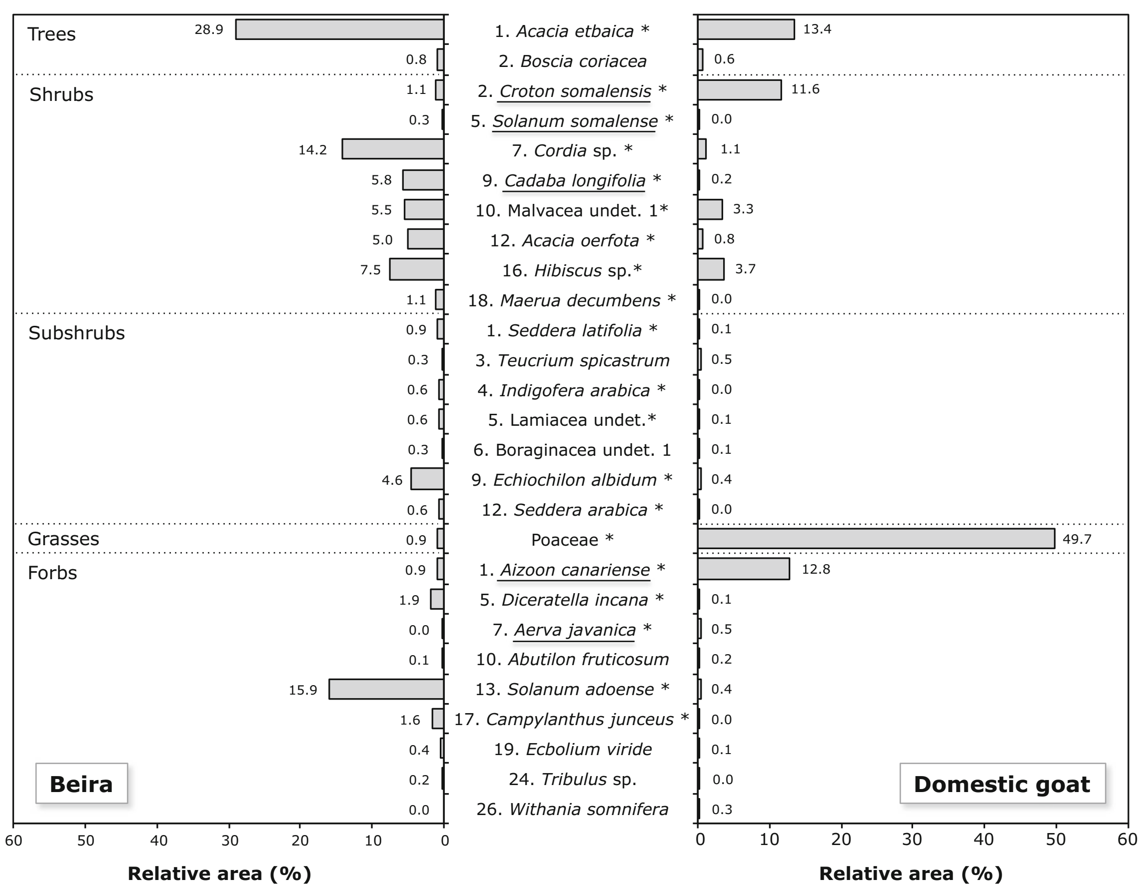

Fig. 1 Estimated relative areas of epidermis of the 27 plant species (or families) occurring in at least 25 % of the faecal samples from the beira or the domestic goat. Within each morphological category (trees, shrubs, etc.), species are listed in decreasing order of abundance in the plots (the number preceding each plant's name refers to its rank within the category, species rarely or not found in the faecal samples included). Plants known to be favoured by overgrazing are underlined (see Discussion). *Asterisk* represents the species whose estimated relative area differs significantly between beira and goat at the threshold $\alpha_{corr} = 0.05/27 \approx 0.0018$ (permutation test)

Aizoon canariense (12.8 %), whereas the beira preferred the much less abundant *Solanum adoense* (15.9 vs 0.9 % for *A. canariense*; $T = 0$, $n = 37$, $P < \alpha_{corr} = 0.05/351 \approx 1.42 \times 10^{-4}$). Similarly, among the shrubs, *Croton somalensis* was a major component of the goat's diet (11.6 %) but a marginal food item for the beira (1.1 %), which preferred less abundant shrubs such as *Cordia* sp. (14.2 %; $T = 7$, $n = 39$, $P < 1.42 \times 10^{-4}$) or *Hibiscus* sp. (7.5 %; $T = 27$, $n = 37$, $P < 1.42 \times 10^{-4}$). Nevertheless, *Hibiscus* sp. was not neglected by the goat, which preferred this species to other, more abundant shrubs such as *S. somalense* (3.7 vs 0.0 %; $T = 1$, $n = 32$, $P < 1.42 \times 10^{-4}$). Subshrubs, despite their abundance in the plots (about three times as great as that of the Poaceae; Table 1), constituted a very low proportion of the estimated areas of epidermis for the goat (total 1.3 %); the proportion was higher for the beira (total 8.0 %; permutation test: $P = 0.0001$), primarily because the latter fed substantially on *Echiochilon albidum*, a moderately abundant subshrub species.

Overall, ranking plant categories in decreasing order of epidermis area and underscoring the pairs of categories whose epidermis area did not differ significantly (Wilcoxon's *T* test, $n = 39$, $\alpha_{corr} = 0.05/10 = 0.005$) led to shrubs > <u>trees</u> > <u>forbs</u> > subshrubs > Poaceae for the beira and Poaceae > shrubs > <u>forbs</u> > <u>trees</u> > subshrubs for the goat.

Discussion

Certain food items may be entirely digested, or their remnants destroyed by the faecal samples' preparation (Holechek et al. 1982; Samuel and Howard 1983), and we cannot be sure that a plant never found in the faeces was not ingested. Among the plants that were common in the study area but absent or very rare in the faecal samples, the question especially arises for the forbs *Reseda amblycarpa* and *Launaea massauensis*, which have glabrous leaves and were found to have very thin and fragile cuticles. The uncertainty is lower for the species having pubescent leaves such as the shrub *Iphionopsis rotundifolia*, the subshrub *Barleria* sp. 1 or the forb *Pulicaria* sp. Hairs appeared to be particularly resistant; in the faecal samples examined, we never found cuticle fragments of a pubescent species without also finding its hairs (attached or isolated), whereas we often found isolated hairs without finding any cuticle fragment of the corresponding species. It is thus likely that the species with pubescent leaves that were abundant in the study area but rare or absent in the faeces (Table 1) were little consumed.

As expected on the basis of the literature (see Introduction), the domestic goat was found in the present study to be an intermediate feeder, eating ca. 50 % of grasses. In contrast, the beira was found to be a strict browser, feeding almost exclusively on the leaves of woody plants and forbs. More generally speaking, our findings suggest that the beira is more selective (or less opportunistic) than the goat. Nevertheless, both animal species exhibited clear signs of dietary selectivity: none of them seemed to eat large quantities of the subshrubs that were abundant in the study area, and both appeared to prefer *Hibiscus* sp. to other, more common shrubs.

It is worth noting that three plant species known to be favoured by overgrazing (Audru et al. 1994a,b; Ibrahim 1998; Laurent et al. 2002; Fig. 1) were found to be ingested in a non-negligible way. Among them, the shrub *Cadaba longifolia* was mainly consumed by the beira. However, whereas the species is considered as an indicator of overgrazing by Ibrahim (1998), it never seems to become a major component of the flora when overgrazing occurs. The scheme is different for the forb *A. canariense* and the shrub *C. somalensis*. The two species, little consumed by the beira, constituted major food items for the goat. Moreover, both can cover large areas (NG and EM, pers. obs.), and in the event of severe overgrazing, the altitudinal *A. etbaica* wooded steppe is known for turning into herbaceous-subshrub steppe dominated by *A. canariense* (Audru et al. 1994a,b; Ibrahim 1998). In other words, overgrazing by domestic goats induces the spread of plants that the goats consume in abundance but not the beira. With this respect, it certainly constitutes a major threat for the long-term survival of the beira.

Furthermore, we performed our fieldwork during the growing season, but as reported in other herbivore communities (Liu and Jiang 2004; Wingard et al. 2011), diets can be expected to converge when trophic resources decline. Soon after the beginning of the dry season, the herbaceous plants of the study area turn out to be unavailable, their aerial parts desiccating when the whole plant does not die. Among these species are the Poaceae, *A. canariense* and *S. adoense*, consumed in abundance by the goat or the beira when available. Early in the dry season, the diets of the two animal species should thus become much more similar, and include in particular an enhanced proportion of *A. etbaica*, the main item that they have in common. With this respect, the high densities of domestic goats foraging in the arid hills from southern Djibouti (Giotto et al. 2009) may deplete a key food resource for the beira during the dry season. Nevertheless, a further study is needed to confirm this assumption.

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