EFFECTS OF COMPETITOR DENSITY AND RAINFALL REGIME ON THE LONG-TERM POPULATION DYNAMICS OF AN HERBIVORE COMMUNITY IN A WESTERN AFRICAN SAVANNAH

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RÉSUMÉ.— *Effets de la densité des compétiteurs et du régime des pluies sur la dynamique de population à long terme d'une communauté d'herbivores dans une savane ouest-africaine.*— En dépit de beaucoup d'articles scientifiques consacrés à l'écologie des communautés des ongulés dans les savanes africaines, seules quelques études se sont focalisées sur l'Afrique de l'Ouest. Dans cet article, sur la base de line-transects sur le long terme (1985-2008), nous analysons les interactions entre les espèces d'ongulés de savane dans le Ranch de Gibier de Nazinga (Burkina Faso) en relation avec les pluies et la densité de leurs compétiteurs potentiels. Nous avons estimé la taille des populations de toutes les espèces par comptage à distance. Il n'est pas apparu d'effet année sur la taille des populations pour toutes les espèces mais, en analysant par groupes de cinq années, des fluctuations significatives ont été décelées au moins pour certaines espèces. Des modèles linéaires généralisés sur les relations interspécifiques (tant positives que négatives) entre paires d'espèces suggèrent que les fluctuations interannuelles de la taille des populations des divers ongulés seraient vraisemblablement imputables aux variations de l'intensité du braconnage, à l'influence du régime des pluies (pour au moins trois espèces brouteuses) et à une densité-dépendance négative.

SUMMARY. – Despite many scientific articles were devoted to study aspects of community ecology of ungulates in African savannahs, only very few studies focused on communities from Western Africa. In this paper, we analyse the interspecific interactions of savannah ungulates in the Nazinga Game Ranch (Burkina Faso) in relation to rainfall patterns and potential competitor density, using long-term (1985-2008) line-transect data. We estimated the population sizes of all species by using distance sampling. There was no effect of the year on the population sizes of all the species, but, when 5-year-period groups were analyzed, there were significant fluctuations over time intervals for at least some of the species. Generalized Linear Models on the interspecific relationships (either positive or negative) between pairs of species would suggest that interannual population size fluctuations of the various ungulates were likely attributable to fluctuations in poaching intensity, the influences of rainfall regimes (for at least three browser species), and negative density dependence.

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There has been a long tradition of field studies on the ecology of herbivore communities of African savannahs, with emphasis on regulating mechanisms, including interspecific and intraspecific competition, predation, facilitation, and the effects of wildfire and rainfall regimes (e.g., Sinclair, 1985, 1995; Mills *et al*., 1995; Owen-Smith & Ogutu, 2003; Stelfox *et al*., 2003; Owen-Smith *et al*., 2005; Ogutu & Owen-Smith, 2006; Ogutu *et al*., 2008, 2009). From this wealth of studies, it has been highlighted that seasonal wildfires maintain the tree–grass balance and that herbivores directly affect vegetation structure by consuming plants and indirectly by consuming herbaceous vegetation fuelling wildfire (Bond & Keeley, 2005; Eby *et al.,* 2014). Regrowth of high-quality herbaceous forage after wilfire (e.g. high protein: lignin content or low nutrient: carbon ratio) make herbivores to prefer grazing in recently burnt sites (Eby *et al.,* 2014). Thus,

during the peak of the dry season not only the wildfires are particularly frequent (thus destroying much of the existing herbaceous cover), but there is also a high concentration of herbivores trying to forage for high quality food in the burnt places. Therefore, during the dry seasons and not during the rainy seasons, food resource should be limited and interspecific competition for browse should be high. Hence, based on the above-mentioned considerations, it can be predicted that:

(i) the density of some species should decrease when the density of other species would increase;

(ii) the intensity of competition should be higher during the dry seasons;

(iii) the intensity of interspecific competition should be higher among browsers than among grazers.

However, it is still unclear when positive or negative interactions will dominate (Anderson *et al.*, 2016). One reason for which the knowledge on these interspecific interactions is still incomplete is because there has been no satisfying coverage of study species and ecological scenarios across African savannahs. Indeed, the great majority of these studies relate on ungulate communities from eastern Africa (Murray & Brown, 1993; Mduma & Sinclair, 1994; Keesing, 1997; Sinclair *et al.*, 2000; Owen-Smith & Ogutu, 2003; Owen-Smith *et al.*, 2005; Ogutu *et al.*, 2009) or southern Africa (e.g., Mason, 1990; Owen-Smith & Mills, 2008), with studies from western Africa lagging behind (e.g., Fischer & Linsenmair, 2001; Marchal *et al.*, 2012; Bouché *et al.*, 2016). This scarcity of studies from western African savannahs is linked to the fact that, due to the fragmentation of pristine savannah habitats (Galvin *et al.*, 2008; Marchal *et al.*, 2012; Ripple *et al.*, 2015), most large mammals are restricted to small and isolated protected areas subjected to increasingly high pressure from human population's demand for land and food (Marchal *et al.*, 2012; Tranquilli *et al.*, 2014; Bouché *et al.*, 2016). Therefore, in order to better understand the coexistence dynamics of sympatric herbivores, it would be necessary to add several western African case studies to the available scientific literature.

In this paper, we analyse the potential competition intensity among seven ungulate species inhabiting a western African savannah: the Nazinga Game ranch (hereafter NGR) in south-central Burkina Faso, where long-term monitoring of mammal species has been implemented since 1980. We focus on whether any negative density dependence can be uncovered between seven species of sympatric ungulates (three grazers and four browsers), in the assumption that, if this negative density dependence does exist, the interspecific competition between the two target-species should be effective. We also explore whether negative density dependence can be uncovered more frequently among browsers than among grazers, as predicted by general theory (see above). Finally, we investigate whether rainfall patterns influence the population dynamics of these sympatric ungulates. Our prediction is that, if interspecific competition between two species is effective, it should be minimized during the rainy season (when herbaceous vegetation is at its peak) and, as a consequence, the population size of competing species should be facilitated by years with high rainfall because of the relative relaxation of the interspecific competition strength. Thus, if theoretical predictions are correct, browsers should be more affected by rainfall volumes (higher density during high rainfall years) than grazers. In this regard, NGR offers an exceptional opportunity for studying all these aspects because of its tradition of long-term field studies on mammal densities (e.g., Marchal *et al.*, 2012; Bouché *et al.*, 2016; Hema *et al.*, 2017a, 2017b).

MATERIALS AND METHODS

TAXONOMIC NOTE

Western African ungulates have recently undergone considerable taxonomic revision, and some authorities considered the Western African several populations to be separate species from other conspecific populations from elsewhere in Africa (Groves & Grubb, 2011). These taxonomic changes would include: *Alcelaphus major* that was elevated as a full species

from *Alcelaphus busephalus*; *Ourebia quadriscopa* from *Ourebia ourebi*; *Tragelaphus phaleratus* from *Tragelaphus scriptus*. In this paper, we prefer to use the classical taxonomy for practical reasons, also waiting for a stable decision about ungulate taxonomy in western Africa in the years to come.

STUDY AREA

The field study was carried out at NGR (about 940 km^2 surface; coordinates: 11°1'-11°18' N, 01°18'-01°43'W), a protected area of south-central Burkina Faso (Western Africa) (Fig. 1). The vegetation is tall-grass tree-shrubs savannah, with main plant species being *Vitellaria paradoxa, Terminalia* spp., *Combretum* spp., *Acacia* spp., and *Detarium microcarpum*, and with main grasses being *Andropogon ascinoides* and *Schizachyrium sanguineum* (Croes, 1988). Annual rainfall varies between 540 and about 1600 mm, with peaks in July and August (Tab. I). There was no year effect on the rainfall patterns (expressed as yearly average of the monthly rainfall; one-way ANOVA: $F_{20,231}=0.433$, $P = 0.985$), whereas there were significantly monthly effects (one-way ANOVA: $F_{11,240}= 50.57$, $P < 0.001$; see Appendix). However, there was a increasing trend of rainfall over the years (Bouché *et al.*, 2016).

Figure 1.— Map of Burkina Faso, showing the Nazinga Game Ranch.

TABLE I

Pluviometric data for the Nazinga Game Ranch over the study period

	DRY SEASON					WET SEASON				DRY SEASON			
Year	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Total
1987	0	0	11.9	8.1	45.4	187.5	183.6	286.3	139.5	31.6	0	0	893.90
1988	0	0	2.2	65.1	37.9	176	158.6	244.6	131	21	13.9	0	850.30
1989	0	0	36.7	4.3	22.7	148.3	261.7	383.5	191.8	52.7	0	40	1141.70
1990	0	0	0	53.5	124	33	229.2	161.2	93.1	22.1	17.7	23.6	757.40
1991	0	2.3	114.1	43.8	174.6	160.9	142.5	370.4	88.1	184.3	0	0	1281.00
1992	0	0	0.2	69.7	113.7	108.9	172.4	221.9	148.2	48.5	10.8	0	894.30
1993	0	0	22.4	24.2	68.4	251.5	193.9	292.3	116	30.2	3.7	0	1002.60
1994	0	0	23.3	54.5	185.4	44.2	306.8	439.5	138.1	76.6	0	0	1268.40
1995	0	0	8.3	60.1	36.4	178.5	153.6	320.8	117.7	32.2	0.2	16.6	924.40
1996	0	0	8.1	15.2	111.1	306.9	115.8	363.6	215	17.3	0	0	1153.00
1997	0	0	2.1	52.1	101.7	115	112	165.6	212.2	99.4	0	0	860.10
1998	0	9	0	87.9	138.5	124.3	161.9	215.3	271.9	59.6	0	0	1068.40
1999	0	0.1	0	75.7	165.9	76.1	391.4	318.3	193.8	68.8	0	0	1290.10
2000	0.1	0	0	52.1	73.5	191.7	120.3	225.4	143.9	55.8	0	0	862.80
2001	0	0	0	17.1	48.2	125.2	145.1	236.4	113	43.1	0	0	728.10
2002	0	0	0	62.9	73.2	111.6	201.9	210.4	148.6	36.6	5.2	0	850.40
2003	0	2.2	56.6	43.2	87	169.9	181.4	326.1	269	68.3	2.5	0	1206.20
2004	0	0	10.3	43	48.2	196.9	203.2	275.9	130.8	24.2	0	0	932.50
2005	0.4	62.9	0	37.1	120	162.5	206.1	195.6	237.7	557	0	0	1579.30
2006	0	1.3	0	80	56.5	194.4	192.1	209.4	306.7	52.5	0	0	1092.90
2007	0	0	0	102.5	77.4	120.9	30.59	46.3	156.1	7.5	0	0	541.29

Field research was conducted between 1985-2008. Data collection protocol involved 30 equally spaced transects of 1.4 km, and South-North arranged systematically with a random start, over the entire area of the ranch (Hema *et al.*, 2010b, 2010c). A zoning performed on the track network base allowed us to consider seven blocks and 79 portions of transects. The total length of transects translate to about 45 km in 920 km^2, with an overall covered length of transects of about 600 km. These transect lengths compared well with the available literature, given that there is a high variation across studies: for instance, 23.6 km in 3544 km^2 in Mlele Game Controlled Area Tanzania; Caro, 2016); 187.5 km in 730 km^2 in Upper Lupande and 240 km in 930 km^2 in Lower Lupande (Zambia; Jachmann, 2002); and 176 km in 5,053 km² in Gonarezhou National Park (Zimbabwe; Madhlamoto *et al.*, 2014). Collecting field data lasted seven days per year, with the linear transect unlimited bandwidth method being applied (Burnham *et al.*, 1980; Buckland *et al.*, 1993; 2001).

The transects were covered by 12 teams of three people. Each team consisted of a scientist (team leader) and two observers (a native of neighboring villages and a park field guide). The teams walked along strictly straight transects. They were equipped with GPS, compasses, rangefinders, cards, a range weapon by the tracker team and sheets on which all the notes on the species, the number of individuals observed, the radial distance to the viewing angle, gender age, type of activity, illegal activity by humans, etc., were recorded. Walks started in early morning as soon as daylight allows to distinguish objects accurately.

STATISTICAL ANALYSES

Data for the various species densities along line transects were analysed using Distance software version 6.0 (Thomas *et al.*, 2010). Models were selected following the procedures in Jachmann (2001), with the selected model for each species being that (i) with the lowest Akaike Information Criterion (AIC) score among the candidate models and (ii) a good detection function curve with a non-significant χ^2 value. By this procedure, the most frequently selected model was the Half-normal key, followed by the Uniform model and the Hazard-rate model (all with Cosine extension). Data before 1994 were not collected in the field with such details needed for an analysis with Distance software, so we calculated for each sighting a median distance from transect identical to the median recorded in the field from 1995 to 2012 and applied it to the data for generating the population size estimates.

Generalized Linear Models (GLZ, Hosmer & Lemeshow, 2000) were used to quantify the effects of monthly rainfall on the population sizes by year, and the population size relationships of each species with all the other target species of our study. The models with rainfall were performed only during the period 1987-2007 (apart 1990 and 1999, when population size data for the various ungulates were not available). We standardized all variables to remove the effect of differences in the original scale of measurement. The standardization of values was made by replacing all values of selected variables by standardized values, which are computed as follow:

Standardized score = (raw score – mean) /Standard Deviation.

In the model, a stepwise forward regression procedure was used to test the statistical significance of each variable in turn and were excluded the variables when they did not correlate significantly to dependent variable (Wald test P > 0.05). The eventual significant variables could be computed using the best subset procedure. In the models of population size relationships among species, the variables (population size of each species) were computed using the best subset procedure. In every model, the population size of a given species was used as dependent variable and the population sizes of all the other species were used as predictors. In all models, the identity link function and a normal distribution of error were used (McCullagh & Nelder, 1989).

RESULTS

INTERANNUAL POPULATION SIZE FLUCTUATIONS

Seven sympatric ungulate species were observed, three being grazers and four browsers (Tab. II). The population size fluctuations for all the selected species over the years are given in Fig. 2. There was no effect of the year on the population sizes of all the species (one-way ANOVA, $F_{1,21}=0.599$, P = 0.912), that is no year was particularly favourable or particularly negative for all the species. Similarly, there was no effect of the year on either the grazers (one-way ANOVA, $F_{1,21} =1.587$, P = 0.145) or the browsers (one-way ANOVA, $F_{1,21} = 1.126$, P = 0.351).

However, when 5-year period groups were analysed, there were significant fluctuations over time intervals for at least some of the species. Indeed, the species that did not fluctuate remarkably across 5-year periods were *Tragelaphus scriptus* (one-way ANOVA, $F_{1,3} = 0.246$, P = 0.862), *Sylvicapra grimmia* ($F_{1,3} = 0.959$, P = 0.437), and *Alcelaphus buselaphus* ($F_{1,3} = 1.467$, P = 0.263). On the other hand, populations fluctuations over 5-year periods were significant in other three

species, including *Hippotragus equinus* ($F_{1,3} = 4.745$, $P < 0.02$). For this species, a Tukey HSD post-hoc pairwise comparison revealed that this difference was due entirely to the differences between the period 1992-1997 versus 2004-2008 ($P < 0.01$; much higher density in this latter time period).

TABLE II

Synoptic table of the population size relationships among species of ungulates at Nazinga Game Ranch, using GLZ models. Pos = significantly positive relationship; Neg = significantly negative relationship; blank = No significance in the pairwise relationship between species

| Species	Feeding habits	*Alcelaphus buselaphus*	*Hippotragus equinus*	*Phacochoerus africanus*	*Kobus ellipsiprymnus*	*Tragelaphus scriptus*	*Ourebia ourebi*
Alcelaphus buselaphus	mostly grazer	*****					
Hippotragus equinus	mostly grazer		*****				
Phacochoerus africanus	mostly grazer			*****			
Kobus ellipsiprymnus	browser		Pos		*****		
Tragelaphus scriptus	browser					*****	
Ourebia ourebi	browser			Pos			*****
Sylvicapra grimmia	browser	Neg	Pos	Neg			Pos
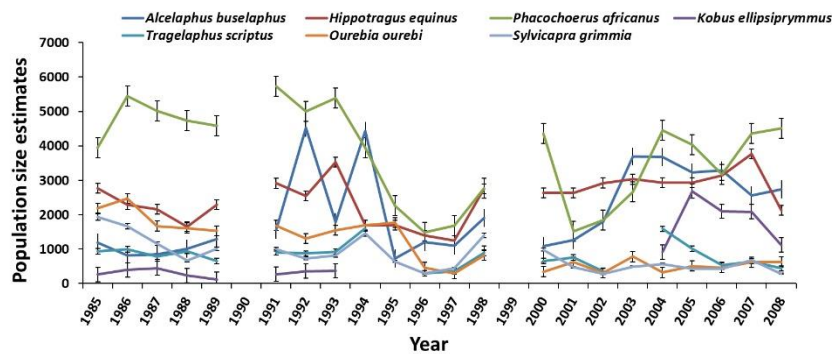
Figure 2.— Fluctuations in population size estimates, determined by a Distance methodology, for the selected ungulate species at Nazinga Game Ranch, Burkina Faso. 95 % confidence intervals of the estimate, as generated from Distance software, are also presented. Gaps would indicate the years in which the density of the various species could not be estimated.

The second species with significant fluctuations was *Kobus ellipsiprymnus* ($F_{1,3} = 63.593$, $P < 0.0001$). For this species, a Tukey HSD post hoc test showed that the population size increased significantly after 2008 (differences at least $P < 0.01$). The third species exhibiting significant fluctuations was *Ourebia ourebi* ($F_{1,3} = 6.6329$; $P < 0.01$), with Tukey HSD post-hoc test showing that the population sizes decreased significantly after 1998 (at least $P < 0.01$ for the last two periods of 5-year timespan). *Phacochoerus africanus* population size fluctuations are examined in another paper (Hema *et al*., 2017a) and therefore are not evaluated in this paper.

496

Phacochoerus africanus. There were no significant relationships beetwen population size of these suids and monthly rainfall during the period 1987-2007 (all computed scores < 2.607, all computed P > 0.106).

Ourebia ourebi. The GLZ model showed that the probability of population size increases for this species was correlated positively with an increase of precipitation in August (estimate = 0.558, Wald = 8.594, P < 0.01). The model explained 68.90 % of the total deviance.

Alcelaphus buselaphus. There were no significant relationships between the species population size and monthly rainfall during the period 1987-2007 (all computed scores < 2.948, all computed P > 0.086).

Hippotragus equinus. There were no significant relationships beetwen the species population size and monthly rainfall during the surveyed period (all computed scores < 2.886, all computed P > 0.089).

Kobus ellipsiprymnus. The GLZ model showed that the probability of high population sizes of this species increased with an increase of precipitation in August (estimate = 0.698, Wald = 11.386, P < 0.001). The model explained 51.32 % of the total deviance.

Sylvicapra grimmia. There were no significant relationships between population size of this species and monthly rainfall during the study period (all computed scores < 2.321, all computed P > 0.127).

Tragelaphus scriptus. The GLZ model showed that the probability of the species population size increased with an increase of precipitation in July (estimate = 0.527, Wald = 6.523, P < 0.05). The model explained 72.27% of the total deviance.

INTERSPECIFIC RELATIONSHIPS AMONG SPECIES

The summary table of the population size relationships among species, estimated by GLZ models, is given in Table 2. According to our models, the population size of *Phacochoerus africanus* was correlated positively to the population size of *Ourebia ourebi* (estimate = 0.958, SE = 0.294, Wald = 10.601, P < 0.01) and negatively to that of *Sylvicapra grimmia* (estimate = -1.591, SE = 0.424, Wald = 14.112, P < 0.001).

GLZ models showed that *Alcelaphus busephalus* population size was significantly and negatively affected by population sizes of *Sylvicapra grimmia* (estimate = -1.913, SE = 0.815, Wald = 5.507, P < 0.05), whereas all other species did not have any significant effect (at least, estimate = 1.235, P = 0.105).

Population size of *Hippotragus equinus* was positively correlated to the population sizes of both *Kobus ellipsiprymnus* (estimate = 0.427, SE = 0.203, Wald = 4.408, P < 0.05) and *Sylvicapra grimmia* (estimate = 0.934, SE = 0.470, Wald = 3.947, P < 0.05).

Population size of *Kobus ellipsiprymnus* was positively correlated only to the population size of *Hippotragus equinus* (estimate = 0.532, SE = 0.253, Wald = 4.408, P < 0.01).

Population size of *Ourebia ourebi* was significantly positively correlated to that of *Phacochoerus africanus* (estimate = 0.432, SE = 0.133, Wald = 10.601, P < 0.01) and *Sylvicapra grimmia* (estimate = 1.070, SE = 0.284, Wald = 14.186, P < 0.001).

Sylvicapra grimmia population size was negatively correlated to that of *Alcelaphus busephalus* (estimate = -0.140, SE = 0.059, Wald = 5.507, P < 0.05) and *Phacochoerus africanus* (estimate = -0.305, SE = 0.081, Wald = 14.112, P < 0.001) and positively to that of *Hippotragus equinus* (estimate = 0.223, SE = 0.112, Wald = 3.946, P < 0.05) and *Ourebia ourebi* (estimate = 0.454, SE = 0.121, Wald = 14.186, P < 0.001).

Population size of *Tragelaphus scriptus* was not significantly correlated to that of any species (at least, estimate = 0.390, P = 0.164).

DISCUSSION

POPULATION FLUCTUATIONS

Our study shows that considerable internannual fluctuations occurred in all seven species of herbivores at NGR, with just a few species showing a constantly declining trend (see below). These results are generally consistent with the patterns provided by Bouché *et al*. (2016) that also showed considerable interspecific variation in the long-term density estimates for these species. Overall, we consider that these fluctuations are due to both human-made reasons (poaching; type of management of the protected area) and ecological processes (negative density dependence in a few species due to limited food resource during the dry seasons, especially in the years when rainfall precipitations were relatively moderate also during the wet season).

Concerning *Hippotragus equinus* population fluctuations, the density peak occurred in 2004-2008. We suggest that this peak was essentially due to anthropogenic reasons, i.e. to a reduction in poaching intensity due to increased patroling within the park borders (Hema *et al*., 2017a) due to the substantial funds received by NGR from the 'Fonds pour l'Environnement Mondial' (FEM) project through the Global Environmental Facility (GEF). Increased patroling certainly decreased the poaching intensity within the park borders (Hema *et al*., 2017a). The FEM project run up to the year 2006. After the end of FEM project, shortage of funds caused a reduction in patroling support and, very likely, a new poaching increase with consequent *Hippotragus equinus* population collapse during the years 2009-2012 (our unpublished observations; data for the other ungulates not available for these latter years). The same pattern of positive population trend in 2004-2008 was also seen in *Kobus ellipsiprymnus* (this study) and *Phacochoerus africanus* (Hema *et al*., 2017a). Concerning *Phacochoerus africanus,* Hema *et al*. (2017a) showed that the various management phases of NGR had remarkable effects on the population dynamics of this species, and likely also of *Kobus ellipsiprymnus* and *Hippotragus equinus*.

Conversely, *Ourebia ourebi* showed a declining trend (see also Bouché *et al*., 2016; Hema *et al*., 2017b), that we tentatively attribute mainly to overhunting by poachers (Hema *et al*., 2017b). It is also possible that the highly increasing population sizes of baboons (*Papio anubis*) and crocodiles (*Crocodylus niloticus suchus*), that heavily feed on these small antelopes (our unpublished observations), may have played a role, but further research is needed to confirm this hypothesis.

RELATIONSHIPS AMONG POPULATION FLUCTUATIONS, FORAGING HABITS AND RAINFALL REGIME

Rainfall has been considered as the prime climatic factor underpinning the dynamics of African savannah ungulates (Ogutu *et al*., 2008). Indeed, it has been reported that savannah ungulates respond both to cumulative past rainfall and seasonal fluctuations in rainfall (Ogutu & Owen-Smith, 2003, 2006; Owen-Smith & Ogutu, 2003; Owen-Smith & Mills, 2006). However, our study revealed that rainfall patterns did not consistently influence the population sizes of the various ungulate species. Indeed, whilst the density of some species was certainly influenced by the rainfall regime (more specifically, by the rains of July and August), for others there was not any detected effect by our models. Interestingly, precipitation increases during July and August (peak of the wet season; Appendix) influenced positively the densities of three out of four browsers (*Kobus ellipsiprymnus, Tragelaphus scriptus, Ourebia ourebi*) but were ininfluent for the population densities of all the grazer species (*Alcelaphus busephalus*, *Hippotragus equinus* and

Phacochoerus africanus) and for one browser (*Sylvicapra grimmia*). We interpret these patterns as a result of both autoecological and synecological processes (see below).

As mentioned above, the density of three species (*Kobus ellipsiprymnus, Tragelaphus scriptus, Ourebia ourebi*) was positively influenced by wet season rainfall regime. *Kobus ellipsiprymnus* and *Tragelaphus scriptus* are, inside the dry savannah vegetation zone, water-dependent species (e.g., Western, 1975; Reilly *et al*., 1990; Dankwa-Wiredu & Euler, 2002; Smit, 2011). The dependence of these species on rainfall regime may be linked to food availability and refuge availability: more rains would mean prolonged availability of water bodies even after the rainy season, that also would produce a higher availability of fruiting trees by dry season (food availability reason). This would in turn influence positively the population dynamics for these browsing ungulates that often feed on fruits at NGR (our unpublished observations). Bouché *et al*. (2016) also showed a significantly positive correlation between rainfall and population size of *Kobus ellipsiprymnus* but did not uncover the same pattern for *Tragelaphus scriptus*. A same positive effect on population sizes of *Kobus ellipsiprymnus* was also demonstrated by Ogutu *et al*. (2008) in East African savannahs. The different statistical methodologies between our study (using GLZ models) and Bouché *et al*. (using linear regressions) may explain the observed differences concerning *Tragelaphus scriptus*.

Both our study and Bouché *et al*. (2016) found a positive effect of (August) rainfall on *Ourebia ourebi* in NGR. This is a habitat generalist species in the ranch (Hema, unpublished observations) and it feeds mainly on leaves and fruits (e.g., Cerling *et al*., 2003). Because flowering and fruiting phenology are clearly related to rainfall patterns with most species maturing their diaspore from the middle to the end of the rainy season (e.g., Munhoz & Felfili, 2007), we suppose that peaks in food availability during years with heavy rainfall may explain the positive relationships between its population size and rainfall.

As mentioned above, our GLZ models did not uncover any significant effect of rainfall on population size of the three grazer species. This evidence is in contrast with the results of Bouché *et al*. (2016), that instead found a positive linear effect of rainfall on population density in *Alcelaphus busephalus* (same also for *Sylvicapra grimmia*). Also in this case, we think that the differences in statistical methodology (GLZ modeling in our case versus simple linear regression in Bouché *et al*., 2016) do explain the detected differences. In this regard, it should be mentioned that, in East African savannahs, Ogutu *et al.* (2008) found that abundances of *Alcelaphus busephalus* newborn calves were highly correlated with monthly rainfall averaged over the preceding 5–6 months. Instead, concerning the other two grazers (*Hippotragus equinus* and *Phacochoerus africanus*), our modeling analyses mirror Bouché *et al.*'s (2016) conclusions that rainfall does not influence their population sizes.

Overall, the fact that rainfall had significant influence on population densities of browsers (but not grazers) mirrors the theoretical prediction of a higher interspecific competition intensity among browsers (see Introduction).

INTERSPECIFIC RELATIONSHIPS

The significant interspecific relationships (either positive or negative) recorded by our models are difficult to explain on the basis of a classical interspecific competition theory, at least for some pairwise comparisons. Negative density dependence was uncovered between *Sylvicapra grimmia* and both *Alcelaphus busephalus* and *Phacochoerus africanus*. Direct competition between these species is unlikely because (i) the former species is a browser and the latter two are grazers, and (ii) predation of whartog on juvenile *Sylvicapra* were never observed at the study area. However, it is likely that some kind of indirect competition may occur: indeed, as warthogs and *Sylvicapra* do overlap greatly in their habitat use, the former may disturb the latter by its rooting activities. Indeed, rooting behavior has marked ecosystem-level effects, and wild suids are therefore

considered ecosystem engineers (e.g. Crooks, 2002; Hone, 2002). Although this has not yet been reported for Africa, wild suids are well known to disturb populations of wild ungulates in open grassy habitats in both the United States (e.g. Taylor & Hellgren, 1997) and Argentina (Perez Carusi *et al*., 2009). Moreover, it is possible that the rooting activities of warthogs may attract baboons (as they may facilitate insect collecting as prey by these monkeys; DeVore & Hall, 1965) into the *Sylvicapra* home ranges, thus producing a depression cascade-effect to the density of *Sylvicapra* due to increased predatory attention of baboons towards juvenile antelopes. In this regard, predation of baboons on juvenile *Sylvicapra* and on the similarly sized *Ourebia ourebi* has been documented several times at NGR (Hema *et al*., unpublished observations) as well as elsewhere (e.g. Harding, 1973).

The negative relationships between *Sylvicapra grimmia* and *Alcelaphus busephalus* are also difficult to explain in competition terms, as these species seem to be too much ecologically divergent for any kind of interspecific competition to apply. However, *Alcelaphus* is not only a grazer but also a browser (Ejidike *et al*., 2013). So, it is possible that when grass is not readily available during the dry season peaks, *Alcelaphus busephalus* may enter into bushlands to browse leaves and to eat fruits, thus entering in direct competition with *Sylvicapra grimmia*. If our hypothesis is correct, interspecific competition between the two species should certainly be limited to the driest period of the year, and especially to the driest years.

Positive relationship between *Sylvicapra grimmia* and *Ourebia ourebi* can be explained because they live in the same habitat type (woodlands inside savannahs; Mduma & Sinclair, 1994; Oualiou *et al*., 2007), both are browsers (Oualiou *et al*., 2007) and both have similar body sizes (Kingdon, 1997). They do not form interspecific groups (as they are mostly solitary or in strictly familiar groups) (Brashares & Arcese, 2002), and apparently, they do not compete as their populations are not big and therefore they would probably not consume the resource available. Therefore, it is unlikely that they may exploit the carrying capacity of their habitat. These species also likely share the same pressures, either from poaching or environmental issues, thus being positively correlated in terms of their interannual population size trends.

The positive relationship between *Sylvicapra grimmia* and *Hippotragus equinus* can be explained by the fact that it uses habitat selection to avoid predation mainly by associating with other larger species for protection (Mduma & Sinclair, 1994).

Our GLZ models revealed that *Tragelaphus scriptus* density is apparently not influenced by any species. We consider that this depends on the fact that it inhabits strictly riverine forests inside the park (Hema *et al*., unpublished observations), where all other species are either absent or just occasional. *Kobus ellipsiprymnus* is also very much linked to water bodies in the riverine forest. Since both species are browsers and apparently feed on leaves and fruits of the same species (*Detarium microcarpum* and *Combretum* spp., Hema *et al*., unpublished observations), it can be argued that these latter do not represent a limiting factor in the forests of the park, at least in most of the years.

The positive density dependence between *Alcelaphus busephalus* and *Hippotragus equinus* is likely due to both similar habitat preferences and similar response to poaching, as these species are among the most priviledged targets for poachers. Thus, during the years with good availability of funds for running field activities by patrols in NGR, the two species would benefit at the same time.

The positive density dependence between *Ourebia ourebi* and *Phacochoerus africanus* are probably due to the fact that they do overlap greatly in terms of habitat preferences inside NGR (Hema *et al*., unpublished observations), thus responding in parallel ways to the eventual habitat changes.

ACKNOWLEDGEMENTS

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APPENDIX

Descriptive statistics for rainfall (mm) patterns at Nazinga Game Ranch throughout the study period

	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Number of years	21	21	21	21	21	21	21	21	21	21	21	21
Min	0	0	0	4.3	22.7	33	30.59	46.3	88.1	7.5	0	0
Max	0.4	62.9	114.1	102.5	185.4	306.9	391.4	439.5	306.7	557	17.7	40
Mean	0.024	3.704	14.104	50.1	90.938	151.628	184.004	262.323	169.628	75.680	2.571	3.819
Standard error	0.019	2.992	5.941	5.728	10.404	13.904	16.211	19.680	13.507	25.431	1.124	2.249
Variance	0.008	188.05	741.378	689.103	2273.202	4059.872	5518.912	8134.105	3831.702	13582.44	26.565	106.311
Standard deviation	0.089	13.713	27.228	26.250	47.678	63.717	74.289	90.189	61.900	116.543	5.154	10.310
Median	0	0	2.1	52.1	77.4	160.9	181.4	244.6	148.2	48.5	0	0