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Selective disturbance by elephants (*Loxodonta africana*) on eight tree species in a West African savannah

Abstract African elephants (*Loxodonta africana*) are ecosystem engineers in African savannahs, but their role in the modifications of the populations of trees by means of their browsing activities has been poorly studied so far in West Africa. We studied the disturbance of elephants to eight selected species of trees in the Nazinga Game Ranch (Burkina Faso), in 54 transects at the end of dry season 2008. We fitted simple models describing the number of dead individuals for each tree species in relation to their initial population density, and in relation to dung-pile density, in the assumption that there should be a positive relationship between elephant density and dung-pile density. Generalized Linear Model analyses and regression analyses showed that the more dense the woodland cover, the least the percentage of damaged plants by elephants. For each plant species, the initial density and density of elephant dung-piles explained a high proportion of the variance in the density of dead individuals. Stochastic models, generated by a purposely created simple computer program written in GW-BASIC programming language, predicted changes in tree and shrub abundance under different assumptions about elephant numbers. The models suggested that elephant browsing may cause considerable change in the selected plant populations, especially with regard to such species as *Acacia gourmaensis*, *Vitellaria paradoxa* and *Maytenus senegalensis*. These changes may possibly increase the meat harvest from controlled hunting activities, thus improving the income for surrounding communities.

Keywords Elephants · Tree vegetation · Population · Decline · Nazinga · Burkina Faso

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Introduction

As the African magafauna continues to decline under the pressure of habitat degradation and poaching, it has today become clear that without strong and immediate conservation efforts, the future status of many species is in serious trouble (Mallon et al. 2016). However, it is interesting to note that the status of animal populations may vary considerably across the continent (Mallon et al. 2016; Smith et al. 2016), and, for example, in the case of elephants, the intensity of the population declining phenomenon as well as habitat changes at sub-regional level may differ across the continent (Mallon et al. 2016; Smith et al. 2016). In West Africa, the landscape is changing rapidly as human populations expand due to high birth rates and migrations within the Sahelian region due to droughts (World Food Program 2012). Most populations of African savannah elephants in West Africa are both

small and isolated, and shifting human populations are putting increasing pressures upon their remaining habitats (Roth and Douglas-Hamilton 1991; Poilecot 2010; Bouché et al. 2011). The actual status of the sub-regional elephant's population remains unknown, and especially the savannah populations are particularly threatened (Bouché et al. 2011). However we know that the sub-regional elephant's populations are scattered, isolated (Barnes 2002) and mostly confined to protected areas. During the last 10 years, tentative estimates of 11 489 ± 2 583 (including Definite + Probable + Possible + Speculative estimates) for the sub-region may be calculated from the IUCN/SSC African Elephant Specialist Group web site elephant's status reports (available at http://www.elephantdatabase.org/preview_report/2013_africa_final/2013/Africa). Thus, the elephant is under serious threat in the whole of the West African subregion.

One of the most conspicuous elephant populations in West Africa occurs in southern Burkina Faso adjacent to the border with Ghana (Barnes et al. 2006; Bouché 2007), where a network of protected areas and movement corridors have been designed especially in order to preserve the elephant populations as well as the remnant savannah habitats. At the centre of this network lies the Nazinga Game Ranch (NGR), that is now one of the most important protected areas of the subregion (Belemsobgo 1995; Hema et al. 2010a; 2010b). The elephant population at NGR has fluctuated remarkably over the years, and has been intensely studied (e.g., Hien 2003; Hien et al. 2007; Ouédraogo et al. 2009). In 1979, when the ranch was first established in an area of about 38,300 ha, it was occupied by about 40 elephants (C. Lungren, pers. com., in Jachmann 1988). In 1982, there were 230 (95% CI: 38–414) in and near the south-east portion of the nearby Kabore-Tambi National Park (Bousquet unpublished data in Jachmann 1989). As the project expanded to its current extent of about 981 km² and law enforcement improved, and permanent water was provided, elephants moved into the NGR from the unsafe adjacent ranges where poachers were active (Jachmann and Croes 1991). Corridors linked the ranch to the Pô National Park (now known as Kabore-Tambi National Park) to the northeast, the Sissili valley to the south and the Boucle du Mouhoun to the east (Sebogo and Barnes 2003; Barnes et al. 2006). Consequently elephant numbers rapidly increased within the ranch. Aerial sample surveys in January 1982 gave population estimates of 300 (95% confidence interval: 0–110) elephants in and near the Nazinga Game Ranch (Bousquet unpublished data in Jachmann 1992); and an estimate of a population of 610 (95% CI: 0–1270) a few years later by Jachmann (1991). Meanwhile ground foot counts by Jachmann (1988) estimated the population at 322 (95% CI: 0, 725) and at 487 (95% CI: 210–774) in 1987 by O'Donoghue (unpublished data) in Jachmann (1991). The elephant population increased rapidly because most of the elephants in Kabore Tambi National Park moved to NGR. By then, elephant browsing was obviously modifying the woodland structure (Fig. S1) (Jachmann

and Croes 1991; Damiba and Ables 1994; Ouédraogo 2005), as these animals are well-known ecosystem engineers (e.g., Dublin et al. 1990; Jones et al. 1994). Overall, elephant population increased three fold since the mid 1980s (Bouché et al. 2016).

The ecological effects of elephants upon tree populations was a major issue not only for ecologists but also for the managers of protected areas in the 1960s and 1970s in eastern and southern Africa (Jachmann and Bell 1979; Barnes 1983, 1985), and will likely re-emerge in the twenty-first century as elephants are increasingly restricted within protected areas (van Aarde and Jackson 2007; Nyirenda et al. 2012). In the case of the NGR, it is interesting to investigate the eventual effects of elephant browsing on savannah tree species not only because of its purely scientific interest for the science of ecology, but also because these effects may have an influence upon the ranch's relationships with the surrounding villages. In particular, it would be possible that eventual modifications in the woodland trends may influence in turn also the revenues earned by the local communities from harvesting the ungulate populations.

In this paper, we aim at evaluating the selective disturbance behaviour of elephants on eight of the most common tree species of NGR. For each species, we estimate the size of the cohort of standing individuals and the numbers of dead individuals, and then we present a tentative model for explaining the eventual modifications of the cohort due to elephant browsing, in order to predict the scale of the vegetation changes that are likely in the near future within the protected area.

Materials and methods

Study area

The Nazinga Game Ranch lies in southern Burkina Faso between 11°1′ and 11°18′ of latitude north and between 1°18′ and 1°43′ of longitude west (Fig. 1). It covers about 97,536 ha. The area is relatively flat with a mean altitude of 300 m (Spinage 1984), and is traversed by the valley of the Sissili river and two of its tributaries, the Dawevélé and the Nazinga rivers, all of which flow seasonally.

The climate is characterized by a single dry season from October to May and a rainy season from June to September. The mean annual rainfall is about 900 mm (Table S1). The vegetation is tall grass tree/shrub savanna with the main vegetation types being riverine forest, savanna woodlands and shrub savanna dominated by *Combretum* and *Terminalia* species (Dekker 1985; Guinko 1985; Arbonnier 2000; Ouédraogo 2005). The main management activities in the ranch include education and community based activities, law enforcement, habitat management and research. Economic activities based on sustainable use of wildlife include game viewing safari hunting, cropping and
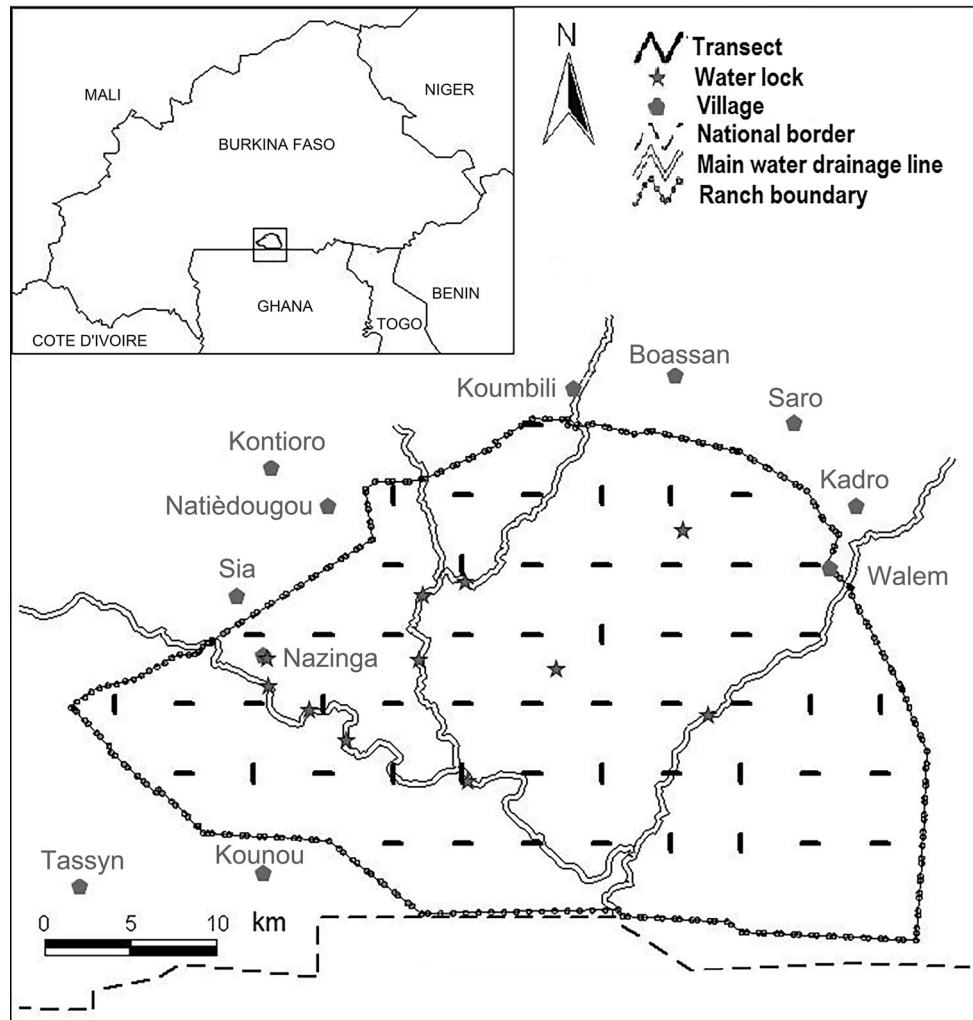
Fig. 1 Location of Nazinga Game Ranch in Burkina Faso (inset) and map of the ranch showing the distribution of transects

community fishing. Animals shot in the managed hunting programme include Warthog (*Phacochoerus africanus*), Roan antelope (*Hippotragus equinus*), Hartebeest(*Alcelaphus buselaphus*), Bushbuck (*Tragelaphus scriptus*), African buffalo (*Syncerus caffer*), Common duiker (*Sylvicapra grimmia*), Oribi (*Ourebia ourebi*), Waterbuck (*Kobus ellipsiprymnus*) and Baboon (*Papio anubis*). Ten villages lie outside the ranch, four within 2 km of the boundary. With less than 10 habitants per km², NGR and its surrounding areas has one of the lowest human densities of the country. However, since the Sahelian drought in the 1970s, the area has been subject to high immigration from the north (Kessler and Geerling 1994; Ouédraogo 1997).

Field protocol

Tree and dung piles surveys

The impact of elephants upon the vegetation was evaluated by a cross-sectional survey design. Simultaneous surveys of elephant droppings and woody vegetation were conducted in the ranch at the end of the 2008 dry season, between 5th April and 3rd May. We used the most recent Geographic Information System database for the ranch to prepare maps using ArcView 3.2; and a systematic transect design (Buckland et al. 2001) to collect field data. A grid of sides 2 km was placed over the study area. Then from a random start 54 transects were laid at 4 km intervals, such that they ran through the center of each selected cell (i.e., every other cell). Each transect was 1 km long and oriented north–south or east–west so as to cut across the drainage lines (Fig. 1).

For the vegetation survey, we enumerated only adult tree individuals of the eight commonest species (see below). Here, we considered as adults those trees and shrubs that were over 1 m height. The quadrats were placed at the beginning, mid-point and end of each transect (Fig. S2). Each quadrat was 25 m × 25 m. Each tree or shrub within the quadrat was enumerated. A tree or shrub was considered damaged if it was dead, pushed down, broken at the base or severely wounded by ele-

phant action in such a way as to ensure death (Fig. S1). Burning was measured as the linear burnt length (m) along the transect that were burnt, as this variable was significantly positively collinear with the number of burnt trees. Elephant-induced damages to trees were easily identified in the field because only elephants are known to make serious damage to trees at NGR, including breaking trees, pulling shrubs out, pushing trees down, etc. Another agent that may cause tree damages is the human activity, especially by cattle men. Nonetheless, cattle men cuttings (using cutlasses) are clearly distinguished in the field.

Density of dung piles was used as a proxy of the elephant abundance along the various transects. The line transect survey method (Buckland et al. 1993; Buckland et al. 2001) was used to estimate dung pile abundance (Barnes 1993; Buckland et al. 1993). The survey team consisted of three people who walked in a straight line along the transect. The following notes were made for each dung-pile: distance along transect, the stage of decomposition (Barnes and Jensen 1987; Barnes 1993) and the perpendicular distance from transect centre-line.

Statistical analyses and modeling

For this analysis we selected the eight commonest woody species in the ranch (Hema et al. unpublished observations), that were recorded in at least 20 transects. These plant species were: *Vittelaria paradoxa* C. F. Gaertn (Sapotaceae), *Acacia dudgeoni* Craib. ex Holl. (Mimosaceae), *Acacia gourmaensis* A. Chev. (Mimosaceae), *Detarium microcarpum* Guill. et Perr. (Caesalpiniaceae), *Terminalia laxiflora* Engl. and Diels (Combretaceae), *Gymnosporia senegalensis* (Lam.) Exell. (Celastraceae), *Piliostigma thonningii* (Schumach.) Milne-Redh. (Caesalpiniaceae) and *Combretum glutinosum* Perr. ex DC. (Combretaceae). For each species, we calculated an estimate of the initial density (N), as the density of live + dead individuals measured during the survey.

Only those dung-piles that fell in the decomposition stages A to D defined by Barnes and Jensen (1987) were included in the analysis. These four stages were defined as follows: Stage A = Boli intact, very fresh, moist, with odour; Stage B = Boli intact, fresh but dry, no odour; Stage C1 = Some of the boli are disintegrated, but more than half are still distinguishable as boli; Stage C2 = Less than 50% of the boli are distinguishable; the rest was disintegrated; Stage D: All boli completely disintegrated; dung pile now forms an amorphous flat mass. Dung-piles at stage E (sensu Barnes and Jensen 1987) were not included in the analyses. Stage E = Decayed to the stage where it would be impossible to detect at 2 m' range in the undergrowth, it will not be seen on a transect unless directly underfoot.

Effective strip width (ESW/ESD in Distance software) of dung count transects was 15.41 m (modelled value). For each transect, the mean density of elephant dung-piles (E_j) was estimated from the equation (Burnham et al. 1980):

$$E_j = \frac{n_j \cdot f(0)}{2 \cdot L_j}$$

where n_j is the number of dung-piles recorded on the jth transect, and L_j is the length of that transect; and f(0) is the reciprocal of half the effective strip width for survey, calculated using DISTANCE 4.1.2. The half-normal key adjusted cosine fitted best the data after a AIC selection procedure (i.e., that one was the model exhibiting the lowest AIC score).

Our goal was to fit the simplest model that described the apparent changes in abundance of the tree species associated with elephant browsing. For each species browsed by elephants, the mortality varies with the initial number of trees (Barnes 1983), thus it is obvious that the number of dead trees is a function of the number of live trees, with the elephant density being a factor in the tree probabilities to die. Indeed, Jachmann (1989) showed that elephants pushed over trees selectively on preferred trees species, and were not necessarily influenced by tree density.

Since data were not normally distributed (after Kolmogorov–Smirnov tests), the raw data for the pertinent variables were log-transformed prior to be entered into any statistical analysis. For each species, the response variable was the logarithm, ln(1 + Y) of the number of damaged individuals, Y. The predictor variables were the initial number of tree individuals N and the density of elephant droppings E, both expressed as the logarithm. The basic model was therefore:

$$\ln(Y+1) = a + b \cdot \ln(N+1) + c \cdot \ln(E+1), \tag{1}$$

where a was the intercept and b and c were the regression coefficients for the initial tree density and dung density respectively. To account for any curvilinear relationships we tested the addition of a quadratic term for tree abundance:

$$\ln(Y+1) = a + b \cdot \ln(N+1) + c \cdot [\ln N+1)]^2 + d \cdot \ln(E+1). \tag{2}$$

If it made a significant contribution to explaining the variance in ln(1 + Y) then it was retained in the model; otherwise it was dropped.

Fire plays an important role in killing trees (Laws et al. 1975; Dublin et al. 1990) and secondly in removing dead trees. We tested the effect of fire by adding the measure of burning (number of meters of the transect that were burnt, B) to the model. We also tested the interaction of elephant abundance and burning, lnExB, since it cannot be excluded that elephants may avoid burnt areas at the study area (Bell and Jachmann 1984). If burning made a significant contribution to explaining

the variance in ln(1 + Y) then it was retained; otherwise it was dropped. In this regard, our model has some limitations in that, according to Shannon et al. (2011), there is a strong indication that tree mortality after being damaged by elephant, was driven by fire and drought. In our case, we could not separate fire from elephant, but drought was not an issue because the rainfall regimes did not change remarkably year-by-year (Table S1) and because there are several permanent water bodies inside the park.

Generalized linear models (GLMs) were used to model the relationship between stem mortality and number (= density) of stems, density of elephant dung piles and the effect of fire, expressed as length of un-burnt area (Hosmer and Lemeshow 2000). In the model, ''stem mortality'' was used as dependent variable and the identity link function and a normal distribution of error were used (McCullagh and Nelder 1989). The model was computed using the best subset procedure. The Akaike Information Criterion (AIC) was employed to find the smallest subset of variables that best predicted the response of a dependent variable (Akaike 1973). GLM were computed in STATISTICA 6.0 (http://www.statsoft.com).

Modeling the tree density changes in relation to their initial density and dung-pile density

We used regression models to estimate the effects of initial tree density and dung-pile density on the number of damaged trees, across the study area at a given moment in time. Here we make the assumption that this cross-sectional relationship between damaged trees and the two predictor variables will also apply longitudinally in time. It is also assumed that there is no spatial variability within the study area, which is of course a simplistic assumption of the model.

For each species, a simple computer program, written in GW-BASIC (that is a dialect of the BASIC programming language developed by Microsoft from BA-SICA, originally for Compaq), started with the initial density and calculated the number of damaged individuals Y' for one time step using the regression equation for that species:

$$\ln(Y' + 1) = a + b \cdot \ln(N + 1) + c \cdot [\ln N + 1]^2 + c \cdot \ln(E + 1) + d \cdot B + z$$

(3)

where z was a random number drawn from a normal distribution of mean zero and variance equal to that of the residuals of Eq. 1. This was therefore a stochastic model because the random variation was added to the value of Y'.

Assuming all damaged trees and shrubs died during that time step, at the end of the time step the number of remaining individuals (N_t) was then $N_t = N - Y'$. That number of live individuals then entered the next time step. The program cycled through five time steps. A time step could represent between two and five years depending upon the average time a damaged tree or shrub remains visible. This will vary from one species to another and with the frequency of fires. The program repeated this procedure 1000 times, giving 1000 estimates of the remaining live individuals (N_t) after five time steps. The final estimate was the median of the 1000 estimates, while the 95% confidence limits were given by the 2.5 and 97.5 percentiles.

Results

Tree damages and dung piles data

The summary of the data on the number and density of damaged and undamaged woody individuals per transect is given in Table S2. The number of undamaged woody individuals (expressed as the individual tree/stem data per transect and per plot) was positively correlated with the number of damaged tree individuals (Pearson's $R = 0.318$, $P < 0.0001$; Fig. 2a). The density of trees/ stems (per ha, including both damaged and undamaged ones) in each transect was negatively correlated to the proportion of trees/stems damaged by elephants (%) (Pearson's $R = -0.241$, $P < 0.01$; Fig. 3b), that is: the more dense the woodland cover, the least the percentage of damaged plants by elephants.

Along 54 transects, a total of 3819 dung piles were observed. Distance methodology analysis (N parameters = 3; $\chi^2 = 67.64$, df = 21, $P < 0.0001$) returned a dung pile density per km^2 = 2273.6 (variance = 180, 854.57; % coefficient of variation = 19%; 95% upper confidence limit = 3297.5; lower confidence limit = 1567.6).

For all eight selected species, the regression models were significant ($P < 0.05$) when the initial tree or shrub density and elephant dung density were fitted as predictors (Table 1). The models were not improved after adding either the quadratic term for tree abundance (*DeltaAIC* = 2.315) or the variable for burning (in each case *DeltaAIC* = 1.774). For four species (*Acacia dudgeoni, Combretum glutinosum, Deterium microcarpum*, and *Piliostigma toningii*), their initial density and elephant dung density accounted for more than half the variation in the density of damaged individuals (Table 1). Only for *Acacia gourmaensis* did these two variables account for less than one-third of the variance. For all species, the regression coefficient for initial density (*b*) was significant. For three species (*Acacia dudgeoni, Combretum glutinosum* and *Vitellaria paradoxa)* the regression coefficient for dung density (*c*) was significantly negative (Pearson's $R > -0.35$, $P < 0.05$) (Table 1).

Generalized Linear Model revealed significant positive relationship between the stem mortality and the dung piles density and and the length of unburnt area (thus showing moderate effect of fire on stem mortality)
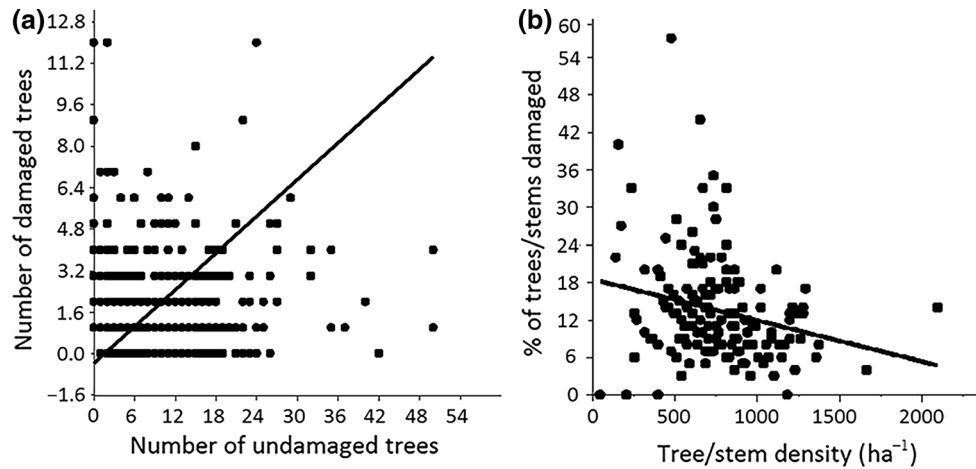
Fig. 2 Relationships **a** between number of undamaged woody individuals (expressed as the individual tree/stem data per transect and per plot) and number of damaged individuals across transects at the study area; **b** density of tree/stems (per ha) and % of trees/stems damaged by elephants per transect. For the statistical details, see the text
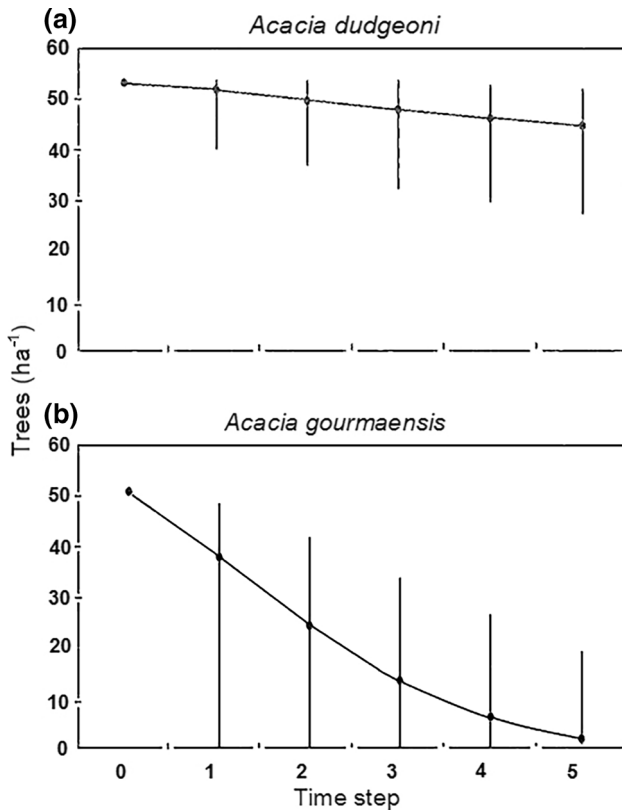

Fig. 3 Predicted changes (= declines) of two species over five time steps according to the stochastic simulation models. The declines of the species that declined least [*Acacia dudgeoni* (**a**)] and the one that declined most [*Acacia gourmaensis* (**b**)] are shown. *Vertical bars = error bars*

(Table 2). These variables were the most parsimonious combination expressed by the performed GLM (Table 3). Thus, this model showed that the probability of finding dead stems was directly related to density of the elephant dung piles and the lenght of unburnt area, thus revealing that fire was not a significant predictor of tree mortality. This model explained 65.52% of total deviance.

Modelling changes in the populations of eight selected tree species

The stochastic simulation models predicted remarkable changes in the populations of the eight selected plant species, and all the selected plant species were predicted to decline, although with a great interspecific variation of intensity (Fig. 3). For example, 97% of the *Acacia gourmaensis* trees and shrubs were predicted to die after five time steps; more than two-thirds of *Vitellaria paradoxa* and about half the population of *Maytenus senegalensis* (Table 4). About a third of the *Combretum glutinosum, Deterium microcarpum, Piliostigma toningii* and *Terminalia laxiflora* cohorts would also die, with the species predicted to suffer the least impact being *Acacia dudgeoni* (Table 4; Fig. 2). Concerning these models, it should be however noted, that for all species the 95% confidence intervals were wide. The distribution of Y' produced by Eq. 2 was lognormal with a long tail towards the higher values. Since Y' was then subtracted from N to give the number of remaining trees or shrubs (N_t), the distribution of N_t had a long tail towards the lower values and therefore the confidence intervals were asymmetrical. For two species, *Acacia gourmaensis* and *Vitellaria paradoxa*, the confidence interval embraced zero, indicating a risk that they could be eliminated in the near future.

In order to predict the effects on woody plants of changing elephant populations (that is, changes in dung density) due to movements into or out of the area along the corridors, for each woody species the dung pile density was increased by 50% in one simulation (in order to simulate a 50% increase in elephant numbers) and decreased by 50% in a second simulation. An increase in elephant numbers predicted heavy decline of *Acacia gourmaensis* and of *Vitellaria paradoxa* (Fig. 3). On the

Table 1 Regression models describing the number of damaged trees or shrubs Y in relation to the initial trees or shrub density, and the measure of elephant abundance (elephant dung density in 2008)

Species	Variable	Regression coefficient	SE for regression coefficient	P	R^2	P for R^2	Number of transects
Acacia dudgeoni	Intercept	−6.637	1.976	0.004	0.577	< 0.001	21
	ln(1 + initial tree density)	1.572	0.356	0.000			
	ln(1 + dung density)	0.487	0.113	0.000			
Acacia gourmaensis	Intercept	−0.298	1.312	0.823	0.304	0.046	20
	ln(1 + initial tree density)	0.650	0.283	0.035			
	ln(1 + dung density)	0.249	0.142	0.098			
Combretum glutinosum	Intercept	−4.427	1.182	0.001	0.549	< 0.001	28
	ln(1 + initial tree density)	1.173	0.313	0.001			
	ln(1 + dung density)	0.372	0.156	0.025			
Deterium microcarpum	Intercept	−4.588	1.461	0.004	0.597	< 0.001	27
	ln(1 + initial tree density)	1.306	0.237	< 0.001			
	ln(1 + dung density)	0.160	0.177	0.373			
Gymnosporia senegalensis	Intercept	−5.802	1.975	0.009	0.479	0.004	20
	ln(1 + initial tree density)	1.679	0.461	0.002			
	ln(1 + dung density)	0.389	0.190	0.057			
Piliostigma toningii	Intercept	−4.304	1.034	0.000	0.521	< 0.001	31
	ln(1 + initial tree density)	1.257	0.245	< 0.001			
	ln(1 + dung density)	0.195	0.152	0.212			
Terminalia laxiflora	Intercept	−4.026	1.232	0.003	0.397	< 0.001	36
	ln(1 + initial tree density)	1.065	0.297	0.001			
	ln(1 + dung density)	0.280	0.185	0.140			
Vitellaria paradoxa	Intercept	−3.096	1.368	0.030	0.349	< 0.001	40
	ln(1 + initial tree density)	0.984	0.307	0.003			
	ln(1 + dung density)	0.460	0.158	0.006			

The response variable was ln(1 + Y)

Table 2 Results of the Generalized Linear Model exploring the relationship between stem mortality (dependent variable), dung piles density and and the length of unburnt area

	Estimate	SE	Wald	P
Intercept	3.361745	3.101061	1.175192	0.278337
Number of stems	0.093742	0.021032	19.86564	< 0.0001
Dung density	0.000698	0.000259	7.278507	0.006978
Fire (length of unburnt area)	−0.00236	0.005277	0.200211	0.654551
Scale	5.864148	0.564278	108	0
Explained deviance	65.52%			

SE standard error

other hand, if the elephant population were to be halved, then about 10% of the *Acacia gourmaensis* population, and almost half the *Vitellaria paradoxa* population, would survive (Table 2). However, because the confidence intervals were wide, the three simulations for each species (that is, current elephant density, 50% increase and 50% decrease) produced estimates with overlapping

confidence intervals and therefore no significant differences in final density can be detected.

Discussion

Our study suggests that elephants can have remarkable effects on the vegetation of the NGR, as 100% of the selected plant species were influenced by their browsing activities. Nonetheless, this fact does not obviously imply that the entire woodland would be affected by elephants, as our study focused on a limited number of tree species (that, however, were the commonest in the landscape). Indeed, our study neither (1) surveyed the effects of elephants on all tree and shrub populations of the park, (2) the proportion and composition of those trees and shrubs killed directly by elephants versus by other agents such as fire, and (3) the spatial variability of the selected tree species in relation to elephant habitat use.

Table 3 Most parsimonious combination of variables expressed by the performed GLM, and ordinated by their AIC values

Variable 1	Variable 2	K	AIC	L.Ratio	P
Number of stems	Dung density	2	350.4818	22.83447	0.000011
Number of stems	Dung density	3	352.2819	23.03431	0.000040
Number of stems		1	355.2200	16.09622	0.000060
Number of stems	Fire (length of unburnt area)	2	357.1100	16.20627	0.000303
Dung density		1	365.2674	6.04889	0.013915
Dung density	Fire (length of unburnt area)	2	367.1982	6.11807	0.046933
Fire (length of unburnt area)		1	371.2905	0.02571	0.872622

Table 4 Changes in tree or shrub density after five time steps predicted by the stochastic simulation models (note that all predicted changes are negative, i.e. predicted declines) and changes in tree or shrub density after five time steps predicted by the stochastic simulation models, following a 50% decline or 50% increase in elephant density

Species	Starting density (ha⁻¹)	Final density - Median (95% CI) (ha⁻¹)	% change	50% increase in elephant density		% decline	50% drop in elephant density		% decline
				Median final density (ha⁻¹)	95% CI		Median final density (ha⁻¹)	95% CI	
Acacia dudgeoni	53.3	44.4 (27.4, 51.9)	−16.7	41.5	24.7, 50.0	22.1	47.3	34.9, 53.3	11.4
Acacia gourmaensis	85.3	2.9 (0.0, 32.0)	−96.6	0.8	0.0, 30.1	99.1	7.8	0.0, 38.2	90.9
Combretum glutinosum	48.0	33.0 (14.3, 43.2)	−31.3	30.6	10.4, 41.6	36.2	36.9	18.4, 44.6	23.2
Deterium microcarpum	80.0	57.0 (33.3, 70.1)	−28.7	56.1	31.2, 69.9	29.9	59.4	36.9, 72.2	25.7
Gymnosporia senegalensis	56.0	27.1 (2.9, 43.4)	−51.6	24.2	2.8, 40.5	56.8	32.1	4.5, 46.0	42.7
Piliostigma toningii	80.0	51.0 (16.2, 69.5)	−36.2	49.7	13.6, 67.7	37.9	54.7	24.1, 70.4	31.6
Terminalia laxiflora	85.3	60.3 (21.1, 77.6)	−29.3	57.8	15.7, 75.9	32.3	64.2	27.0, 79.8	24.8
Vitellaria paradoxa	69.3	22.3 (0.0, 51.6)	−67.9	15.3	0.0, 45.7	78.0	31.2	0.8, 55.6	55.0

For all species, both the initial density (as expected) and the density of elephant dung-piles explained a high proportion of the variance in the density of damaged trees: more than half the variance for three species. This result is noteworthy because it shows that dung pile density certainly influenced the amount of dead trees, and it did so in a similar magnitude as the initial tree density. Our models considered that the most affected species would be *Acacia gourmaensis, Vitellaria paradoxa* and *Gymnosporia senegalensis*. However, since our models did not include the regeneration rate (= recruitment) of the selected plant species, it is obvious that the absolute values of decline (up to over 96% in *Acacia gourmaensis*) should not be considered as real estimates but just as an indication of the species-specific differences in the potential exposure to elephant disturbance in the NGR. In other words, the predicted 96.6% decline of *Acacia gourmaensis* should be not taken as an indication of any imminent extinction of this species from the park, but should be considered merely as an evidence that this species will suffer from elephant browsing activities much more than the other seven selected tree species, especially if the elephant density would increase in the next decades. Indeed, field surveys during the years 1984–2014 revealed that *Acacia gourmaensis* declined by about 70% (Nama Neti personal communication).

Unexpectedly, fire was not a significant predictor of tree mortality across transects. This fact was due to that most transects were intensely burnt (mean burnt area of each transect exceeded 90%). The lack of variation between transects in burning meant that the effect of this variable could not be computed (Kleinbaum et al. 2008), in spite of this, this variable had certainly a considerable relevance in tree mortality. As the human population expands outside the ranch, more fires are likely to sweep into the ranch and it is unlikely that the proportion of burnt territory within the ranch (>90%) will tend to diminish.

In order to predict the trend in each population one would need data on both regeneration rates and seedling survival rates; these were beyond the resources of this project but must be addressed in subsequent studies. In this regard, in Ruaha National Park (Tanzania), Barnes (1983) reported abundant regeneration at the end of the wet season. However, all this abundant regeneration was or destroyed by fire or eaten by elephants during the dry season, so by the end of the dry season none was left. In other words, adult trees and shrubs were being killed by elephants and fire, but regeneration was zero. The same is possibly true at Nazinga, where the combination of intense dry season burning combined with the large ungulate populations and dense elephant populations is likely to result in little successful regeneration (Dublin et al. 1990). Even 20 years ago, when the elephant density was much less than today, there was little regeneration (Jachmann and Croes 1991). Given the increased number of elephants and the fact that regeneration was already low when elephant density was much lower, one could imagine that some tree species

should already have disappeared. Since their disappearance did not occur, that means that there are other factors that allowed these species to survive. Maybe the dissemination by elephants is part of the surviving solution for these heavily impacted tree species. It would also be interesting to study the resilience of tree species to early fires (October–November most common fire period) that are quite smoother for vegetation in general.

Another major limitation of this study was the lack of information on the time that a damaged tree remains visible, that is, the length of each time step. This will vary from one species to another, with the size of tree and with the frequency of fires. It can only be estimated by observing a large sample of marked damaged trees and shrubs over a period of years. Thus at present the rate of decline of each species can only be expressed in time steps. Another limitation is the wide confidence intervals of the predictions for each species. Here we had 54 transects distributed across the study area, and the most common tree (*Vitellaria paradoxa*) was recorded in 40 of them. In order to reduce the size of the confidence intervals, a very large sample would be necessary (at least 120 transects).

Our study may have also some conservation implications for the management of the Nazinga Game Ranch. Indeed, an important question for the ranch management and the surrounding communities is: how will the large herbivore populations, and the trophy hunting, be affected as the woodland landscape would change under the elephant browsing activity? Although the effects of woodland changes by both burning and elephants are often perceived as deleterious (Owen-Smith 2006), we think that in the present case they can have also positive cascade effects. For example, opening out the tree canopy will encourage grazers such as hartebeest, waterbuck and especially buffalo (Jachmann and Croes 1991). However, it should be noticed that most herbivores (even grazers) change habitat along the day according to weather and time of the day, and the buffalo is not a strict grazer but a mixt grazer-browser. Moreover in West Africa some grazers can occasionally become browsers in case of food shortage (hartebeest, reedbuck) (Hema et al., unpublished observations), as trees conserve the last primary biomass in case of drought.

If large-bodied herbivores are favoured by elephants and fire, at least in some periods of the years, an increase in their populations will offer a greater harvest of meat from legal hunting. Thus if poaching were to be controlled then the woodland trend could be to the benefit of the surrounding village communities. Currently, the entire area of the ranch is affected by illegal poaching activity, but with less intensity in the part of the ranch where the field staff and the ranch administration are based. Areas with high densities of illegal activities also corresponded to areas with low animal density (Ouédraogo et al. 2009; Marchal et al. 2012). Animals avoided peripheral areas with high human pressures. The north and south-eastern parts were the most affected, and since 2010, the number

of carcasses of mammals recorded along transects was high (Hema et al. unpublished data).

Revenues to the ranch from eco-tourism could be also intensified with an higher density of ungulates that can easily be spotted by people. The enhancement of the numbers of ecotourists would be interesting to monitor, as there were about 500 visitors during the study period. Thus, it is predicted that elephant engineering action on the NGR may help the poverty alleviation of the area via a positive action towards the density of the ungulate communities inhabiting the ranch. In this case a careful costs-benefits analysis should be done in the years to come, because (1) the elephant-mediated environmental changes in the ranch could possibly produce an increase in the local population's income via increased hunting harvests (main form of wildlife valorization at NGR) due to the increase of the population of large ungulates but (2) the development of villages and the increasing human population around the ranch will continue, and the nearness between elephants and villages will continue to generate high human-elephants conflicts rates with local residents especially during the dry season when the fields are not guarded. Thus, the dynamics of this process should be studied in detail in the years to come.

References

Akaike H (1973) Information theory and an extension of the maximum likelihood principle, in Petrov, B.N.; Csáki, F., 2nd International Symposium on Information Theory, Tsahkadsor, Armenia, USSR, September 2–8, 1971, Budapest: Akadémiai Kiadó, pp. 267–281

Arbonnier M (2000) Arbres, arbustes et lianes des zones sèches d'Afrique de l'Ouest. CIRAD Paris

Barnes RFW (1983) Effect of elephant browsing on woodlands in a Tanzanian national park: measurements, models and management. J Appl Ecol 20:521–540

Barnes RFW (1985) Woodland changes in Ruaha National Park (Tanzania) between 1976 and 1982. Afr J Ecol 23:215–221

Barnes RFW (1993) Indirect methods for counting elephants in forest. Pachyderm 16:24–30

Barnes RFW (2002) The problem of precision and trend detection posed by small elephant populations in West Africa. Afr J Ecol 40:179–185

Barnes RFW, Jensen KL (1987) How to count elephants in forests. IUCN Afr Elephant Rhino Spec Group Tech Bull 15:1–6

Barnes RFW, Adjewodah P, Ouédraogo L, Héma ME, Ouiminga H, Zida PC (2006) Transfrontier corridors for West African elephants: the PONASI-Red Volta and Sahelian corridors. Unpublished report, IUCN, Ouagadougou, Burkina Faso

Belemsobgo U (1995) Le modèle "Nazinga": réussite technique et incertitudes sociales. Le Flamboyant 35:22–27

Bell RHV, Jachmann H (1984) Influence of fire on the use of *Brachystegia* woodland by elephants. Afr J Ecol 22:157–163

Bouché P (2007) Northern Ghana elephant survey. Pachyderm 42:58–69

Bouché P, Douglas-Hamilton I, Wittemyer G, Nianogo AJ, Doucet J-L, Lejeune P (2011) Will elephants soon disappear from West African savannahs? PLoS One 6(6):e20619. doi: 10.1371/journal.pone.0020619

Bouché PL, Bailly V, Muyle M, Zinque MH, Mercier A, Cornélis D, Lungren C, Portier B, Marchal A, Renault F, Yaméogo D, Kafando P, Sawadogo P, Vermeulen C (2016) Conserving wildlife amongst the cotton fields. A third of a century of experience at the Nazinga Game Ranch, Burkina Faso. Environ Monit Assess 188(7):1–13

Buckland ST, Anderson DR, Burnham KP, Laake JL (1993) Distance sampling: estimating abundance of biological populations. Chapman and Hall, London

Buckland ST, Anderson DR, Burnham KP, Laake JL, Borchers DL, Thomas L (eds) (2001) Introduction to distance sampling: estimating abundance of biological populations. Oxford University Press, New York

Burnham KP, Anderson D, Laake JL (1980) Estimation of density from line transect sampling of biological populations. Wildl Monogr 72:202

Damiba TE, Ables ED (1994) Population characteristics and impacts on woody vegetation of elephants on Nazinga Game Ranch, Burkina Faso. Pachyderm 18:46–53

Dekker AJFM (1985) Edition de la carte de végétation de Nazinga. FAO, Ouagadougou, DP/UPV: 82/008

Dublin HT, Sinclair ARE, McGlade J (1990) Elephants and fire as causes of multiple stable states in the Serengeti-Mara woodlands. J Anim Ecol 59:1147–1164

Guinko S (1985) La végétation et la flore du Burkina Faso. Ministère de l'Environnement et du Tourisme, Direction de l'Aménagement Forestier et du Reboisement, Ouagadougou, Burkina Faso

Hema ME, Barnes RFW, Guenda W (2010a) Distribution of savannah elephants (*Loxodonta africana africana* Blumenbach 1797) within Nazinga game ranch, southern Burkina Faso. Afr J Ecol 49:141–149

Hema ME, Barnes RFW, Guenda W (2010b) The seasonal distribution of savanna elephants (*Loxodonta africana africana* Blumenbach 1797) in Nazinga Game Ranch, southern Burkina Faso. Pachyderm 48:33–40

Hien B (2003) Les éléphants du Ranch de Gibier de Nazinga (Burkina Faso): données passées, situation actuelle, perspectives de conservation. Pachyderm 35:43–52

Hien BM, Jenks J, Klaver RW, Wicks ZW (2007) Determinants of elephant distribution at Nazinga Game Ranch, Burkina Faso. Pachyderm 42:70–80

Hosmer DW, Lemeshow S (2000) Applied logistic regression analysis, 2nd edn. John Wiley and Sons, New York

Jachmann H (1988) Numbers, distribution and movements of the Nazinga elephant. Pachyderm 10:16–21

Jachmann H (1989) Food selection by elephants in the 'miombo' biome, in relation to leaf chemistry. Biochem Syst Ecol 17:15–24

Jachmann H (1991) Evaluation of four survey methods for estimating elephants densities. Afr J Ecol 29:188–195

Jachmann H (1992) Movements of elephants in and around the Nazinga Game Ranch, Burkina Faso. J Afr Zool 106:27–37

Jachmann H, Bell RHV (1979) The assessment of elephant numbers in the Kasungu National Park, Malawi. Afr J Ecol 17:231–239

Jachmann H, Croes T (1991) Effects of browsing by elephants on the *Combretum/Terminalia* woodland at the Nazinga Game Ranch, Burkina Faso, West Africa. Biol Conserv 57:13–24

Jones CG, Lawton JH, Shachak M (1994) Organisms as ecosystem engineers. Oikos 69:373–386

Kessler JJ, Geerling C (1994) Profil environnemental du Burkina Faso. Université Agronomique de Wageningen, Département de l'Aménagement de la Nature, Les Pays-Bas

Kleinbaum DG, Kupper LL, Nizam A, Muller KE (2008) Applied regression analysis amd other multivariable methods. Thomson Brooks/Cole, Belmont, California

Laws RM, Parker ISC, Johnstone RCB (1975) Elephants and their habitats. Clarendon Press, London

Mallon DP, Hoffmann M, McGowan PJK, Grainger MJ, Hibert F, Van Vliet N (2016) An IUCN situation analysis of terrestrial and freshwater fauna in West and Central Africa. IUCN, Gland

Marchal PL, Bouché P, Ouédraogo M, Sawadogo P, Yaméogo DD, Yanogo F, Vermeulen C (2012) Status of medium-sized ungulate populations in 2010, at the Nazinga Game Ranch, Burkina Faso (Western Africa). Biotechnol Agron Soc Environ 16:307–315

McCullagh P, Nelder JA (1989) Generalized linear models. Chapman and Hall/CRC, London

Nyirenda VR, Myburgh WJ, Reilly BK (2012) Predicting environmental factors influencing crop raiding by African elephants (*Loxodonta africana*) in the Luangwa Valley, eastern Zambia. Afr J Environ Sci Technol 6:391–400

Ouédraogo NA (1997) Quels régimes fonciers pour les aménagements hydro-agricoles? Actes du séminaire atelier < < Quel environnement pour le développement de l'irrigation au Burkina Faso ≫ ; IIMI, Ministère de l'Environnement, Direction des Etudes et de la Planification, Burkina Faso

Ouédraogo M (2005) Régulation de la dynamique des populations de buffles (*Syncerus caffer* Sparrman) et de waterbucks (*Kobus ellipsiprymnus* Ogilby) et moyens de gestion à mettre en œuvre pour préserver l'équilibre des communautés végétales dans le ranch de Nazinga (Burkina Faso). Thèse de Doctorat; Faculté Universitaire des Sciences Agronomiques de Gembloux; Belgique

Ouédraogo M, Delvingt W, Doucet JL, Vermeulen C, Bouché P (2009) Estimation des effectifs des populations d'éléphants par la méthode d'inventaire pédestre total au Ranch de Gibier de Nazinga, (Burkina Faso). Pachyderm 45:57–66

Owen-Smith N (2006) Elephants, woodlands and ecosystems: some perspectives. Pachyderm 41:90–94

Poilecot P (2010) Le braconnage et la population d'éléphants au Parc National de Zakouma (Tchad). Bois For Trop 303:93–102

Roth HH, Douglas-Hamilton I (1991) Distribution and status of elephants in West Africa. Mammalia 55:489–527

Sebogo L, Barnes RFW (2003) Action plan for the management of transfrontier elephant conservation corridors in West Africa. IUCN

Shannon G, Thaker M, Tam Im Vanak A, Page BR, Grant R, Slotow R (2011) Relative impacts of elephant and fire on large trees in a savanna ecosystem. Ecosystems 14:1372–1381

Smith FA, Doughty CE, Malhi Y, Svenning JC, Terborgh J (2016) Megafauna in the Earth system. Ecography 39:99–108

Spinage C (1984) Analyse des données de climat de Pô et de Léo en référence à Nazinga. FAO/FODP/UPV/82/008 document de travail no 4, Ouagadougou, Burkina Faso

van Aarde RJ, Jackson TP (2007) Megaparks for metapopulations: adressing the causes of locally high elephant numbers in southern Africa. Biol Conserv 34:289–297

World Food Program (2012) Drought affects millions in the Sahel. https://www.wfp.org/stories/drought-returns-sahel, Accessed 22 Oct 2016