Density-dependent body condition and recruitment in a tropical ungulate

N. Gaidet and J.-M. Gaillard

Abstract: In tropical areas, annual rainfall and predation have been reported to drive population dynamics of most species of large herbivores studied so far, with little direct empirical evidence for density-dependent responses of life-history traits. We here investigated in a game ranch in Zimbabwe density-dependent responses of body condition and recruitment in an impala (*Aepyceros melampus* (Lichtenstein, 1812)) population that underwent an experimental drastic reduction of density within 2 years under similar rainfall and predation pressure. Body condition of all sex and age classes was lower during the high-density year than during the low-density year, suggesting increased competition for restricted resources at high density. In addition, we observed a significant increase in population recruitment (from 0.47 to 0.80 juveniles/female) as population density declined. Our study provides a rare example of a direct density-dependent response of body condition at the individual level in a tropical ungulate species, and indicates that food resource variation controls population dynamics of impala under constant and moderate predation pressure as is commonly reported in temperate populations of large herbivores.

Résumé : Dans les régions tropicales, on a montré que les précipitations annuelles et la prédation sont les facteurs qui contrôlent la dynamique de population de la plupart des espèces de grands herbivores étudiées à ce jour; en revanche, il y a peu de données empiriques sur des réactions dépendantes de la densité dans les caractéristiques démographiques. Nous étudions ici dans un ranch de gibier du Zimbabwe les réactions dépendantes de la densité de la condition corporelle et du recrutement dans une population d'impalas (*Aepyceros melampus* (Lichtenstein, 1812)) qui a subi une réduction expérimentale considérable de sa densité au cours de 2 années pendant lesquelles les précipitations et la pression de prédation sont restées constantes. La condition corporelle chez toutes les classes d'âge et de sexe était plus basse durant l'année de forte densité que durant l'année de faible densité, ce qui laisse croire à une compétition accrue pour les ressources limitées à la forte densité. De plus, nous avons observé une augmentation significative du recrutement de la population (de 0,47 à 0,80 jeunes/femelle) au cours du déclin de la population. Notre étude fournit un rare exemple d'une réaction directe dépendante de la densité de la condition corporelle à l'échelle individuelle chez une espèce tropicale d'ongulés; elle indique ainsi que la variation des ressources alimentaires contrôle la dynamique de population des impalas dans les conditions de pression de prédation constantes et modérées comme on observe souvent dans les populations tempérées de grands herbivores.

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Introduction

The influence of both climatic variation and density dependence on population dynamics of large herbivores has long been studied in a large variety of species (for reviews see Fowler 1987; Sæther 1997; Gaillard et al. 2000). However, while most of these species occur in the tropics, few direct empirical studies of density-dependent responses of life-history traits are available for tropical populations (Gail-

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lard et al. 1998, 2000). Indeed, previous works that have reported evidence of density dependence in populations of large herbivores in tropical areas focussed on time series analyses of population size (e.g., Owen-Smith 2006; Owen-Smith and Ogutu 2003) or biomass densities (e.g., Georgiadis et al. 2007) so that mechanisms by which density dependence operates at the population level have still to be identified. We tried to fill this gap by measuring at the individual level the direct response of some life-history traits of impala (*Aepyceros melampus* (Lichtenstein, 1812)) to an experimental change in density.

In tropical areas, the annual aboveground primary production, and thereby the resource biomass for large herbivores, mostly depend on annual rainfall (e.g., Coe et al. 1976) and soil conditions (Fritz and Duncan 1994). Rainfall has been reported to drive population dynamics of most tropical large herbivores studied so far (Owen-Smith 1990 on greater kudu (*Tragelaphus strepsiceros* (Pallas, 1766)); Mduma et al. 1999 on blue wildebeest (*Connochaetes taurinus* (Burchell, 1823)); Georgiadis et al. 2003 on Burchell's zebra (*Equus burchelli* (Gray, 1824)); Ogutu and Owen-Smith 2003 on ungulate species of Kruger Park; Dunham et al. 2004 on tsessebe (*Damaliscus lunatus* (Burchell, 1823)). Dry years

are generally associated with resource limitation leading to a decline in ungulate population performance (e.g., Sinclair et al. 1985). Predation has also been reported as playing a key role in limiting tropical populations of large herbivores (e.g. Mills and Shenk 1992; Harrington et al. 1999), especially in nonmigratory and smaller bodied species such as the impala (Sinclair et al. 2003). Therefore, assessing density-dependent responses of life-history traits of tropical ungulates requires controlling for variation in rainfall and predator pressure.

We tested for direct density-dependent responses of body condition and recruitment in an impala population living on a game ranch in Zimbabwe. The population density was initially set high through the introduction of animals to meet harvesting objectives, hence providing a context in which density-dependent effects may be expressed. This population underwent a drastic reduction in density within a short time period (2002–2003), because of a combination of harvesting (~20%) and potential poaching and emigration. This provided us with an experimental setting for studying density dependence as recommended by Sinclair (1989). In addition, our 2 year long monitoring took place during dry years (Fig. 1) under a moderate and quite constant predator pressure, allowing us to assess density-dependent responses for given rainfall and predation patterns.

We measured population performance at the end of the hot and dry season in October. Body condition of impala is low during this period (Dunham and Murray 1982) when food resources are limited by senescence of plant tissues and by progressive depletion owing to consumption. According to the range quality hypothesis, which states that among-individual differences in performance should reflect among-individual differences in the quality of habitat available (Sæther and Heim 1993; Gaillard et al. 1996), we predicted that body condition of impala should be positively related to the amount of food supply. We therefore expected (1) to find negative influences of population density on body condition of impala at a given level of annual rainfall. Breeding of impala in southern Africa is highly seasonal, with a short rut period in May and a synchronized lambing period in November–December (Fairall 1968; Murray 1982). Because juveniles have additional energetic requirement for growth, they should be more sensitive to food restriction compared with adults (Hanks et al. 1976; Dunham and Murray 1982). We thus predicted that (2) juveniles should have lower body condition than adults for a given set of density and rainfall conditions and (3) that such between-age differences should be more pronounced when animals face scarce food supply (caused either by high population density and (or) by low annual rainfall). As in most polygynous ungulates, energy allocation to reproduction by male impala is high (Clutton-Brock et al. 1982), leading to higher mass loss during the rut in prime-aged males compared with yearling males (Kojola 1985 on reindeer (*Rangifer tarandus* (L., 1758)); van Rooyen 1993 on impala; Yoccoz et al. 2002 on red deer (*Cervus elaphus* L., 1758)). Hence, in our food-restricted context, we predicted that (4) adult males should have lower body condition than yearling males by the end of the dry season. Impala are sexually dimorphic in size, with mature males being, on average, 30% larger than adult females (Skinner and Smithers 1990). Males are thus expected to have higher absolute energy requirements than

Fig. 1. Rainy season rainfall (November–April) experienced by the study population since its introduction to the ranch, calculated from two proximate stations in the mid-Zambezi valley (Muzarabani and Kanyemba; source from the Zimbabwean Department of Meteorological Services, Harare). The mean rainy season rainfall over the last 23 years (770 mm) is represented as a reference line. The dry seasons when the introduction (October 1999 and 2000) and the study (October 2002 and 2003) were conducted are also indicated.
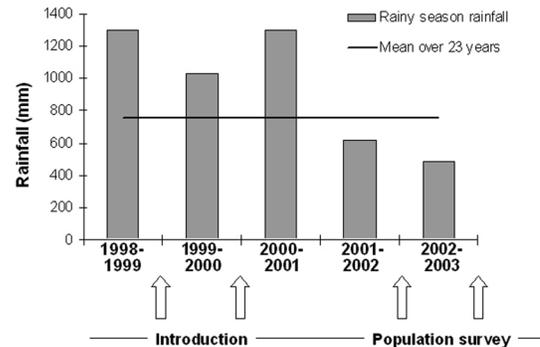
females (Demment and Van Soest 1985) and to be more susceptible to starvation (Clutton-Brock et al. 1985; Loison et al. 1999). We consequently predicted that (5) adult males should have lower body condition than adult females by the end of the dry season and (6) the between-sex differences should be more contrasted at high population density. Males of dimorphic ungulates grow more rapidly and for longer than females (Jarman 1983), and have thus higher nutritional demands during their first year. As a consequence, we predicted that (7) the body condition of juvenile males should be more affected by density than that of juvenile females.

In most ungulate populations, changes in population density affect first recruitment through delayed primiparity and reduction in juvenile survival, whereas female adult survival shows little response to changes of density (Eberhardt 1977; Gaillard et al. 1998, 2000). We hence predicted to find (8) a decreasing recruitment with increasing density for a given level of annual rainfall. Furthermore, following the hypothesis of a differential energetic requirement for growth between sexes, juvenile males should be more likely to die from starvation (Clutton-Brock et al. 1982; Loison et al. 1999; Bonenfant et al. 2002). In our context of restricted food supply, we thus predicted that (9) the sex ratio should be increasingly biased toward females with increasing density for a given level of annual rainfall.

Materials and methods

Study site

The study has been conducted in 2002–2003 in the Chivaraidze Communal Game Ranch, located in the mid-Zambezi valley in northern Zimbabwe (Dande Communal Area). This 3200 ha ranch is surrounded by a 3 m high electric fence and is covered by a mosaic of deciduous dry woodland and shrubland, which is dominated by mopane trees (*Colophospermum mopane* (Kirk ex Benth.) Leonard). There is one rainy season (November–April) with highly variable annual rainfall: the mean rainfall over the last 23 years was 770 mm, with a CV of 36%, and maximum and minimum values of 1300 and 355 mm,

respectively. Rainfall during the rainy seasons preceding the 2 years of the study period were both low, at 630 mm in the 2001–2002 and 480 mm in the 2002–2003, respectively (Fig. 1). Water availability in the ranch consists of some natural water points, river pools, and two artificial water basins pumped during the dry season to provide complementary water supply. The water level of all these water sources was recorded every month to determine the distribution of water availability for ungulates.

When the fence was erected in 1999, the initial resident impala population was estimated from the mean impala density calculated from an initial line-transect count conducted in the area (for further details see Gaidet et al. 2003) at 100 individuals (all nonmarked). The population then increased through successive introductions of 68 impala in 1999 and 334 in 2000. All introduced impala were marked with an ear tag. Although the fence was built to prevent impala from escaping the ranch (a classical game-ranch-like fence 3 m high consisting of 20 wire lines tightened with vertical droppers every 2 m), some impala were observed on few occasions jumping successfully through the wire lines despite the resistance of the fence. Hunting activity was initiated in 2002 ($n = 12$) and increased in 2003 ($n = 76$). Hunting focussed on male impala from December to June. A community of several ungulate species, including kudu, bush duiker (*Sylvicapra grimmia* (L., 1758)), Sharpe's grysbok (*Raphicerus sharpie* Thomas, 1897), warthog (*Phacochoerus africanus* (Gmelin, 1788)), and bushpig (*Potamochoerus larvatus* (F. Cuvier, 1822)), was originally present. African elephants (*Loxodonta africana* (Blumenbach, 1797)) were chased away from the ranch in 1999 before the introduction of impala, with no intrusion ever since. Therefore, the presence of African elephants, which can influence the performance of mesoherbivores such as the impala through competition (Fritz et al. 2002, Rutina et al. 2005), was not an issue in the present study. Other species of large herbivores were introduced, including eland (*Taurotragus oryx* (Pallas, 1766)), sable antelope (*Hippotragus niger* (Harris, 1838)), tsessebe, waterbuck (*Kobus ellipsiprymnus* (Ogilby, 1833)), blue wildebeest, and Burchell's zebra.

Predation was not measured directly, but the presence of predators was assessed during the study period through spoor detection on the network of dust roads (60 km over the entire ranch) continuously covered for management and field research activities (at least twice a week). Potential local predators consisted of resident leopard (*Panthera pardus* (L., 1758)) and caracal (*Caracal caracal* (Schreber, 1776)) for impala adults, and side-striped jackal (*Canis adustus* Sundevall, 1847), yellow baboon (*Papio cynocephalus* (L., 1766)), martial eagle (*Polemaetus bellicosus* (Daudin, 1800)), and python (*Python sebae* (Gmelin, 1788)) for impala fawns. A short intrusion (10–15 days) by a small group of nonresident lions (*Panthera leo* (L., 1758)) (4 individuals) was detected in both years, but spotted hyenas (*Crocuta crocuta* (Erxleben, 1777)) and African wild dogs (*Lycaon pictus* (Temminck, 1820)) were absent (N. Gaidet, personal observation). No predator intrusion (except lions) or disappearance was recorded during the study period, neither predator removal conducted, suggesting a quite constant predation pressure.

Data collection and analysis

The study has been conducted in October 2002 and October 2003, corresponding to the end of the hot and dry season. As a consequence of the low rainfall, water surface was restricted to few sites (three water points in 2002 and only two in 2003), where we built some blinds and platforms to conduct observations from within 30 to 50 m on groups of animals coming to drink. In both years, we monitored each water point for 4 consecutive days from 0600 to 1800, on the 2nd and 3rd week of October (i.e. 2 weeks before the first rains in both years), following an identical procedure for comparative purposes.

Population density estimates

We estimated population density from the proportion of marked animals observed during the water point survey using the Petersen–Lincoln method (Bailey 1951) corrected for long-term application (Gaillard et al. 1986). We used a capture–mark–recapture (CMR) method (Lebreton et al. 1992), from the program MARK (White and Burnham 1999), to estimate probabilities of apparent survival (i.e. a compound of survival and emigration; Lebreton et al. 1992) and tested for various models (Table 1) to assess yearly variation in survival and resighting probabilities. We used Akaike's information criterion (AIC) to select the best model: the model with the smallest AIC value was retained as the best compromise between accuracy (low deviance) and precision (low number of parameters).

Population performance

Body condition is a sensitive and easily measured response of an animal to environmental variation, which is often taken as a measure of the nutritional status of the animal (Sinclair and Duncan 1972). Various indices of body condition have long been tested and used in African ruminants (Sinclair and Duncan 1972). We here used a visual body condition index (VBC), an easily and noninvasive measure that has proven to be a good integrative predictor of energetic status in impala (Dunham and Murray 1982; Gallivan et al. 1995). VBC of individuals was assessed from visual assessment of the animal's hindquarters, using criteria of progressive depletion of fat deposit following Riney (1960). Animals were assigned to one of two condition indices: fair (roundness or slightly angular appearance of rump and flank) or poor (side view of the tail and lumbar vertebrae, and the exterior line of the ischium, appear angular to extremely prominent). For consistency, all VBC measures were assessed by one observer only. To limit observation biases, care was taken to classify animals only from the side and only when standing on flat ground, since sunlight incidence and muscle solicitation while bending on a sand ridge for drinking appeared to affect body appearance, hence visual scoring (Gasaway et al. 1996).

Observations at a closer distance from blinds and platform allowed us to record the exact composition of all groups coming to drink (age and sex classes). Males were aged as juveniles (10 months), yearlings (22 months), and adults (>34 months) based on body and horn sizes. We cannot clearly distinguish yearling females at that time of the year based on body size, thus we considered only two classes for females (juvenile and adult). The lambing period of impala

Table 1. Selection among the capture–mark–recapture (CMR) models that we fitted.

Model	AIC	ΔAIC
Φ (*t+s*) *p*(.)	**866.78**	**0.00**
Φ (*t+s*) *p*(*s*)	867.40	0.62
Φ (*t×s*) *p*(.)	867.59	0.81
Φ (*t*) *p*(.)	878.61	11.83
Φ (.) *p*(.)	900.77	33.99

Note: Survival and resighting probabilities were modelled on an annual basis (from the introduction in 1999 up to 2003), successively testing for an effect of sex (*s*) on resighting probabilities (*p*), and of time (*t*) and sex (interactive (×), additive (+), and main effects) on survival probabilities (Φ) (model notation similarly follows Lebreton et al. 1992). (.) indicates that the resighting or survival probability was modelled independently of any sex or time classes. The best model with the smallest Akaike's information criterion (AIC) value is in boldface type.

is highly synchronized: females give birth to a single young and they can start conceiving on their 2nd year (Murray 1980; Fairall 1983). We estimated recruitment from the ratio of juveniles to adult females.

Impala are water-dependent tropical ungulates that drink on a regular basis when water sources are available. Observations recorded on several consecutive days at the same water points allowed us to measure the frequency of visit from a sample of marked animals (180 in 2002 and 64 in 2003): no marked animal was observed to visit a water point more than once a day (minimum visit interval of 26 h, mean of 49 h; N. Gaidet, unpublished data). We thus analysed each day of observation independently (including records of marked and nonmarked animals) to avoid repeated sampling of the same individuals. Moreover, impala showed a high fidelity to water points, as no marked individual was observed drinking at different water points during our monitoring (each water point being 5 km apart). We consequently pooled observations collected at different water points (three in 2002 and two in 2003), each considered to represent different subsets of the same population. We estimated population parameters based on 4-day replicates in each year.

We used the general linear model (GLM) method to analyse changes in body condition, with VBC score as a binary-dependent variable (good vs. poor) and year, sex, and age classes as fixed factors. We first fitted the most general model (i.e., VBC ~ sex + year + age + age × sex + age × year + sex × year + sex × age × year) that included the interactive effects among the factors age class, sex, and year, testing successively the third and second order interactions among factors, and then tested the main effect of individual factors.

We used a backward stepwise selection procedure with successive removals of interactions and factors. On average, 25% of marked animals were measured for a second occasion during 2 consecutive days of observation at the same water point. We used the generalized estimating equations method (GEE; Liang and Zeger 1986) on the selected model using the day of observation as a random factor to account for pseudoreplication problems (sensu Hurlbert 1984) and to check the reliability of the parameter estimates. As the parameter estimates remained unchanged when using or not the GEE method, we only provided results from the GLM method.

In addition, we measured the individual annual changes in body condition from a subset of marked individuals that were observed in October 2002 and controlled in October 2003. For the analysis of recruitment and sex ratio, we used a GLM approach on day samples to test the between-year differences. We also fitted a GEE including the day of observation as a random factor on the selected model to check the reliability of our estimates. As previously stated, the parameter estimates remained unchanged when using or not the GEE method, so we only reported results from the GLM method.

Results

Population density estimates

A maximum of 189 impala/day were observed during the water point monitoring in 2002, and 128 in 2003, with a large proportion being marked (41% in 2002 and 29% in 2003). From the various CMR models fitted, we selected the model with an additive effect of time and sex on survival probabilities and constant recapture probabilities (Table 1). Survival probabilities estimated were low (from 0.23 to 0.44 in males, and from 0.41 to 0.64 in females), but recapture was high and constant ($P = 0.73$, CV = 0.07, SE = 0.06). Estimates of population density indicated a marked reduction in density between October 2002 and October 2003, from 16.4 to 8.6 individuals/km^2 (Table 2).

Population performance

Body condition

Body condition was recorded for, on average, 107 animals/day in 2002 and 65 animals/day in 2003 (including marked and nonmarked animals), representing 20% and 24% of the total population size estimated, respectively. Including the three-way interaction among sex, age, and year (AIC = 732.32) or any two-way interactions among those factors (best model with AIC = 729.12) did not improve the fitting compared with the additive model (AIC = 727.60). From this model, we found support of our first prediction that body condition was much lower in 2002 than in 2003 (difference of 2.33 ± 0.23 on a logit scale, $P < 0.001$; Fig. 2). Contrary to our second and third predictions, but in support of our fourth prediction, the body condition of both sexes decreased with increasing age: from a mean value of 0.905 on a logit scale for juveniles, the body score tended to decrease in yearlings (difference of 0.192 ± 0.534 on a logit scale, $P = 0.72$) and decreased markedly for adults (difference of 1.474 ± 0.234 on a logit scale, $P < 0.001$).

Contrary to our fifth and sixth predictions, no between-sex difference occurred in body condition (difference of 0.057 ± 0.225 on a logit scale in favour of females, $P = 0.80$). The absence of any significant effect of interactions between year and sex, and between age and sex, led us to reject our fifth, sixth, and seventh predictions.
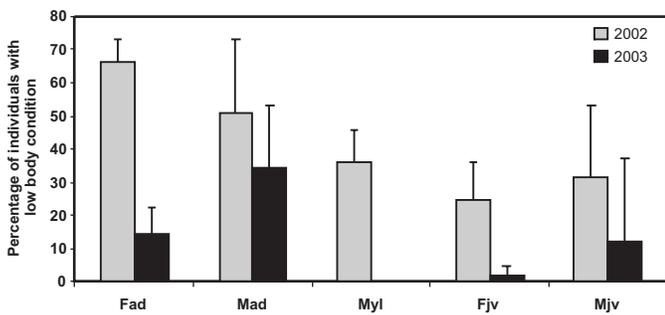
Marked animals that were observed both in October 2002 and controlled in October 2003 were mostly adult females. The analysis of individual change in body condition of these females ($n = 32$) supported results from the GLM analysis: the VBC had increased between 2002 and 2003 for a major-

Table 2. Between-year differences in density and population size of impala (*Aepyceros melampus*) in October estimated from CMR methods.

Year	Model	*n*	*m*	*M* est	*D* est	CV	*N*	*N* low	*N* up
2002	Φ (*t*+*s*) *p*	189	77	215	**16.4**	0.09	**524**	435	612
2003	Φ (*t*+*s*) *p*	128	37	81	**8.6**	0.13	**275**	202	347

Note: The best model (Φ (*t*+*s*) *p*) included a survival time- and sex-dependent and a constant capture probability. *n* corresponds to the total number of different impala contacted; *m* corresponds to the number of marked impala contacted; *M* est corresponds to the estimate of the total number of marked impala present in the population; *D* est corresponds to the density estimate, which is the number of impala per square kilometres; CV corresponds to the coefficient of variation of the density; *N* corresponds to the population size estimate; *N* low corresponds to the lower 95% confidence limit of population size estimate; and *N* up corresponds to the upper 95% confidence limit of population size estimate.

Fig. 2. Sex- and age-specific percentages of impala (*Aepyceros melampus*) with low body condition at high (2002) and low (2003) population densities (Fad, adult females; Mad, adult males; Fjv, juvenile females; Mjv, juvenile males).

Table 3. Individual changes in body condition of some marked adult female impala between October 2002 and October 2003.

Status	*n*	Percentage
Unchanged (poor)	7	21.9
Unchanged (fair)	7	21.9
Increased	18	56.3
Decreased	0	0.0

ity of these females, some had an unchanged VBC score, but no female experienced a reduction in VBC (Table 3).

Recruitment

The annual recruitment increased by 1.482 (±0.227) on a logit scale ($P < 0.001$), from 0.47 (SE = 0.10) in 2002 to 0.81 (SE = 0.22) in 2003. This result supported our eighth prediction of an increase in population recruitment when population density declines. The sex ratio in 10-month-old juveniles was skewed toward females, suggesting a higher mortality in male juveniles. But contrary to our nineth prediction, we found the same proportion of male juveniles in both years (0.42, SD = 0.02 in 2002; 0.40, SD = 0.04 in 2003; $P = 0.42$), suggesting that the sex ratio was not increasingly biased at high density.

Discussion

Our results provided support for only three out of the nine predictions (Table 4). As expected, body condition increased when population density decreased, adult males showed lower body condition than juveniles or yearling males, and the recruitment of the population increased when population density decreased. On the other hand, we did not find any evidence for sex-specific variation in body condition according to age or to changes in density.

Population density changes

Impala is one of the most common ungulates found in the southern Africa savannah (Skinner and Smithers 1990), but local density varies greatly according to habitat and surface-water availability, a key resource in semi-arid ecosystems (i.e., from >150 individuals/km² in the Zambezi alluvial

woodland and floodplain, Zimbabwe (Jarman 1972; Dunham 1994), to 1.6–3.2 individuals/km² in the veld woodland with limited water supply of Lupande Game Management Area in Zambia (Jachmann 2002)). The population we studied was at relatively high density in 2002 (16 individuals/km²) compared with the the population in adjacent areas of the study site (3.4 individuals/km²; Gaidet et al. 2003) and to other mopane woodlands of Southern Africa (Bourgarel et al. 2002; Jachmann 2002).

In 2002, our study population of impala experienced a rapid increase in the biomass of the herbivore community, following the introduction of groups of other ungulate species. However, considering the low soil nutrient availability of the study area (Biodiversity Project 2002) and the mean annual rainfall, the total biomass of medium-sized to large herbivores estimated in the ranch after translocation (1100–1400 kg/km²) was quite far from the maximum carrying capacity estimated for savannah ecosystems, even when we account for the absence of megaherbivores (Fritz and Duncan 1994).

The impala population showed a drastic reduction in density between 2002 and 2003. This population decline is unlikely related to an increase in adult mortality (Gaillard et al. 2000), as supported by the few carcasses that we discovered in the ranch ($n = 11$) despite an intensive field-work all year long. After their first introduction within the ranch (1999 and 2000), impala experienced 3 years of very high rainfalls (1000–1300 mm/year; Fig. 1). The year 2002 was their first year with a below-mean rainfall, and most of their usual water sources in the ranch consequently dried out at the onset of the dry season (July 2002), in particular the water point where impala were initially introduced and kept for several weeks for acclimatization. As a result, groups of impala may have escaped by jumping through the fence driven by their will to find new water points, despite the provision of water at two artificial water points.

Table 4. Summary of the predictions tested on performance response of an impala population to changes in density for a given pattern of annual rainfall.

Prediction	Outcome
Body condition	
(1) Positive influence of a decrease in density on individual condition	Supported
(2) Juveniles have a lower body condition than adults at a given density	Rejected
(3) Between-age differences are more pronounced at high population density	Rejected
(4) Adult males have a lower body condition than yearling males	Supported
(5) Adult males have a lower body condition than adult females	Rejected
(6) Between-sex differences in body condition of adults are larger at high than at low population density	Rejected
(7) Juvenile males are more influenced by the decrease in density than juvenile females	Rejected
Recruitment	
(8) Population recruitment increases from high to low population density	Supported
(9) Female-skewed sex ratio at 10 months of age is higher at high than at low population density	Rejected

Body condition

The strong between-year difference that we found in individual body condition, irrespective of age or sex, supports our first prediction that body condition should decline at high density and is consistent with the range quality hypothesis (Sæther and Heim 1993; Gaillard et al. 1996). During the dry season, the depletion of resource quality and quantity have led animals to mobilize their fat reserves. At high density, increased competition for restricted resources should force the animals to exhaust more rapidly their body reserves (Sæther and Heim 1993). Despite a lower rainfall and possible delayed effects of the previous drought on soil water content, impala maintained a higher body condition in the dry season of 2003 than in 2002. Such a negative impact of high density on body condition and body mass is consistent with studies of Holarctic species of large mammals (Fowler 1987; Sæther 1997). While evidence of density dependence assessed by time series analyses of counts or biomass (in impala, giraffe (*Giraffa camelopardalis* (L., 1758)), and Burchell's zebra, Owen-Smith and Ogutu 2003; Burchell's zebra and giraffe, Georgiadis et al. 2007), as well as an association between decreased performance and low food supply (white-eared kob (*Kobus kob* (Erxleben, 1777)), Fryxell 1987; red lechwe (*Kobus leche* Gray, 1850), Williamson 1991; blue wildebeest, Mduma et al. 1999) have been reported at the population level in some tropical ungulates, our study provides a first study case reporting evidence of direct density-dependent responses of body condition at the individual level in a tropical large herbivore.

Contrary to our prediction, adults of both sexes were more susceptible to food shortage than juveniles, suggesting that nutritional stress related to reproduction has a greater impact on body condition than energetic requirement for growth. This finding supports the relative greater sensitivity of adults to variation in food reported in white-eared kobs (Fryxell 1987). However, for impala, lactation coincides with the wet season (Dunham and Murray 1982) so that juveniles cannot benefit from milk supply throughout the dry season. Therefore, our results contradict previous studies that reported lower fat reserves in younger impala (Hanks et al. 1976; Dunham and Murray 1982; Gallivan et al. 1995). The poor body condition that we reported for adults at both high and low densities may indicate that the lower density in

2003 was still high enough to limit access to resource, especially during a severe dry season. This interpretation is supported by the density in our study being consistently higher than the densities currently reported for impala in this type of habitat (see above). The low primary production associated with harsh climatic conditions during our study period could have led to nutritional stress.

As expected from our fourth prediction, adult males had lower body condition than yearlings. Such a lower body condition in territorial males compared with younger bachelor males has been reported for impala at the end of the rut in May (van Rooyen 1993). During the rut, breeding males experienced a severe decline in fat reserves, associated with a reduction in the time spent feeding for territorial tenure and mating activities (Jarman and Jarman 1973; Murray 1980). A second short rut period has been reported in September on rare occasions, which could cause body reserve depletion in males in October. However, we did not observe any sexual behaviour in September 2002 (N. Gaidet, personal observation). After the rut, male body condition deteriorates until August and then steadily increases up to April (Anderson 1965). However, during severe dry seasons, male condition can deteriorate until November (Howells 1974). During our study period, food restriction might have affected adult males that seem to have not yet recovered in October from nutritional requirements of their previous reproduction.

We found no evidence for sex-specific responses of body condition to environmental changes. Our predictions that males should sustain higher energetic demands for growth or maintenance than females owing to their larger body size (Demment and Van Soest 1985) was, therefore, not supported. A higher susceptibility of growth to environmental variation in young males than in young females has often been reported in highly dimorphic temperate ungulates (red deer, Clutton-Brock et al. 1982 and Bonenfant et al. 2002; white-tailed deer (*Odocoileus virginianus* (Zimmermann, 1780)), Leberg and Smith 1993), but not in weakly dimorphic ones (western roe deer (*Capreolus capreolus* (L., 1758)), Gaillard et al. 1996). The moderate sexual size dimorphism (1.33) of impala might account for similar responses of body condition between young males and females. An absence of between-sex differences was already reported for juveniles and yearlings (Gallivan et al. 1995),

but in adult age classes, males were generally reported to be more susceptible to starvation than females (Gallivan et al. 1995; Bourgarel et al. 2002). In our study, we compared body condition at the end of the dry season, when adult males and females were not facing the same energetic demands for reproduction. Critical period of the reproductive cycle occurs in May–June for males (rut), and between December and February for females (late pregnancy and early lactation), hence female condition remains generally relatively high throughout the dry season (Anderson 1965; Howells 1974; Dunham and Murray 1982; van Rooyen 1996). However, in poor years with restricted food resources, the nutritional demand for gestation might lead to an earlier decline in female body condition (van Rooyen 1996).

Recruitment

As expected, the recruitment increased when density decreased. However, changes in annual recruitment as assessed by calf to cow ratios are difficult to interpret (Bonenfant et al. 2005) because variation in juvenile mortality cannot be distinguished from variation in fecundity.

Proportions of adult males recorded (0.18 and 0.14 in 2002 and 2003, respectively) were lower than reported in natural populations (0.39, Jarman 1972; 0.35, Fairall 1983), but was within the recommended ratios proposed to increase the production of impala populations without insemination failure (1 male for 5–10 females, Fairall 1985; van Rooyen 1994). The sex-selective harvesting thus should have not influenced the conception rate, hence the recruitment.

Pregnancy rate of female impala older than 2 years of age are usually high (e.g., 100% of 254 females and 98.4% of 131 females in the Zambezi valley in 1969 and 1970, respectively, Smith 1970; 95% of 860 females in Kruger NP, South Africa, Fairall 1983) and fairly constant under a wide range of climatic conditions (Fairall 1983). Yearlings have a lower and more variable conception rate (50% of pregnancy, on average, ranging from 0% to 87%; Fairall 1983). Although we were not able to distinguish yearlings from adult females, changes of yearling fecundity alone are unlikely to account for the marked change of annual recruitment that we reported between years of contrasting density.

Survival of juveniles is the most sensitive demographic parameter to density changes in populations of large herbivores (Gaillard et al. 1998, 2000). A high mortality has been reported for impala during the first months of life (Jarman and Jarman 1974). We suggest that the between-year changes in recruitment occurred throughout a density-dependent response of juvenile survival. A between-sex difference in juvenile mortality has been reported in impala (Dasmann and Mossman 1962). However, we found similar sex ratios in both years despite marked changes in density, suggesting that increasing density affected young males and females similarly.

Concluding remarks

Our study supports the hypothesis that food-resource variation controls for population dynamics of impala under constant and moderate predation pressure as reported previously for other tropical ungulates (Sinclair et al. 1985; Owen-Smith 1990; Mduma et al. 1999). As population dynamics of wild large herbivores are likely driven by the interactions between density and climate, the influence of population density on forage competition is expected to occur only when resources are limited (Owen-Smith 1990, 2006; Gaillard et al. 1996).

Even though the role of predation on the population decline could not be totally ruled out, a marked change in predation pressure was unlikely to account for observed changes in performance of impala because changes of predation pressure can hardly account for the marked between-year difference in body condition within 1 year. Moreover, marked changes of predation pressure cannot account for the drastic increase in recruitment that we observed within 1 year in the absence of a noticeable change in predator presence on the ranch.

In environments where changes in food production depends on highly variable climatic fluctuations, density dependence has to be interpreted for a given rainfall pattern. Our impala population might have displayed no density dependence during a period of above-average rainfall with the same population density. Furthermore, the annual distribution of rainfalls may also influence the performance of impala. The amount of rains during the early season should influence vegetation growth, and especially the nutritional quality of grass, whereas the occurrence of occasional rains during the dry season should reduce the constraint of water availability. The timing of rainfall was very similar in both years of study, with no rain during the dry season. The distribution profile showed higher rainfall in early season in the year of high density (420 mm in October 2001 to January 2002 vs. 200 mm in October 2002 to January 2003), suggesting a relatively higher resource availability in the year when impala had lower performance. Patterns of rainfall during the study period were thus conservative regarding our results because we should have observed even greater density-dependent responses in condition and recruitment with the same rainfall amount and distribution between years of contrasting density.

The concomitant density-dependent change that we observed in individual body condition is consistent with the hypothesis of food-driven recruitment, indicating that our population was close to the food-resource ceiling (sensu Gasaway et al. 1996). This is consistent with the high density level of our study population relative to standard densities of impala in similar habitats.

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