Effects of annual rainfall and habitat types on the body mass of impala (*Aepyceros melampus)* in the Zambezi Valley, Zimbabwe

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Abstract

Body mass is often considered as a good indicator of body condition of individuals in ungulates, hence of their fitness, and thus, may be used as an index to monitor the status of populations subject to harvesting schemes. Here, we report the influence of annual rainfall (a proxy for primary production) and habitat on the body mass of impala in a population cropped for meat in a communal area of Zimbabwe. We analyzed the data from 2 contrasted years for rainfall, in two different habitats. In the good year (i.e. high annual rainfall) impala were heavier than in the poor year, and adult females seemed to be less affected than males by variation in primary production. We show that adult males were suffering from a seasonal decrease in body mass, supposedly linked to the rut, particularly in good habitat Overall, the habitat effect appeared to be dominated by the rainfall effect, and this may be due to the very high animal densities in the good habitat, i.e. fast resource depletion. Our results also suggest that males (juvenile and adult) are more susceptible to changes in food resource abundance and quality than females, which supports previous studies on sexually dimorphic and polygynous species.

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Résumé

On considère souvent que la masse corporelle est un bon indicateur de la condition physique chez les ongulés, et donc de leur bon état général; on peut donc s'en servir comme index pour contrôler le statut des populations qui font l'objet d'un programme de prélèvements. Nous rapportons ici l'influence des chutes de pluies annuelles (qui sont liées à la production primaire) et de l'habitat sur la masse corporelle des impalas d'une population où l'on prélève des animaux pour la viande, dans une aire communale au Zimbabwe. Nous avons analysé les données de deux années contrastées pour les chutes de pluies, dans deux habitats différents. La bonne année (c.-à-d. fortes chutes de pluies), les impalas étaient plus gros que la mauvaise année, et les femelles adultes semblaient moins affectées que les mâles par les variations de la production primaire. Nous montrons que les mâles adultes subissaient une réduction saisonnière de leur masse corporelle, sans doute liée au rut, et surtout dans les bons habitats. Partout, l'effet de l'habitat semble être surpassé par l'effet des chutes de pluie, et ceci est peut-être dû à la très forte densité des animaux dans le bon habitat, c.-à-d. un rapide épuisement des ressources. Nos résultats suggèrent aussi que les mâles, juvéniles et adultes, sont plus sensibles que les femelles aux changements dans l'abondance et la qualité des ressources alimentaires, ce

qui confirme des études antérieures sur les espèces dimorphiques et polygames.

Introduction

In most vertebrate populations studied so far, body mass of individuals is a major determinant of their potential reproductive success (Clutton-Brock, 1988; Newton, 1989; Gaillard *et al.,* 2000). Thus, variation in body mass is expected to affect markedly population growth rate so that a good knowledge of sources of variation in body mass is required for a better understanding of population dynamics, and thereby, for a suitable management plan. Previous studies on ungulates often focused on temperate species (e.g. Saether, 1985 on moose; Gaillard *et al.,* 1996 on roe deer; Loison & Langvatn, 1998 on red deer). In addition to obvious differences due to age and sex, environmental conditions, either density-dependent (Fowler, 1987; Gaillard *et al.,* 1996) or driven by climatic variation (Saether, 1985; Gaillard *et al.,* 1996; Loison & Langvatn, 1998) have been shown to affect mean yearly body mass in several ungulate populations. Those populations are often mainly limited by their food resources (White, 1978; Skogland, 1985; Fowler, 1987; Merrill & Boyce, 1991). Such a pattern might also occur in populations of African ungulates (Sinclair, 1975; Owen-Smith, 1990; Mduma, Sinclair & Hilborn, 1999), although predation may be locally the main limiting factor (e.g. Gasaway, Gasaway & Berry, 1996). The notion of food shortage for ungulates in the tropics is determined both by the primary production and their ability to store reserves during the rainy season and the rate at which these reserves are utilized during the dry season. Food limitation is also reflected by the close correlation found to occur between biomass densities of African ungulate communities and aboveground primary production or annual rainfall (Coe, Cumming & Phillipson, 1976; Fritz & Duncan, 1994). Annual rainfall is, thus, a good predictor of primary production across the globe (Lieth, 1975; Lauenroth, 1979), especially in sub-Saharan Africa (Le Houérou & Hoste, 1977).

In this study, we explored the relationship between body mass, annual rainfall and habitat type in a medium-sized ungulate, the impala *Aepyceros melampus* (Lichtenstein). We also incorporated other sources of variation in body mass of herbivores, such as sex and age, in the analyses. We used data from the first 2 complete years of records on the impala cropping operations of the 'Nyama -Faune

et Village' project, specifically implemented to provide meat for rural communities in the Zambezi valley, Zimbabwe (Feron *et al.,* 1998; De Garine & De Garine-Wichatitsky, 1999). The management of such projects, based on large cropping operations, requires the calculation of annual quotas, which in turn requires knowledge of the status and dynamics of the cropped species.

We tested a set of five predictions: (i) we expect to find heaviest individuals in years with highest rainfall (i.e. greatest primary production) because of the close correlation relating food resource and individual body mass. (ii) Impala should be heavier at the beginning of the dry season (cool dry season), when their resource abundance and quality are still high, than at the end of the dry season (hot dry season) when the senescence of plant tissues decreases the quality of the resources and most of the plant standing crop has been consumed. However, this 'season' effect should be weaker in the best habitats (i.e. those with greatest amount of resources) than in the poorest ones. (iii) We expect that female impala should distribute themselves following the Ideal Free Distribution (Fretwell & Lucas, 1970) and consequently have similar mass in all habitats, because they are not territorial and are free to change habitats within their home range (Jarman, 1979; Murray, 1982a). Females should, therefore, occur at higher densities in the habitat with high primary production than in the habitat with low primary production, so that per capita intake rate, a proxy for fitness, should be equal in the two habitats (Fretwell & Lucas, 1970). (iv) Adult males are more constrained by social dominance, particularly during the mating period (from April to June). The dominant males have access to the females that they manage to keep within their territories and should try to select the preferred habitats, where densities of females are highest (Murray, 1982b). We, thus, expect the dominant males to monopolize the best habitats, hence constraining the distribution of the other subdominant or subordinate males (Jarman, 1979). Territorial males have thicker necks than nonterritorial males, and may be heavier at the onset of the breeding season, but the difference does not remain at the end when they have used up most of their body reserves (Jarman, 1979). We, thus, expect to find heaviest males in the best habitats at the beginning of the mating season (i.e. in the cool dry season). (v) The impala is a polygynous ungulate sexually dimorphic in size (60 kg for males vs. 45 kg for females, Estes, 1995) with males being territorial during the rut (April-June in southern Africa, Jarman,

1979; Murray, 1982b; Estes, 1995). Because of the high costs of reproduction sustained by territorial males (van Rooyen, 1993), we expect that males would be more susceptible than females to variation in the quality and quantity of the resources.

Materials and methods

Site

The Nyaminyami District, on the shores of the lake Kariba (Zimbabwe) has one the highest densities of impala in the country. This is one of the major reasons why the 'Nyama - Faune et Village' project of the Centre de Coopération International de Recherches Agronomiques pour le Développement (section Élevage et Médecine Vétérinaire Tropicale) was implemented in this area in 1993, within the framework of the Communal Areas Management Program for Indigenous Resources (CAMPFIRE) programme, because its main objectives were to organize community-managed sustainable cropping schemes in order to provide these remote rural areas with meat. Within the Nyaminyami District, our study was carried out in the Omay Communal Area, which is characterized by two very distinct habitats: (i) the lake shores and (ii) the inland woodlands. The lake shores habitat is a very open savanna, with an average visibility of 250 m, and is composed of two main types of grasslands: floodplain grasslands *(Digitaria eriantha, Panicum maximum)* and *P. repens* grasslands. The inland habitat is a mosaic of Miombo *(Julbernadia globiflora, Brachystegia boehmii* and *B. spiciformis)* and Mopane *(Colophospermum mopane)*

woodlands and savanna woodlands, with an average visibility of 100 m (Murindagomo, 1997). The lake shores are considered to be a very favourable habitat. The flood-plain grasslands have a digestible herbage primary production on average 1.5 times higher than the inland woodland habitats, and the *P. repens* grasslands benefit from the progressive decrease of the lake water level, which allows grass production during the hot dry season on the areas that were submerged after the Rainy season (Taylor, 1985). This is thought to be a major reason why ungulate densities remain very high in this area through-out the year, in addition to the permanent availability of surface water (Taylor, 1985).

In Zimbabwe, the year is classically divided into three seasons: a Rainy season from November to April, a cool dry season from May to July, and a hot dry season from August to October (Fritz, De Garine-Wichatitsky & Letessier, 1996). In the Nyaminyami District, the average annual rainfall over the last 18 years was 789.1mm; with a coefficient of variation among years equal to 29.9% (Fig. 1). It has been argued that for ecosystems with high interannual coefficient of variation (CV ≥ 30%), animal populations may be driven by the stochasticity of climatic events (i.e. density-independent processes), but particularly for areas receiving less than 500 mm annual rainfall (Ellis, Coughenour & Swift, 1993). The annual rainfall average in our study site is well above this threshold value, therefore, it is likely that animal populations will be driven by density-dependent processes, and annual rainfall is likely to be a good indicator of the quality of the year in terms of availability of food resources.
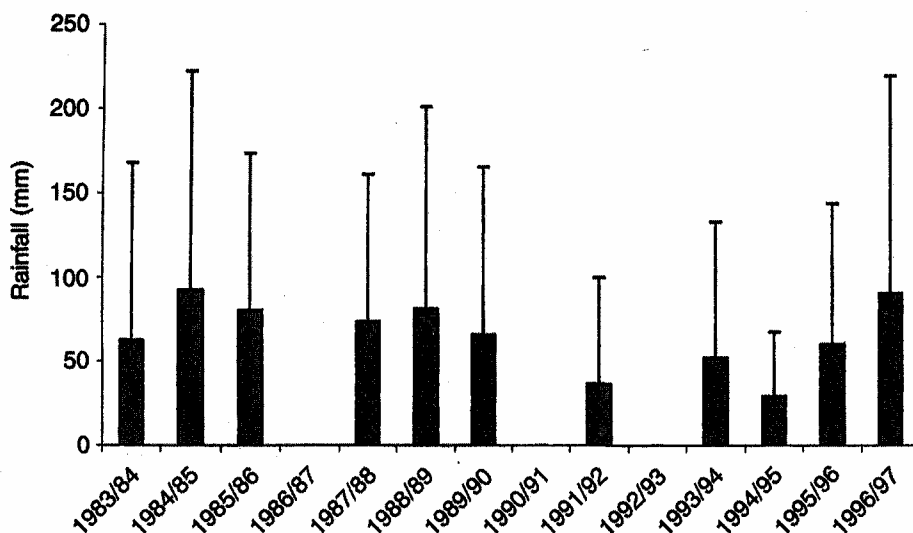

Fig 1 Yearly rainfall (mean monthly values +1 SD) in Siakobvu (Nyaminyami district) between 1984 and 1998 (from the data collected by the National Meteorological Services of Harare). The average annual rainfall over this period was 789.1 mm (SD = 236.35 and CV = 29.9)

Database

For each animal, records included the following information: the date, the place (GPS coordinates), the carcass mass, the sex and the age (three classes: juveniles between 0- and 1-year-old, subadults between 1- and 2-years-old and adults older than 2 years). Age was estimated by the Veterinary Services Inspector who was in charge of the operation, using horns (Bothma, 1989) and body morphology. It was fairly easy to classify both juvenile males and females and adult and subadult males, but it was more difficult to distinguish adult and subadult females (both being hornless). In this case, age was estimated from the body size. The error can be important because a female adult at the end of the dry season can appear thinner or smaller than a subadult female at the beginning of the dry season. Consequently, only adults and juveniles have been considered for this analysis. We are aware that among the individuals classified as adult females, there might be some subadults.

A scale was used to weigh the carcass of the animal after removal of the head, the lower limbs, the gut and sexual organs. This was defined as the carcass mass (Feron *et al.,* 1998). Hereafter, 'mass' will refer to the carcass mass as defined above.

The database contains 1174 individuals (Fig. 2). The number of individuals hunted during the rainy season was relatively low, thus, only the cool dry season and the hot dry season have been used for the comparison between seasons. The database comprised only 2 years for which data were complete and large enough in the two dry seasons (1994/95 and 1995/96). A dry season is directly related to the preceding rainy season that starts in November the year before, hence what we call year 1994/1995 starts in November 1994 and ends in October 1995. The annual rainfall was 348.5 mm for 1994/1995 and 720.4 mm for 1995/1996, which allowed us to classify 1994/1995 as a poor year and 1995/1996 as a good year according to primary production.

Statistical analyses

Our analyses followed the principles of an experimental design with one dependent variable (mass) and five factors with several modalities: sex (males and females), age (adults and juveniles), year (1994/1995 and 1995/ 1996), season (cool dry season and hot dry season) and habitat (lake shores and inland). We have used General Linear Model Univariate procedure (SPSS Inc, 1998) to analyse and test null hypotheses about the effects of factors on the means of a single dependent variable, investigating both third- and second-order interactions among factors, as well as the main effects of individual factors.
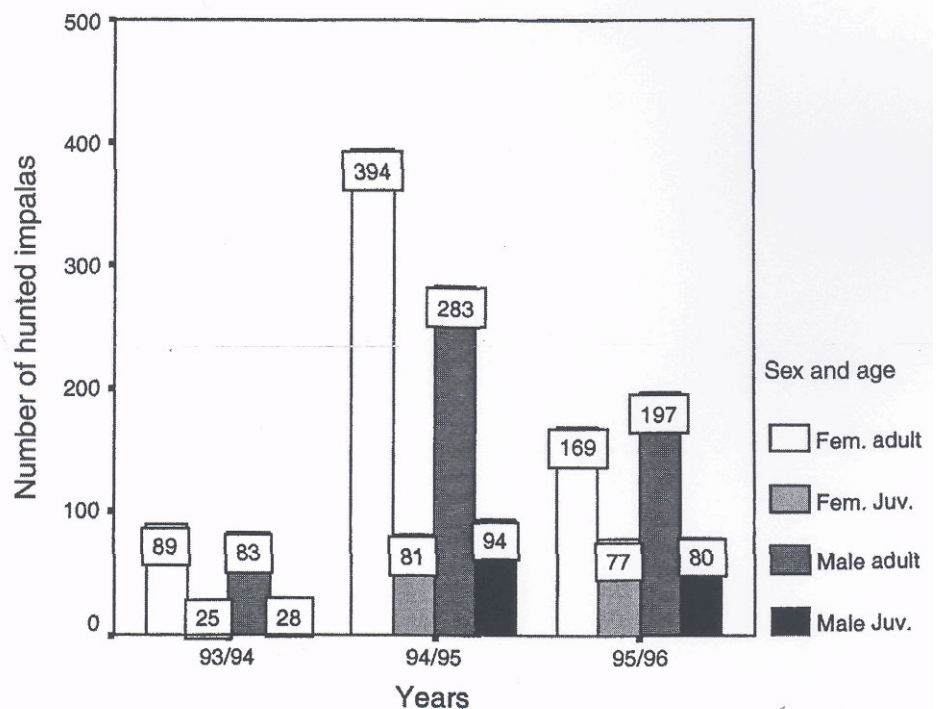

Fig 2 Number of impala hunted each year per age and sex classes

This statistical procedure can be used with a small number of individuals (Sherrer, 1984), but requires the assumption of homoscedasticity to be fulfilled. The data were $\log_{10}$-transformed to meet the requirement of our parametric data analysis.

Results

Adult females

No adult female was shot in the inland habitat during the hot dry season 1995/1996. We, therefore, tested the effects of year and season on lake shores habitat only (first ANOVA) and we tested the effects of season and habitat on year 1994/1995 only (second ANOVA).

From the first ANOVA, we did not find any significant second-order interaction between effects of year and season ($F_{1,335} = 0.110$, $P = 0.740$). There was no effect of season ($F_{1,336} = 0.280$, $P = 0.597$). Only the year effect was significant ($F_{1,336} = 9.093$, $P = 0.003$). The average body mass of adult females was higher during the good year 1995/1996 (mean 22.0 kg, SD = 2.729, $n = 77$) than during the poor year 1994/1995 (mean 20.5 kg, SD = 3.629, $n = 262$).

From the second ANOVA, we did not find any significant interaction or main effect involving the factors habitat and season (all $P > 0.273$). Mean body mass of female impala averaged 20.4 kg (SD = 3.548, $n = 346$).

Juvenile females

We did not find any significant third- ($F_{1,108} = 0.106$, $P = 0.745$) or second-order interaction among the effects of year, season and habitat (all $P > 0.134$). Conversely to adult females, we did not find any significant difference of mass between the 2 years ($F_{1,112} = 0.006$, $P = 0.936$), the two seasons ($F_{1,112} = 0.760$, $P = 0.385$) or the two habitats ($F_{1,112} = 1.904$, $P = 0.170$). Mean body mass of juvenile female impala averaged 13.2 kg (SD = 3.203, $n = 116$).

Adult males

We did not find a significant third ($F_{1,296} = 0.000$, $P = 0.987$) order interaction among the three factors. However, the second order interaction between the effects of year and season was significant ($F_{1,297} = 9.884$, $P = 0.002$), whereas the second order interactions between year and habitat ($F_{1,297} = 0.029$, $P = 0.866$) and between season and habitat ($F_{1,297} = 0.677$, $P = 0.411$) were not significant. This suggests the seasonal effect differed between years (i.e. according to the quality of the rainy season). For the poor year 1994/95 (low rainfall), body mass during the cool dry season (mean 26.2 kg, SD = 4.868, $n = 126$) was higher than that measured during the hot dry season (mean 22.9 kg, SD = 4.287, $n = 94$), whereas there was no between-season difference in mass during the good year 1995/1996 (mean 25.0 kg, SD = 3.930, $n = 59$ in the cool dry season versus mean 25.5 kg, SD = 2.839, $n = 25$ in the hot dry season).

Juvenile males

We did not find any significant interactions among the factors year, season and habitat (all $P > 0.623$), but both the main effects of season and year were significant ($F_{1,124} = 8.817$, $P = 0.004$, and $F_{1,124} = 5.047$, $P = 0.026$, respectively). The weight of juvenile males was greater in the good year 1995/1996 than in the poor year 1994/1995, and was greater in the hot dry season than in the cool dry season (good year: mean 14.7 kg, SD = 2.452, $n = 34$ in the cool dry season versus mean 16.6 kg, SD = 4.835, $n = 10$ in the hot dry season; poor year: mean 13.3 kg, SD = 2.527, $n = 31$ in the cool dry versus mean 15.4 kg, SD = 4.146, $n = 53$ in hot dry season). That the juvenile males were still growing may account for these results.

In summary, out of our five predictions, three appeared to be supported (i, iii, v) one was partly supported (ii) and the other one (iv) was rejected (Table 1). Such results were consistent with the hypothesis of a close

Table 1 Outcome of the tests of the five predictions about ecological variation in body mass of impala according to age and sex classes

Predictions	Outcome of the test
(i) Individuals are heavier in years with high rainfall	Supported
(ii) Individuals are heavier in cool dry seasons	Supported for adult males only
(iii) There are no differences in the body mass of females between habitats	Supported
(iv) Males are heavier in the best habitat at the beginning of the rut (i.e. in the cool dry season)	Rejected
(v) Males are more susceptible than females to changes in food resources	Supported

relationship between primary production and population dynamics in tropical ungulates.

Discussion

We found a year effect in three of the four analyses we performed. The first of our five predictions on the effects of the annual rainfall (i.e. the amount of primary production) on the body mass of impala was thus supported. This is consistent with the hypothesis of limitation of tropical ungulate populations by their food resources (e.g. Sinclair, 1975, 1989).

We did not find any effect of habitat in the multifactorial analyses, and only found the expected effects of season for adult males, with a higher mass during the cool dry season than during the hot dry season. These results only weakly support our second prediction that impala should be heavier at the beginning of the dry season. The absence of effect for juveniles (both males and females) might be accounted for by the fact they are still growing. Indeed, juveniles are still gaining mass during both the cool and the hot dry seasons. However, the absence of effect for adult females supports our hypothesis of between-sex differences in the relationship between primary production and body mass (predictions iii, iv, v).

The fact that we did not find any effect of habitat for females supports our third prediction that females distribute themselves following the Ideal Free Distribution and therefore have similar food intakes and ultimately body mass and fitness in both habitats (Fretwell & Lucas, 1970). Males and females were not individualized during these dry season counts. However, the annual censuses carried out during 2 years showed great differences in impala densities between the two habitats. In September 1997, the average density for the lake shores habitat was more than 20 times higher than that of the woodland habitats (120 vs. five individuals km^{-2}, Murindagomo, 1997). Similar results were obtained in May 1998 (135 vs. five individuals km^{-2}, Bourgarel, 1998). The highest density found in the best habitat is consistent with the Ideal Free Distribution theory, but this marked between-habitat difference in density is likely to happen over a short time scale only because primary production on the lake shores does not match such differences in densities. Local increase of impala group size following local increase in food availability has been described previously in the Sengwa Wildlife Research Area (Dunham, 1979). If males are highly territorial on the lake shores

and, as is often the case, females are more numerous than males in impala populations (60% female, Jarman, 1979), it is likely that the high density in the lake shores habitat is mainly due to the increasing density of females. This would also be consistent with our third prediction that female densities should be higher in the best habitat.

The absence of any effect of habitat on the mass of adult males was surprising with regard to our fourth prediction. A closer investigation showed that for the poor rainy year, cool dry season mass of males in the lake shores habitat tended to be higher than the mass of males in the inland habitat, although not significantly. However, the habitat types seemed to play a role in the poor year, with a seasonal change of mass for adult males in the lake shores habitat, but not inland. The decrease of mean body mass was thus greater in the best habitat in poor years, which contradicts the second part of our second prediction. This may be explained by an increase in competition through food resource depletion at high densities, particularly at the end of the dry season when the availability of surface water may temporarily increase densities on a daily basis. Density-dependent responses have been frequently reported in populations of tropical ungulates (e.g. Sinclair, 1977 on buffalo; Mduma *et al.,* 1999 on wildebeest). In addition, in years with drought (i.e. poor grass production), browse provides a good alternative food resource in the inland wooded habitats. The absence of any effect or trend during good years also suggests that the difference in the quality of habitats was reduced by the quality of the rainy season.

Our results show that juvenile males, but not females, were affected by the quality of the rainy season. Adult males reacted to variation in the quality of the year as adult females did, but were also affected by seasonal changes in food resource, probably due to their territorial and fighting behaviour during the rut (i.e. high energy expenditures). These between-sex differences support our fifth prediction that males, in general, are more susceptible to variation in resource abundance than females, as in most polygynous and dimorphic ungulates (e.g. Clutton-Brock, Albon & Guinness, 1987; Owen-Smith, 1993).

Our approach to factors influencing impala body mass and potentially population dynamics, was based on data collected from shot animals. This obviously has the bias associated with these types of operations, but because cropping schemes were aimed at producing meat and not trophies, the size bias was certainly reduced. Further-

more, our results are fairly consistent with predictions drawn from ecological theories, which suggests that the use of these types of data is robust and may be used as indicators of population status when implementing monitoring schemes of ungulate populations subject to intensive management operations.

Acknowledgements

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