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Herbivore population regulation and resource heterogeneity in a stochastic environment

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Abstract. Large-mammal herbivore populations are subject to the interaction of internal density-dependent processes and external environmental stochasticity. We disentangle these processes by linking consumer population dynamics, in a highly stochastic environment, to the availability of their key forage resource via effects on body condition and subsequent fecundity and mortality rates. Body condition and demographic rate data were obtained by monitoring 500 tagged female goats in the Richtersveld National Park, South Africa, over a three-year period. Identifying the key resource and pathway to density dependence for a population allows environmental stochasticity to be partitioned into that which has strong feedbacks to population stability, and that which does not. Our data reveal a density-dependent seasonal decline in goat body condition in response to concomitant density-dependent depletion of the dry-season forage resource. The loss in body condition reduced density-dependent pregnancy rates, litter sizes, and pre-weaning survival. Survival was lowest following the most severe dry season and for juveniles. Adult survival in the late-dry season depended on body condition in the mid-dry season. Population growth was determined by the length of the dry season and the population size in the previous year. The RNP goat population is thereby dynamically coupled primarily to its dry-season forage resource. Extreme environmental variability thus does not decouple consumer resource dynamics, in contrast to the views of nonequilibrium protagonists.

Key words: African semi-arid grazing system; capital-income breeder; consumer resource dynamics; density dependence; dry season; environmental stochasticity; equilibrium; key resource; life history strategy; nonequilibrium; rangeland debate; wet season.

INTRODUCTION

Density dependence and environmental stochasticity are both important determinants of large-herbivore population dynamics (Coulson et al. 2000, 2004, Sæther et al. 2007). Recent developments in stochastic demographic modeling show that environmental variability can profoundly influence estimates of population growth rates, and hence our ability to predict future population sizes (Boyce et al. 2006, Sæther et al. 2007). The challenge to population ecologists is thus to establish how internal physiological constraints and external resource and environmental conditions interact, which is of particular relevance in an increasingly variable world (Stenseth et al. 2002, Boyce et al. 2006). Consequently, focus has shifted toward determining the pathways by which density dependence operates in a population (Bonenfant et al. 2009). This facilitates identification of the vital rates and spatiotemporal contexts that interact most strongly with environmental variability to shape the population trajectory (Sæther 1997, Illius and O'Connor 1999, 2000).

Variation in an environment has temporal and spatial components, which both vary in their patterning and degree of heterogeneity (Boyce et al. 2006). Temporal variability has been associated with an increase in herbivore density dependence, most probably due to more frequent per capita forage deficits (Wang et al. 2006, 2013). In contrast, spatial heterogeneity can buffer populations against temporal variability by increasing the asynchrony in plant phenology, allowing herbivores to access a greater proportion of the forage resource while in its most nutritious state (Wang et al. 2006, 2009, Hobbs and Gordon 2010) and dispersing them before they critically deplete these preferred resources (Walker et al. 1987, Owen-Smith 2004). The central role of forage

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availability in determining individual body condition and thus survival and reproduction (Parker et al. 2009), and the fact that climate can play a substantial role in determining vegetation productivity, has led to an alternate viewpoint that weather effects on food availability, and not density dependence, determine herbivore abundance (White 2008). Extreme environmental variability has also been proposed to decouple consumers from their resource base, and effectively consign the population to a nonequilibrial state (Ellis and Swift 1988, Behnke et al. 1993; but see Illius and O'Connor 1999). However, these arguments overlook that the adequacy of forage can only be assessed relative to population size, and thus while climatic variation can considerably modify forage abundance, the population response to these changes will be contingent on its size (Caughley and Gunn 1993, Berryman 2004).

The "key resource" concept explicitly links population dynamics to the forage resource via individual body condition (Illius and O'Connor 1999, 2000). The key resource for a population is the resource subset that determines the size of the population vital rate that exerts most influence on the population trajectory (i.e., the key factor sensu Varley and Gradwell 1960, Scoones 1991, Illius and O'Connor 1999). Identifying the key resource for a population requires estimating the relative importance of life stage specific contributions of fecundity and mortality to shaping the population trajectory, and mechanistically linking variation in these vital rates to changes in resource availability. Isolating the key resource for a population is thus central to determining the pathway to density dependence. Environmental stochasticity can then be partitioned into that which strongly affects the availability of the key resource, and hence population stability, and that which does not (Illius and O'Connor 2000).

Mortality linked to resource availability when plants are seasonally dormant has been identified as the critical vital rate for a wide range of species, including ibex (Sæther et al. 2002, Jacobson et al. 2004), reindeer (Aanes et al. 2000, Tyler et al. 2008), kob (Fryxell 1987), and wildebeest (Sinclair et al. 1985, Mduma et al. 1999). However, Gaillard et al. (2000) argue that the large temporal variability of recruitment parameters generally make them more influential to determining large-herbivore population size. Time lags in the depletion or replenishment of fat reserves generate delays in the population response to seasonality (Sæther 1997), and needs to be accounted for when isolating the key resource. A species' position on the capital–income breeder continuum strongly influences the extent of these seasonal carryover effects on fecundity rates (Jönsson 1997, Kerby and Post 2013). Capital breeders develop large fat reserves during the plant growth season, buffering them against resource limitation when plants are dormant, and thus display pronounced seasonal carryover effects. In contrast, income breeders have more limited fat reserves and are more responsive to resource deficits during gestation.

Here we explore the consequences of extreme environmental variability for the dynamics of a goat (*Capra hircus*) population living in the desert landscapes of the Richtersveld National Park, South Africa. We monitored body condition, fecundity, and survival rates of >500 uniquely identifiable individuals over three years, and related variation in these parameters to environmental conditions, forage availability, and animal density. Goats are income breeders, and we thus expect their recruitment and survival rates to respond to dry-season forage availability. We first establish whether a pathway to density dependence can be identified, and then explore the interaction between environmental stochasticity and consumer resource coupling.

METHODS

Climate and landscape

The Richtersveld National Park (RNP) is on the South Africa–Namibia border, 100 km inland from the Atlantic Ocean (Fig. 1A). Mean annual precipitation is very low and extremely variable, with 114 mm/yr (CV = 58%) recorded at Koeroegabvlakte from 1996 to 2009. The winter wet season typically comprises 2–3 frontal rainfall events occurring between June and August. Annual rainfall decreased over the three years of this study: 176.2 mm in 2007, 123.4 mm in 2008, and 62.2 mm in 2009. Summers are hot (average minimum, 17.5°C to maximum, 33.0°C, with >45°C recorded in all months from November to April) with very low humidity, while winters are cooler (9.7°C to 24.0°C). The rugged mountainous desert landscape is intersected by broad gravel plains that taper into dry river beds leading down to the perennial Orange River (Fig. 1B). In years with good winter rainfall, this otherwise brown and dusty landscape is transformed into a lush carpet of flowering annuals among the scattered and revitalized low, perennial shrubs (July to September). The Orange River, fed by summer rainfall regions over 1000 km to the east, supports a thin ribbon of riparian woody vegetation that remains green year-round. However, moderate flooding in the mid-dry season (February to April), in response to far-off rainfall, often produces a brief flush of new growth (see Plate 1 and Appendix A for study site photos).

Nomadic pastoralism

Nama pastoralists have a long history in the region, and persist under the harsh conditions by migrating with their goats and sheep to the plains in the central RNP following winter rainfall (July to September). Births typically occur in August/September, following conception in April/May. Herds are then moved to the Orange River riparian zone in spring (October), because the animals require frequent access to drinking water as the plains forage dries out (Hendricks et al. 2005*b*). Herds are frequently relocated along the Orange River as the summer dry season progresses. In drought years, herds

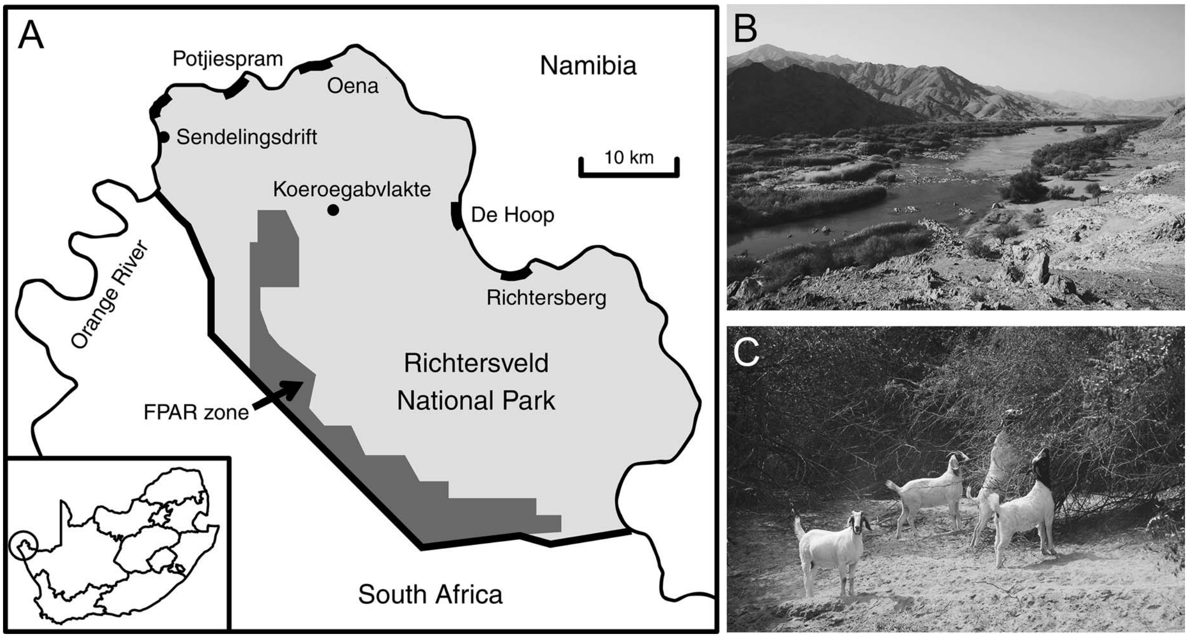

FIG. 1. (A) Location of the Richtersveld National Park, with the Orange River forming the northern and eastern border of the park. The dark-gray fraction of photosynthetically active radiation FPAR zone is the region of reliable FPAR values used to provide an index of plant growth conditions across the whole RNP. The five dark blocks situated along the river are the areas where browse availability was monitored. Photo (B) shows the Orange River at the De Hoop study site, and photo (C) shows goats browsing in the riparian zone (photo credit: G. P. Hempson).

remain along the Orange River year-round (Hendricks et al. 2005*b*). Here we consider the plains as the wet season range (WSR) for RNP herds, and the region within 5–10 km of the Orange River as the dry-season range (DSR). It is important to emphasize that herd movement decisions are based on what is perceived to be best for optimizing animal body condition (Hendricks et al. 2004), and should thus be a reasonable representation of natural seasonal migration patterns.

Overall mean animal densities are low in the RNP (<0.15 animals/km^2). The number of herds in the RNP typically ranges from 12 to 18, with a median herd size of $\sim$350 animals. Herds can be composed exclusively of goats, but may be up to 50% sheep (average: $\approx$15%). The five study herds comprised $\sim$50%, 70%, 80%, 100%, and 100% goats. However, sheep are likely to have little impact on the results we present here due to dietary differences with goats (Hendricks et al. 2005*a*), particularly in the riparian zone where goats rely primarily on browse. Management strategies maximize the number of adult females (Hendricks et al. 2004). A herd of 350 animals may have as few as five adult males, because juvenile males are typically sold when aged 3–5 months (November/December, i.e., early dry season). The sale of virtually all juvenile males has limited influence on the analyses that we present, because density estimates are based on individuals older than one year, sales occur after the period considered for the preweaning survival rate analysis and that of main lactational demand, and because we only tagged females. A small amount of local sales and slaughter occur year-round (mostly sheep; Hendricks et al. 2004; G. Hempson, *personal observation*). Eight study goats (0.016%) were slaughtered over the three-year study period.

Data collection

Forage availability.—Browse canopy volume in the riparian zone of the Orange River was monitored at five locations during 10 sampling trips from February 2008 to October 2009 (Fig. 1A). These sites were frequently used by pastoralists. Six 50×20 m plots were located at 500-m intervals along the river at each study site. Browse canopy volume below 2 m was estimated by measuring the length, breadth (both to nearest 50 cm), and height (10 cm intervals) of sections of tree canopy (leaf material) within each plot, and multiplying this volume by an estimate of the percentage of maximum potential leaf density (adapted from Walker 1976). These data were aggregated to provide a species-level estimate of browse canopy volume at 10 cm height intervals for each plot.

FPAR (fraction of photosynthetically active radiation) imagery was obtained from the NASA database[7] and used to assess general foraging conditions across the RNP ($\sim$1-km^2 pixel, 8-day time interval). A 200-km^2 region (Fig. 1A: FPAR zone) was used to provide a general index of foraging conditions from 2000 onwards,

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[7] http://modis.gsfc.nasa.gov/data

as much of the remainder of the RNP is too sparsely vegetated to produce meaningful FPAR values.

Individual level goat data.—Tagged female goats were weighed and monitored at 2–3 month intervals from February 2007 to October 2009 ($n = 15$). An initial group of 45 females, consisting of 15 juveniles (<1 year), 15 yearlings (1–2 years) and 15 adults (>2 years), was fitted with a numbered green ear tag in each of five study herds in February 2007. These 225 marked individuals were added to by marking their female offspring (usually at 2–4 months old). Additional individuals were included as required to supplement diminished life stage specific sample sizes arising from mortalities. A total of 502 goats were marked in the RNP during the course of the study.

Goat mass was estimated using a portable walk-on scale (UWE Scales, Xindian City, Taiwan, 0.2-kg precision). Weighing sessions took place early in the morning before herds began foraging. We assessed reproductive status (not pregnant, early/late pregnant, lactating) when conducting each weighing, and asked herders for details on births during the sampling trip interval (i.e., the number and sex of offspring, date of birth, whether they were still alive, fetus aborted, etc.). These data were judged to be unreliable for some herds in 2007, and litter size and pre-weaning survival analyses were thus restricted to 2008 and 2009. Herders were also questioned about the fate of marked goats that were absent at the time of weighing (e.g., cause of death, sale, slaughter, missing, etc.). Where no explanation was available, an animal that subsequently did not reappear was recorded as having died from an unknown cause during the first interval in which it had gone missing. These unknown causes comprised 75% of the potential mortality cases. Here we treat these unknowns as natural mortality (hereafter "mortalities"), because: (1) herd management is aimed at maximizing goat herd size (Hendricks et al. 2004), (2) sheep are preferentially slaughtered for household consumption, (3) sales are largely limited to 3–5 month old males, and (4) the green ear tags used in the study made migration between herds easily detectable. Nonetheless, we acknowledge that this assumption may not hold in all instances, but expect this observation error to be randomly distributed across the study period.

Herd level data.—Herd position and size were used to estimate goat densities in the RNP. Weekly herd positions ("stockpost" locations) were recorded for the period from August 2006 to November 2009 by the RNP field rangers. Herd censuses have been conducted at 3–6 month intervals since 1995, with individuals classified as being younger or older than 12 months. Weekly herd size estimates were made assuming linear changes in herd sizes between censuses. Weekly maps of goat densities were created by assigning the size of a herd (individuals >12 months only) to a 2.5-km radius (average daily foraging range [Hendricks et al. 2005*b*]) around its current stockpost location, with animal numbers summed for any area of overlap among neighboring herds. Weekly goat density estimates for each herd were expressed as the mean number of goats per hectare within 2.5 km of the stockpost (animals per hectare). Ideally, animal densities should be expressed relative to the available forage, but this was not possible due to the lack of a single RNP-wide measure of forage availability. However, for the riparian browse availability analyses, goat density estimates were refined by expressing animal numbers relative to the area of riparian tree cover ($\text{animals}\cdot\text{ha}_{(\text{Tree})}{}^{-1}$) calculated from Google Earth imagery. Density surfaces were prepared using ArcInfo 9.3 (ESRI) and the adehabitat package (Calenge 2006) in R version 2.14.1 (R Development Core Team 2011).

Analyses

Model fitting and selection.—All analyses were performed in R (version 2.14.1; R Development Core Team 2011). General linear mixed models (GLMMs) were fitted using the lme4 package (lmer function; identity or logit link [Bates and Maechler 2010]). Model selection was based on the Akaike Information Criterion (AIC); only the best models are presented. Significance values for GLMMs were calculated using the languageR package (pvals.fnc function; nsim = 10 000 [Baayen 2011]), with variables considered significant at the 95% confidence level. Generalized linear models were fitted (GLMs) where candidate random effect terms did not account for variation in the data.

Riparian browse availability.—Browse availability of the five most common species (≈80% total canopy volume) in the riparian zone was modeled in two steps to accommodate the zero-inflated data set (Fletcher et al. 2005): (1) as a binomial response variable with browse either present (1) or absent (0); and (2) as the $\log_e$ of browse volume (in cubic meters) for the cases where browse was present. Browse was scored present if the plot-level canopy volume estimate within each 10-cm height interval was >5% of the maximum canopy volume recorded at that level for that species. Goat density (preceding four weeks), year, and ease of forage accessibility due to goat physical stature (canopy height classes: <1.3 m, 1.3–1.7 m and >1.7 m) were fitted as fixed effects. Species, height interval, site, plot, and sampling trip were included as random effects (see Appendix B for details).

Goat body condition.—Body mass (in kilograms) was modeled to determine the effect of individual status and environmental conditions on goat body condition. Reproductive status, age in months (as a quadratic term, to allow for changes in growth rates from juveniles to adults and potential senescence), and their interaction were fitted as fixed effects to account for individual status on body mass. Goat density (preceding four weeks), season ("wet season and early to mid-dry season" or "mid- to late-dry season"), year, and the full set of interactions were fitted as fixed effects. Herd and individual identities were fitted as random effects (see Appendix C for details).

Goat vital rates.—Recruitment was separated into three components and analyzed using binomial GLMs (logistic link): (1) pregnancy rate ($0 =$ not pregnant, $1 =$ pregnant), (2) litter size ($0 =$ singleton, $1 =$ twins or triplets), and (3) pre-weaning survival ($0 =$ died, $1 =$ survived to first sampling trip after birth). Age (months; quadratic), goat density (either a 0 to 4 week, 5 to 8 week, or 9 to 12 week time lag), year, and season (as previously described) were fitted in each full model. Litter size ("singleton" or "twin/triplet") was included in the pre-weaning survival model. Note that litter size and pre-weaning survival analyses were restricted to 2008 and 2009 (see previous discussion and Appendix D for details)).

Survival was analyzed at the life stage level for each herd, using a two-step approach to accommodate the zero-inflated data set (Fletcher et al. 2005): (1) as a binomial response where mortality was either zero (0) or greater than zero (1) ("mortality occurrence"), and (2) as the $\log_e$ of the daily mortality rate for cases where mortality was recorded ("mortality extent"). Life stage, year, season, and density were fitted as fixed effects, and herd and cohort size categories fitted as random effects. Subtracting the product of the probabilities of mortality occurrence and extent from 1 provided an estimate of annual survival. Mid- to late-dry season adult mortalities (April to August) were analyzed to test for evidence for causal linkages between dry season forage resource depletion and associated body condition on survival. A binomial GLM was fitted with individuals scored as 1 if they survived through to August that year and 0 if they died during the late-dry season interval. The proportional change in body mass from February to April (mid-dry season), goat densities (March to May), reproductive status (April) and year were fitted in the full model (see Appendix E for details).

Population size.—RNP goat population census data from 2000 to 2007 (cf. 2007–2009 seasonal data) were analyzed by multiple linear regression to assess annual population growth in response to: (1) time spent in the DSR that year, and (2) population size at the end of the preceding year. Time spent in the DSR was estimated for the period between 1 January and 30 September each year based on FPAR data and a threshold value at which herds typically migrated to the WSR (see Appendix F). Population size estimates were obtained from the last census in that year (range: August to November), and variation includes herd migration to and from areas beyond the RNP borders. FPAR data are only available from 2000 onwards, and a full census of the RNP goat population was not conducted in 2008.

RESULTS

Our results move sequentially along the hypothesized pathway to density dependence: first we examine if forage resource bottlenecks occur, whether these have consequences for individual body condition, and thereafter whether there are subsequent impacts on fecundity and survival rates and hence the population trajectory.

Riparian browse availability

Goats depleted riparian browse resources in a density-dependent manner, with the most easily accessible forage being consumed first, and with depletion occurring more rapidly in the more severe dry season. Browse presence (Fig. 2A) and volume (Fig. 2B) in the riparian zone was determined by goat density: presence model (PA), $\chi^2_3 = 22.07$, $P < 0.01$; volume model (V), $\chi^2_3 = 75.47$, $P < 0.001$; forage accessibility, PA, $\chi^2_4 = 204.15$, $P < 0.001$; V, $\chi^2_4 = 112.49$, $P < 0.001$); year, PA, $\chi^2_1 = 4.67$, $P < 0.05$; V, $\chi^2_1 = 13.68$, $P < 0.001$; and the interaction between year and forage accessibility, PA, $\chi^2_2 = 13.17$, $P < 0.01$; V, $\chi^2_2 = 9.99$, $P < 0.01$ (Appendix B). The probability of browse being present, and the volume of browse when present, both decreased in response to higher goat densities, and were also lower in parts of the canopy more easily accessible to goats. Browse availability was lower in 2009, which was a drier year than 2008 with a longer dry season. The interaction between browse accessibility and year shows that browse depletion was more severe in 2009 than in 2008 at all canopy levels, and was most pronounced low down in the canopy (Fig. 2A). There was a shallower absolute decline in browse volume with increased goat densities at each canopy level in 2009 than in 2008, as would be predicted by a constant fractional offtake rate, but lower browse availability in 2009 (Fig. 2B). The difficulty that goats had in utilizing browse above 1.7 m is evident in the shallow absolute decline in browse volume above this height, despite the high browse volume. Density-dependent browse depletion by goats means that this resource will be most limited toward the end of the dry season and in years with longer dry seasons and greater goat population sizes.

Goat body condition

Body mass was determined by an animal's state (age, $\chi^2_{10} = 3496.2$, $P < 0.001$; reproductive status, $\chi^2_{12} = 1453.0$, $P < 0.001$), and prevailing environmental factors (density, $\chi^2_6 = 100.1$, $P < 0.001$; season, $\chi^2_6 = 106.4$, $P < 0.001$; interannual differences, $\chi^2_8 = 240.0$, $P < 0.001$; Appendix C). Body mass increased with age (with evidence of a decline in body mass in the oldest animals [Fig. 3A]), and through pregnancy (lowest during lactation and when not pregnant). Changes in body mass due to reproductive status increased with age class. Density had a negative effect on body mass during the mid- to late-dry season in all three years of the study, being strongest in 2009 and weakest in 2007 (Fig. 3B). Outside of this period of a priori predicted forage limitation, body mass was positively related to density in 2007 and 2008, but negatively related to density in 2009. Animals of the same age weighed less in 2009 than in 2007 or 2008, for all ages (Fig. 3A). Similarly, for all years, animals weighed less during the mid- to late-dry season than during the rest of

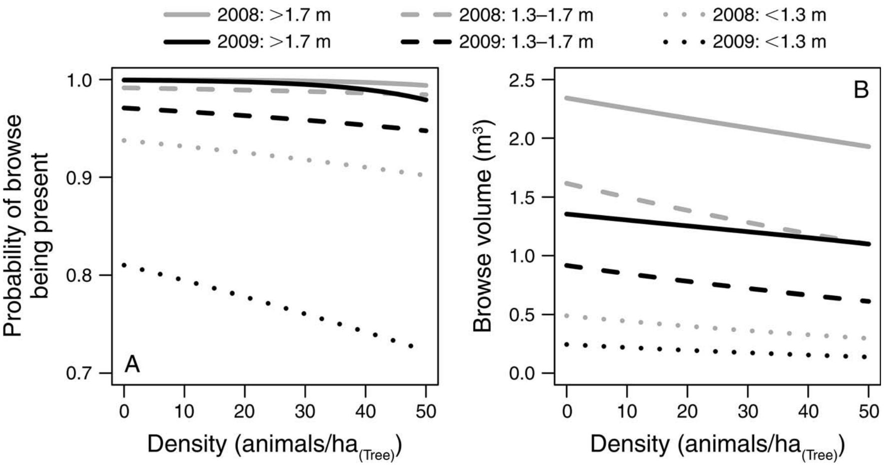

FIG. 2. Predicted plot-level change in browse availability in response to foraging by goats at different densities. (A) The probability (at >5% level) of browse being present or depleted. (B) Where browse was present, the average volume of browse that remained. Goat densities were calculated relative to hectares of tree cover (ha$_{(\mathrm{Tree})}$) rather than land area. See *Methods: Analyses: Model fitting and selection* for model details.

the year once state variables had been accounted for. Goat body condition thus tracks riparian browse depletion in a density-dependent manner as the dry season progresses, with animals regaining condition during the wet and early dry season.

Fecundity

Declines in goat body condition toward the end of the dry season negatively affected recruitment, as predicted for an income breeder. Pregnancy rates are highest at this time of the year, and individuals experiencing greater competition for forage resources had lower pregnancy rates, smaller litter sizes, and produced offspring less likely to survive the pre-weaning phase. This is evident from the negative effect of animal density on the number of pregnant individuals ($\chi^2_1 = 12.0$, $P < 0.001$), their litter size ($\chi^2_1 = 5.9$, $P < 0.05$), and subsequent offspring pre-weaning survival ($\chi^2_1 = 5.1$, $P < 0.05$; Fig. 4; Appendix D). Pregnancy rates were most influenced by animal densities in the period immediately prior to our assessment of reproductive status, suggesting that recent foraging conditions were most influential. Litter size was most sensitive to animal densities during the last trimester of the gestation period, and pre-weaning survival rates to animal densities around the time of birth. Age influenced the probability of an animal being pregnant ($\chi^2_2 = 19.5$, $P < 0.001$) and the litter size it would carry to term ($\chi^2_2 = 37.0$, $P < 0.001$),

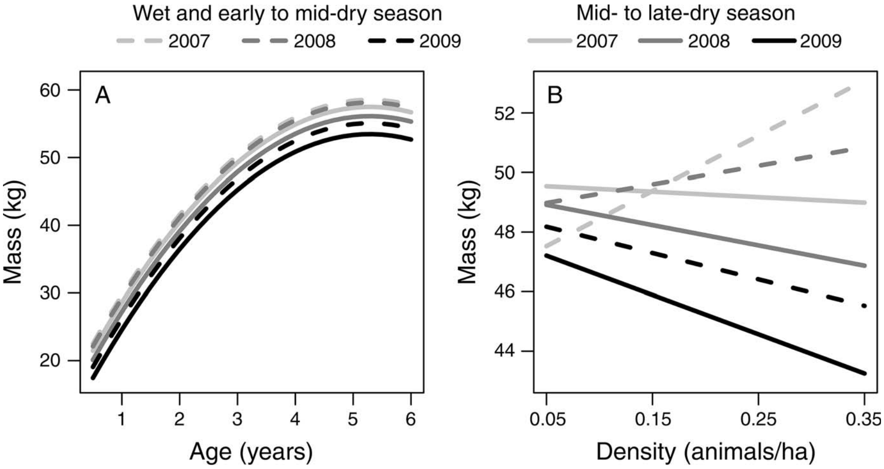

FIG. 3. Predicted goat body mass variation in response to (A) age, and (B) animal densities. In each case, data are shown separately for each year of the study and for the wet and early to mid-dry season and the mid- to late-dry season. In (A), mass estimates are shown for nonpregnant animals at a density of 0.2 animals/ha. In (B), mass estimates are for a three-year-old nonpregnant animal. See *Methods: Analyses: Model fitting and selection* for model details.

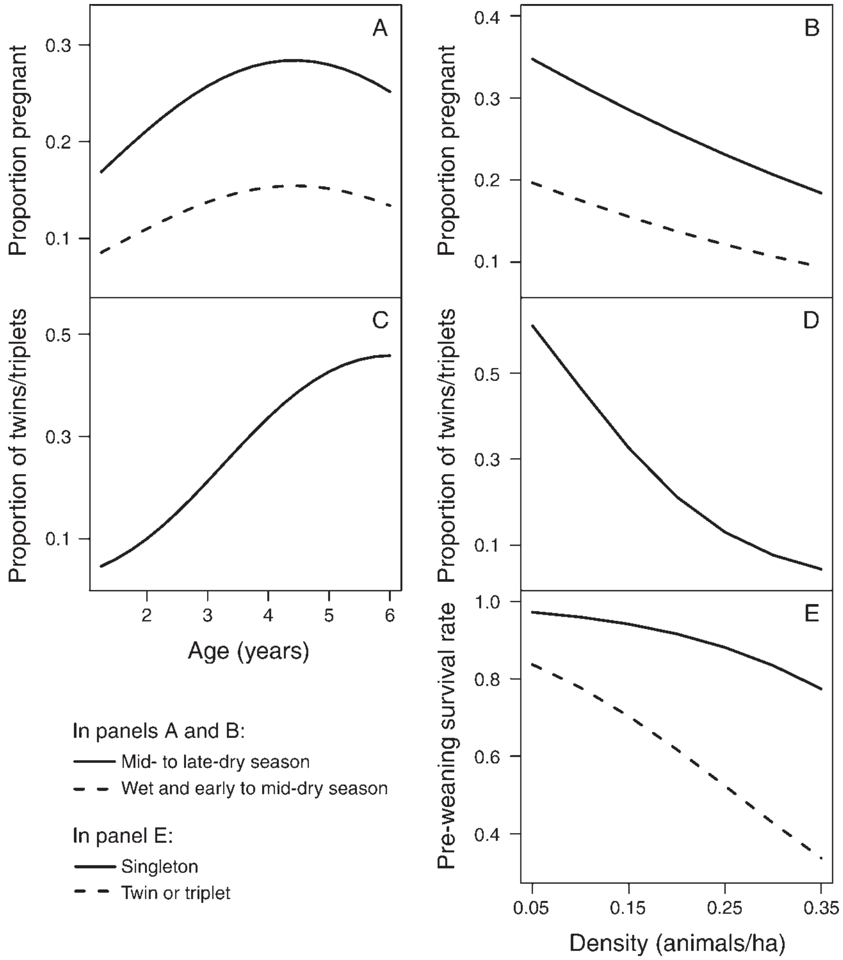

FIG. 4. Fecundity (proportion of females pregnant) in response to (A) age, and (B) animal density, distinguishing the wet and early to mid-dry season from the mid- to late-dry season. Litter size is shown as a function of (C) age, and (D) animal density. In panel (E), pre-weaning survival rates are shown in response to animal density, distinguishing singletons from twins or triplets. In (A) and (C), estimates are shown at a density of 0.2 animals/ha. In (B) and (D), estimates are shown for a three-year-old animal. See *Methods: Analyses: Model fitting and selection* for model details.

while an effect of season was observed on pregnancy rates ($\chi_1^2 = 55.3$, $P < 0.001$) but not on litter sizes. The number of pregnant individuals peaked in 3–5 year old animals during the mid- to late-dry season (Fig. 4A), and litter sizes were highest in 4–6 year old animals (Fig. 4C). There was no effect of maternal age or season on pre-weaning survival; however, there was a strong influence of litter size ($\chi_1^2 = 25.2$, $P < 0.001$), with twins and triplets showing lower survival probabilities than singletons (Fig. 4E). Year effects were not retained in any of the models. Overall, annual recruitment is closely linked to body condition in the late dry season, which in turn is a consequence of the extent of riparian browse depletion.

Survival

Survival patterns broadly matched those of dry-season forage resource bottlenecks and associated declines in body condition. Mortality occurrence and extent gave a similar picture across years (occurrence [*O*], $\chi_2^2 = 10.0$, $P < 0.01$; extent [*E*], $\chi_2^2 = 24.4$, $P < 0.001$) and life stages (*O*, $\chi_2^2 = 6.7$, $P < 0.05$; *E*, $\chi_2^2 = 7.4$, $P < 0.05$), but there was no clear evidence for density or season effects. Annual survival rates were lowest in 2009 and for juveniles (Fig. 5A; Appendix E), and did not differ between yearlings and adults. Adult survival rates over the late-dry season were lower for individuals that lost mass during the mid-dry season ($\chi_1^2 = 7.6$, $P < 0.01$), and were lowest in the long 2009 dry season ($\chi_2^2 = 6.0$, $P = 0.05$; Fig. 5B; Appendix E). Mid-dry season reproductive status was retained in the best model ($\chi_2^2 = 9.9$, $P < 0.01$), but animal density was not. Due to the lack of predators in the study system, these survival patterns largely highlight periods where animals are unable to meet their energetic demands, and further establish the pathway from density-dependent browse depletion and body condition loss to effects on demographic rates that shape the population trajectory.

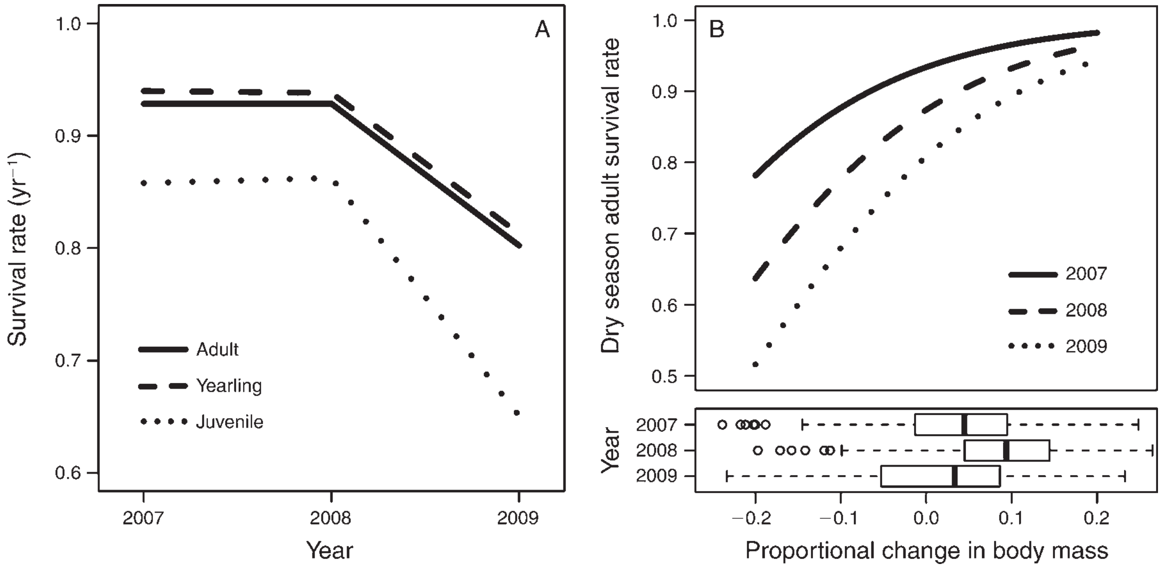

FIG. 5. (A) Annual survival rates for juvenile, yearling, and adult goats in each year of the study. (B) Predicted adult goat survival rates over the mid- to late-dry season (April to August) in response to body mass change during the mid-dry season (February to April; upper panel). The range, inter-quartile, and median of proportional change in body mass in each year are shown in the lower panel; the open circles are outliers. See *Methods: Analyses: Model fitting and selection* for model details.

Population size

Interannual variation in goat population size was strongly related to both the goat population size at the start of the dry season ($F_{1,5} = 24.45$, $P < 0.01$) and the estimated number of days that a herd spent in the DSR between January and September that year ($F_{1,5} = 33.06$, $P < 0.01$; Appendix G). The population size trajectory is traced from 2000 to 2007 in Fig. 6. The marked increase in 2006 (bottom left point, exceeding the +3000 animals contour) is due to both high recruitment and immigration rates. The RNP goat population was projected to decrease in both 2008 and 2009.

DISCUSSION

Our detailed analyses of the mechanisms connecting resource availability to population dynamics reveal clear evidence of density-dependent population regulation in a highly stochastic environment. The extreme variability of conditions in our study system ranks it among those where one is least likely to observe consumer–resource coupling, yet a careful analysis of the sensitivity of appropriate demographic and life history characters to spatial and temporal variation provides incontrovertible evidence for this density-dependent regulation. We thus firmly reject the hypothesis that climatic variability decouples consumer–resource dynamics and causes population trajectories to be determined in a truly density-independent manner (Ellis and Swift 1988, Behnke et al. 1993, White 2008). The key to understanding this consumer–resource coupling is the identification of the critical resource associated with life history transitions, and not to be distracted by the apparent superabundance of other resources.

Pathway to density dependence

Goats in the RNP show a clear density-dependent seasonal decline in body condition as competition-mediated depletion of the dry-season browse resource progresses. This forage bottleneck occurs as females

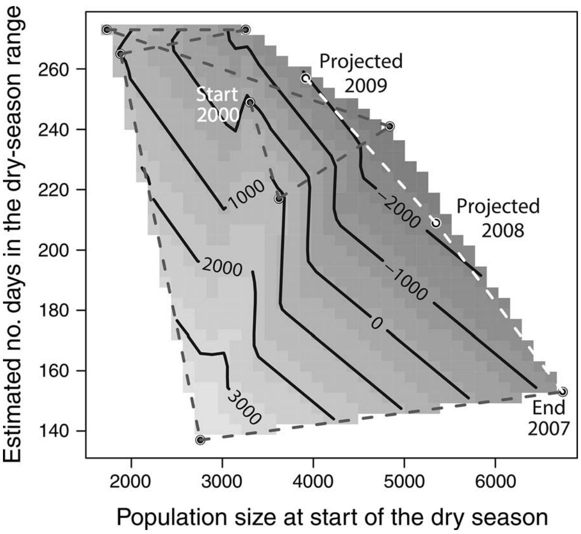

FIG. 6. Contour plot showing the predicted change in the RNP goat population size (values shown on contour lines) in response to population size at the start of the dry season and the estimated number of days spent in the dry-season range in that year. Observed changes for 2000 to 2007 are plotted as dark points, and linked by the dark dashed line. Projected population sizes for 2008 and 2009 are indicated by small white circles and linked by the white dashed line. See *Methods* for further details.

PLATE 1. Goats prior to setting out foraging in the mountainous interior region 10 km south of Potjiespram, Africa. At far left, the crayon markings on the individual's back indicate that it was weighed that morning. Photo credit: G. P. Hempson.

enter the most energetically demanding phase of the reproductive cycle, and, being income breeders, the extent of resource deficits soon have proportionate negative impacts on recruitment rates. Our data suggest that body condition, and hence dry-season forage depletion, is also a major determinant of mortality rates for all life stages. However, density dependence in survival rates may only occur once a threshold density has been exceeded (i.e., possibly only in 2009), as suggested by Owen-Smith (2006), and is seldom demonstrated in adult large-mammal herbivores (Festa-Bianchet et al. 2003). Body condition losses due to dry-season forage resource deficits are thus projected onto the population growth rate via effects on recruitment and survival rates. By contrast, body condition data suggest that there is little competition for resources in the wet season, and that despite regaining the same maximum body condition in the 2007 and 2008 wet seasons, strong differences in dry-season body condition were evident in the subsequent 2008 and 2009 dry seasons. The contribution of carryover effects of wet season body condition into the dry season are thus minimal, as predicted for income breeders (Jönsson 1997). The RNP goat population is thus dynamically coupled to its dry-season forage resource, which constitutes the key resource, but is only weakly coupled to its wet season forage resource, if at all.

Nonequilibrium and density independence

Isolation of the pathway to density dependence for the RNP goat population clearly refutes the view that extreme environmental variability decouples consumer–resource dynamics (Ellis and Swift 1988, Behnke et al. 1993), and that food limitation alone (i.e., independent of population densities) determines population size (White 2008). Rather, while environmental variability can indeed play a large role in determining the amount and duration of reliance on the key resource, the population remains coupled to the riparian browse resource, and the ratio of population size to the availability of this resource determines the population trajectory. The population thus persists in a state of disequilibrium (sensu Illius and O'Connor 1999), with variation in key resource availability and population size continuously redefining the equilibrium population size that would be achieved under constant conditions, and which acts as a moving attractor for population size (Fig. 6 and Caughley and Gunn 1993, Illius and O'Connor 1999). The fact that the system is not usually at numerical equilibrium is thus itself not evidence for the weakness of consumer–resource coupling (Illius and O'Connor 1999). Furthermore, it is crucial to recognize that the strength of consumer–resource coupling is heterogeneous in space and time across the system, and thus somewhat ironically, it is the existence of dynamic coupling with a spatiotemporal subset of resources that potentiates weak or even decoupled consumer–resource dynamics in other parts of the system. This caveat is vitally important, because the potential for large consumer–resource mismatches are greatest where coupling is weak, and hence of periodic extreme depletion and possible degradation of resources (Illius and O'Connor 2000).

Environmental stochasticity and key resources

Temporal variation that impacts the availability and duration of reliance on the key resource will increase the role of density in regulating the population (Wang et al. 2006, 2013) by increasing the frequency of large mismatches between population size and riparian browse availability. Greater temporal variability of the key resource will also reduce mean population size, because populations decline more rapidly in poor years than they can recover in good years (Illius and O'Connor 2000, Davis et al. 2002). Variability in the duration of the dry season, by determining the severity of the dry-season forage depletion bottleneck, is thus a crucial component of environmental stochasticity in tropical systems, most notably via drought-induced population crashes (Fryxell 1987, Walker et al. 1987). By contrast, spatial resource heterogeneity buffers populations against variability (Illius and O'Connor 2000, Wang et al. 2006, 2009, Hobbs and Gordon 2010). In the RNP, seasonal migration into the wet season range allows riparian browse availability to recover in the absence of herbivory, which may limit critical depletion of these resources in at least some years (Owen-Smith 2004). The asynchronous local rainfall-determined pulse of annual forb growth and the flood-induced leaf-out of riparian tree species will also confer stability on goat population dynamics where this spatiotemporal resource heterogeneity is exploited (Wang et al. 2006, 2009, Hobbs and Gordon 2010).

Large-mammal herbivore life history implications

The interaction between the temporal variability of an environment and the position of a large-mammal herbivore on the capital-income breeder continuum may hold important general implications when determining its key resource. Recruitment rates are more sensitive to environmental conditions than survival rates, yet changes in survival rates tend to elicit greater impacts on the population trajectory (Gaillard et al. 2000, Bonenfant et al. 2009). In highly variable environments, the incidence of adult mortality during the winter or dry season is more frequent, and should be important for both capital and income breeders. This suggests that in highly variable systems the key resource will tend to be forage reserves used outside of the plant growth season (Caughley and Gunn 1993, Aanes et al. 2000). However, in environments with only moderate variability, the greater sensitivity of fecundity rates to conditions may indeed cause them to have greater influence on the population trajectory (Gaillard et al. 2000). If so, the key resource for capital breeders is likely a component of those available during the plant growth season, although for income breeders, their sensitivity to current conditions may mean that the key resource remains an element of those used outside of the plant growth season (Kerby and Post 2013). Our study system provides a clear example of an income breeder in a highly variable environment whose fecundity and survival rates are predominantly coupled to forage resource availability in the latter stages of the dry season, which thus greatly amplifies their influence on the population trajectory.

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Supplemental Material

Ecological Archives

Appendices A–G are available online: http://dx.doi.org/10.1890/14-1501.1.sm