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Ecological and behavioral mechanisms of density-dependent habitat expansion in a recovering African ungulate population

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Abstract. Major disturbances can temporarily remove factors that otherwise constrain population abundance and distribution. During such windows of relaxed top-down and/or bottom-up control, ungulate populations can grow rapidly, eventually leading to resource depletion and density-dependent expansion into less-preferred habitats. Although many studies have explored the demographic outcomes and ecological impacts of these processes, fewer have examined the individual-level mechanisms by which they occur. We investigated these mechanisms in Gorongosa National Park, where the Mozambican Civil War devastated large-mammal populations between 1977 and 1992. Gorongosa's recovery has been marked by proliferation of waterbuck (*Kobus ellipsiprymnus*), an historically marginal 200-kg antelope species, which is now roughly 20-fold more abundant than before the war. We show that after years of unrestricted population growth, waterbuck have depleted food availability in their historically preferred floodplain habitat and have increasingly expanded into historically avoided savanna habitat. This expansion was demographically skewed: mixed-sex groups of prime-age individuals remained more common in the floodplain, while bachelors, loners, and subadults populated the savanna. By coupling DNA metabarcoding and forage analysis, we show that waterbuck in these two habitats ate radically different diets, which were more digestible and protein-rich in the floodplain than in savanna; thus, although individuals in both habitats achieved positive net energy balance, energetic performance was higher in the floodplain. Analysis of daily activity patterns from high-resolution GPS-telemetry, accelerometry, and animal-borne video revealed that savanna waterbuck spent less time eating, perhaps to accommodate their tougher, lower-quality diets. Waterbuck in savanna also had more ectoparasites than those in the floodplain. Thus, plasticity in foraging behavior and diet selection enabled savanna waterbuck to tolerate the costs of density-dependent spillover, at least in the short term; however, the already poorer energetic performance of these individuals implies that savanna occupancy may become prohibitively costly as heterospecific competitors and predators continue to recover in Gorongosa. Our results suggest that behavior can provide a leading indicator of the onset of density-dependent limitation and the likelihood of subsequent population decline, but that reliable inference hinges on understanding the mechanistic basis of observed behavioral shifts.

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Introduction

How do individuals and populations respond when they are abruptly released from limiting factors such as competition, predation, or human exploitation? This question is salient for basic and applied ecology, especially in the rapidly changing environments of the Anthropocene. The decline of apex carnivores has relaxed top-down pressure in many ecosystems (Estes et al. 2011). Biological invasions have resulted in the establishment of new populations in habitats that lack the natural enemies present in native ranges (Keane and Crawley 2002, Mitchell and Power 2003). Translocations of animals to facilitate species persistence or to reestablish extirpated populations are increasingly commonplace (Seddon et al. 2014). And in some parts of the world, conservation measures are enabling populations that have long been heavily suppressed to expand into areas where, at least initially, competitive interactions are weak and predation risk is low (Chapron et al. 2014, Perino et al. 2019). Understanding how animals respond to such windows of ecological opportunity—not just demographically but also behaviorally—is important for forecasting and managing population dynamics, species' distributions, and associated ecological impacts (Morris et al. 2009).

Simple models make diverse predictions about how populations can grow in the absence of strongly limiting interactions with other species (May 1976), and empirical studies show that diverse scenarios play out in nature (Duncan et al. 2020). Ungulate populations, for example, may grow until they reach a relatively stable carrying capacity where density-dependent mortality offsets births (Woodgerd 1964, Sinclair et al. 1985, Coulson et al. 2004), or they may exhibit irruptive or cyclical boom-bust dynamics in which populations overshoot carrying capacity and then crash (Caughley 1970, Coulson et al. 2001, Forsyth and Caley 2006, White et al. 2007). Whereas many studies have explored the determinants of population dynamics in large mammals (Sinclair 1977, McCullough 1979, Berger 1986, Fowler 1987, Gaillard et al. 2000, Owen-Smith 2002, Boyce 2009), fewer have detailed the behavioral processes by which rapidly growing populations cope with intensifying resource limitation. It is clear that these responses can be strong and have significant effects on ecosystems (Jewell and Holt 1981, Garrott et al. 1993). For example, as snowshoe hares approach peak abundance in the Yukon, they browse tree species that they ordinarily avoid, resulting in a periodic pattern of tree growth that corresponds to the decadal cycle of the hare population (Sinclair et al. 1993). On subarctic islands, irruptions of caribou have transformed vegetation structure and belowground ecosystem functions (Ricca et al. 2016). Yet we have limited understanding of the proximate individual-level mechanisms that produce such effects.

Rewilding efforts, in which remnant or translocated populations are allowed to grow in places where they (and often their competitors and natural predators) have long been absent or heavily suppressed (Bakker and Svenning 2018, Perino et al. 2019), present an opportunity to study these issues. In Mozambique's Gorongosa National Park, ungulate populations were nearly extirpated during the Mozambican Civil War (1977–1992) and are now recovering (Pringle 2017, Stalmans et al. 2019). The population of waterbuck (*Kobus ellipsiprymnus*), a territorial antelope that is geographically widespread but highly water-dependent and rarely locally dominant (Spinage 1982), has grown particularly rapidly and now exceeds historical levels by more than an order of magnitude (Stalmans et al. 2019). Pre-war aerial surveys in Gorongosa counted an average of ~2,500 waterbuck, almost all of them in the productive Urema floodplain at the core of the park (Tinley 1977); this number was reduced to a few hundred individuals by the mid-1990s, but by 2018, the population had grown to >57,000 (Stalmans et al. 2019). A simple stage-structured logistic-growth model indicated that in 2018, this population was rapidly approaching or perhaps already exceeding plausible estimates of carrying capacity (see *Methods: Study species*), with peak population size predicted to occur in 2022 (Stalmans et al. 2019). Although data from the three most recent aerial surveys might reflect a subtle decline in the growth rate of the population, which increased by 30% from 2014 to 2016 and by 23% from 2016 to 2018 (Stalmans et al. 2019), there was not yet any clear numerical signal of population regulation as of 2018.

Classical theories of habitat selection provide useful reference points for evaluating the behavioral responses of rapidly growing populations such as Gorongosa's waterbuck. According to the ideal free distribution (Fretwell and Lucas 1969; see also Rosenzweig 1992, Morris 2003), populations should exhibit density-dependent habitat selection whereby individuals move freely among habitats of varying quality and conspecific crowdedness, such that per capita resource acquisition and ultimately fitness is similar across habitats. In territorial species, however, individuals may not be entirely free to select habitat, and resource-rich areas may be controlled by competitively dominant individuals such that fitness is unequal across habitats (the ideal despotic distribution; Fretwell and Lucas 1969, Morris 1989). In the extreme, resource-poor areas may be sinks where death rates exceed birth rates (Pulliam 1988); in this case, individual energetic performance should differ markedly across habitats, and abundance in sink habitat should be maintained only by spillover from comparatively resource-rich source habitat. Although the theoretical assumptions of any "ideal" distribution are often violated in nature, ungulates frequently exhibit strong intraspecific competition and density-dependent habitat selection (Pettorelli et al. 2003, McLoughlin et al. 2006, Ricca et al. 2014, van Beest et al. 2014), and the frameworks outlined above suggest testable predictions about the individual-level properties and processes that might accompany density-dependent habitat expansion.

We studied Gorongosa's waterbuck to evaluate the proximate behavioral-ecological mechanisms of density-dependent habitat selection. Our study is guided by the following series of hypotheses. Prior to any marked decline in population growth rate, intensifying intraspecific competition and associated worsening of individual condition should prompt expansion out of historically occupied (and presumably preferred) habitat to mitigate the fitness costs of poor body condition (Morris 2003). This expansion should be nonrandom across individuals with respect to sex, age, and/or breeding status owing to territorial dynamics (Beckmann and Berger 2003); prime-age breeding individuals should remain in the historically selected habitat (as their fitness cost of leaving, in terms of lost mating opportunities, is higher), whereas pre- and post-reproductive individuals should be more likely to expand into historically avoided habitat (as they sacrifice fewer short-term mating opportunities). Habitat expansion should be accompanied by broadening of the population-level dietary niche, arising either from differentiation of individual diets between habitat types (niche variation hypothesis; Van Valen 1965, Bolnick et al. 2007) or from increased individual generalization throughout the population (parallel release; Sjödin et al. 2018). Individual movement, resource acquisition, and exposure to natural enemies should all reflect differences in habitat quality (Morris 2003); thus, for example, individuals expanding into novel, lower-quality habitat might have to travel farther to obtain resources, eat less nutritious diets, and/or have higher parasite loads. Any net difference in energetic performance across habitats should then depend on the relative effects of competition and habitat quality, and on the extent to which individuals in the novel habitat can adjust behaviorally (Svanbäck and Bolnick 2007, Kobler et al. 2009, Courbin et al. 2017). If behavioral plasticity in movement and diet is sufficient to compensate for a reduction in habitat quality, then individuals expanding into a lower-quality habitat with few conspecifics may perform equally well as those in the preferred habitat owing to reduced intraspecific competition (Stewart et al. 2005, McLoughlin et al. 2006, Fortin et al. 2008). Alternatively, if compensatory mechanisms are unavailable or insufficient, then individual energetic performance may decline sharply, and the lower-quality habitat may even act as a sink.

We tested the following specific predictions stemming from these hypotheses, using aerial survey records, GPS telemetry, accelerometry, analyses of diet composition and quality, behavioral assays from camera-trap videos, ecto- and endoparasite counts, body-condition measurements, and a multi-year herbivore-exclusion experiment. (1) As waterbuck density has increased, competition for food in the Urema floodplain has depleted plant biomass in general and preferred food plants in particular. (2) As food availability has decreased, individuals have expanded out of the floodplain and into adjoining savanna habitat where waterbuck historically did not occur (Tinley 1977). (3) Expansion into savanna is skewed toward pre- or post-reproductive individuals, whereas prime-age individuals are more likely to remain and breed in the floodplain. (4) Waterbuck diets in floodplain and savanna are compositionally distinct and more diverse in savanna, reflecting the different plant communities in the two habitats. (5) Savanna is a lower-quality habitat for waterbuck than floodplain, as indicated by diet quality (e.g., lower digestible energy, protein, etc.), more spatiotemporally variable access to drinking water, and elevated parasite loads. (6) Individuals in savanna compensate for lower resource quality by altering their foraging behavior (e.g., time spent eating, bite size/rate) such that waterbuck in the two habitats maintain similar net energy balance. (7) Owing to such behavioral plasticity and weaker intraspecific competition in the less crowded savanna habitat, waterbuck maintain similar body condition in floodplain and savanna. In this framework, predictions 2 (habitat expansion) and 7 (body-condition equivalence) are expected manifestations of density-dependent habitat expansion and are products of predictions 1 (resource depletion), 5 (unequal habitat quality), and 6 (behavioral compensation); prediction 3 (demographically skewed expansion) represents the expected fitness inequality between habitats and is a product of predictions 4 (niche expansion and its attendant costs; Sjödin et al. 2018), 5, and 6.

Methods

Below, we describe the study system and summarize the methods used to test our predictions; full methodological details are in Appendix S1.

Study system

Gorongosa National Park is a floodplain–savanna ecosystem in central Mozambique, occupying roughly 4,000 km^2 at the southern end of the Great Rift Valley (18.96° S, 34.36° E). Mean annual rainfall is approximately 850 mm (interquartile range 644–1,079 mm between 1957 and 2018), most of which falls between November and March (Tinley 1977). During a typical rainy season, Lake Urema expands to cover most of the ~780-km^2 floodplain and then contracts throughout the dry season. Beyond the floodplain, the habitat transitions into intermittently flooded savanna dominated by fever trees (*Acacia* syn. *Vachellia xanthophloea*) and lala palms (*Hyphaene coriacea*), and then into savanna woodland (mixed acacia–*Combretum*, sand forest, termitaria thicket). During the Mozambican Civil War, Gorongosa's ungulate populations declined by >90%, and several large-carnivore species were extirpated (Stalmans et al. 2019). In the last decade, ungulate populations have steadily recovered (Stalmans et al. 2019) under conditions of high food availability (Daskin et al. 2016, Guyton et al. 2020), low carnivore densities (Bouley et al. 2018, Atkins et al. 2019, Gaynor et al. 2021), and effective anti-poaching measures implemented by the Gorongosa Project (Pringle 2017).

Study species

Waterbuck are medium-sized (150–300 kg) antelopes that occur widely throughout Africa, but only "at or near water" owing to their high susceptibility to dehydration and overheating relative to other African bovids (Taylor et al. 1969:630; see also Spinage 1982, Kihwele et al. 2020). Typical habitats include lakeshores, riverine woodlands, and open grasslands (Wirtz and Kaiser 1988). Historically, waterbuck in Gorongosa had "the most restricted dispersion of all the ungulates in the system" and were largely "confined to the green zone pastures [floodplains] which expand and contract with flood and ebb of the Urema Lake" (Tinley 1977:140). In the peak dry season, "almost the entire waterbuck population" occurred in this area (Tinley 1977:147). Waterbuck exhibit strong territorial behavior. Prime-age males defend year-round territories in areas of abundant, high-quality forage, often in close proximity to water (Spinage 1982); females form fluid groups that share common home ranges overlapping male territories (Spinage 1982). Juvenile and older males are effectively excluded from the most resource-rich areas and breeding opportunities by the roughly 10% of adult males that hold territories at a given time (Tomlinson 1981, Wirtz 1981, 1982). The typical diet is dominated by graminoids (Tomlinson 1980, Cerling et al. 2003, Codron et al. 2007), but waterbuck also browse under some conditions (e.g., the dry season; Kassa et al. 2008, Pansu et al. 2019), possibly owing to their high protein requirements (Taylor et al. 1969).

Pre-war aerial surveys estimated Gorongosa's waterbuck density at 1.7 individuals/km^2, representing 4% of biomass among the nine largest-bodied herbivore species; in 2018, park-wide waterbuck density was 32 individuals/km^2, representing 74% of the biomass of those nine species, 75% of all large-herbivore biomass in the floodplain, and 64% of large-herbivore biomass park-wide (Stalmans et al. 2019, Guyton et al. 2020). As such, by 2018, waterbuck were approaching or perhaps already exceeding plausible estimates of carrying capacity (low, medium, and high estimates of 23, 41, and 81 individuals/km^2; see Stalmans et al. 2019).

Quantifying density-dependent habitat shifts

To test the prediction that waterbuck have reduced food availability in the floodplain, we used six 260-m^2 herbivore exclosures and paired unmanipulated control plots established in 2015. We recorded aboveground biomass and percent cover of each plant species 12 times between August 2015 (before exclosure construction) and February 2018. We assumed that effects of herbivore exclusion would be driven primarily by waterbuck, given their disproportionate abundance in the floodplain. We used a linear mixed-effects model to test for differences in plant biomass between treatments. To test whether food plants favored by waterbuck have been especially depleted, we regressed a standardized measure of experimental effect size (ln(exclosure/control)) against previously published data on the selectivity (Jacobs' *D* index) of Gorongosa waterbuck for/against 10 common floodplain plant taxa (Pansu et al. 2019). For these taxa, we also used Wilcoxon tests to determine whether percent cover differed between treatments.

To assess shifts in waterbuck distribution and population structure, we combined aerial wildlife counts (1994–2018) with ground-based surveys of waterbuck age and sex composition (Stalmans et al. 2019). For aerial count data, we used observation locations to quantify the densities of waterbuck in floodplain and savanna. Ground surveys were conducted monthly along road transects from May–September 2019. At each sighting, we recorded the number of individuals, sex and age composition, group structure, GPS location, and habitat (floodplain or savanna). To evaluate our predictions that habitat expansion is biased by reproductive stage and that the floodplain is the prime breeding ground, we tested whether the adult female : male and female adult : subadult ratios were greater in the floodplain (using ANOVA), and whether mixed male–female (i.e., breeding) groups were more common in the floodplain (using permutational multivariate ANOVA, henceforth perMANOVA).

Movements and activity patterns

In 2015 and 2016, we chemically immobilized a total of 30 female waterbuck from savanna ($n = 15$) and floodplain ($n = 15$) and fit them with custom-built collars (Park et al. 2019) that included GPS units, video recorders (National Geographic Crittercam), and triaxial accelerometers. All procedures were approved by the Institutional Animal Care and Use Committee of Princeton University. We obtained usable data from 22 individuals ($n = 10$ captured in the floodplain and 12 captured in savanna). We used GPS data to assess movement patterns (rarefied to an average fix-rate between 5 and 10 minutes), accelerometry data to assess activity patterns, and video data to validate energetic parameters (see *Measuring waterbuck performance* and Video S1). Further details on animal handling, collar specifications, etc., are in Appendix S1.

Because individual waterbuck could move between floodplain and savanna, we classified habitat affiliation using a continuous metric, namely the proportion of time spent in the treeless grassland around Lake Urema (the interior floodplain, henceforth “grassland”; see Appendix S1: Fig. S3). We quantified individual movement patterns (95% home-range isopleths and movement rates; Appendix S1) and used linear regressions to examine how these characteristics varied as functions of proportional grassland use. Given the high water dependence of waterbuck, we also used recursion analysis to assess how waterbuck used water sources—Lake Urema, rivers, and pans (i.e., seasonal or perennial ponds)—in floodplain and savanna. To evaluate activity budgets, we classified waterbuck behavioral states on the basis of triaxial-acceleration and velocity profiles (Park et al. 2019). We used the behavioral-state classifications to calculate the proportion of time individuals spent resting, walking, eating, or running; we then regressed these data against proportional grassland use.

Diet composition and quality

To quantify waterbuck diets, we used metabarcoding of plant DNA sequences amplified from waterbuck fecal samples. Fecal samples were collected directly from anaesthetized individuals in 2016 and opportunistically during vehicular surveys in 2017–2019 ($n \approx 15$ per habitat per year). DNA extraction, plant DNA amplification, and metabarcoding protocols followed those used in our previous studies of large-herbivore diets in Gorongosa (Atkins et al. 2019, Branco et al. 2019, Pansu et al. 2019, Guyton et al. 2020; see Appendix S1 for details). Sequence data were filtered using OBITools (Boyer et al. 2016). Filtered sequences were considered molecular operational taxonomic units (mOTUs) and were identified using both local and global plant DNA reference libraries. To facilitate inter-sample comparisons, we rarefied data to 1,250 reads per sample and converted sequence counts into relative read abundances (RRA) for each plant species. In total, we present dietary data from 111 fecal samples. We visualized the compositional dissimilarity of floodplain and savanna waterbuck using nonmetric multidimensional scaling (NMDS) ordinations and tested for significant differences between habitats using perMANOVA. At a coarser taxonomic grain, we compared the contribution of different plant families to waterbuck diets in each habitat using perMANOVA. We also quantified dietary mOTU richness (using sample-based rarefaction) and Shannon diversity (total niche width; Roughgarden 1972) and compared these attributes across habitats and years.

We combined dietary data with measurements of eight functional traits for 204 plant species to estimate diet quality in each habitat. We measured physical traits (plant height, leaf water content, leaf tensile strength) for approximately three (range of one to six) individuals per plant species (Appendix S1). We measured chemical traits (crude protein, total ash, acid detergent lignin, neutral detergent fiber, percent sodium) using >5 g of the youngest leaves collected from three or more individuals per species. We excluded two fecal samples for which <80% of RRA matched plant species for which we had trait data; the mean RRA of trait-matched mOTUs in the remaining 109 samples was 98%. We then dropped unmatched mOTUs and rescaled the RRA of the remaining trait-matched mOTUs to 100% for each sample. We used RRA-weighted averages of trait values to estimate digestibility, digestible-protein content, water content, tensile strength, plant height, and sodium content of each diet (Atkins et al. 2019, Branco et al. 2019). We analyzed these data using linear models with habitat type, year, and their interaction as factors.

Measuring waterbuck performance

We collected the following body-condition measurements from anesthetized individuals during GPS-collar fitting: chest girth, body length, and hind-foot length (tape measured); thickness of the biceps femoris and longissimus dorsi muscles and maximum rump-fat depth (measured using ultrasonography); and palpation scores of fat deposition at the sacrosciatic ligament, lumbar vertebrae, sacrum, base of the tail, and caudal vertebrae. One individual was excluded from analysis owing to an erroneous hind-foot measurement, leaving $n = 29$ (Appendix S1). We followed Atkins et al. (2019) in developing a body-condition index by using a principal component analysis; the first two components explained 59% of the variation in the condition metrics (Appendix S1: Fig. S2; Tables S1, S2). We compared the scores for each of the first two components across habitats using two-sample t tests. During the 2016 captures, we also recorded the numbers of ticks (Ixodida) and lice (Phthiraptera) on each individual’s face, neck, and ears. We estimated nematode endoparasite loads (Rhabditida: Strongylida) by counting eggs in the fecal samples collected for diet analysis in 2017–2019. Due to the overdispersed nature of egg-count data, we analyzed them using a negative-binomial generalized linear model with habitat type and year as fixed effects.

To assess energetic performance of individuals in each habitat, we estimated bite rates (cropping bites per minute) using camera-trap videos of foraging female waterbuck recorded in June–July 2017 ($n = 22$ videos in the floodplain, 17 in savanna; Video S2). We integrated these data with the dietary and movement measurements described above to calculate energetic balance. Equations and parameterizations for these calculations are in Appendix S1.

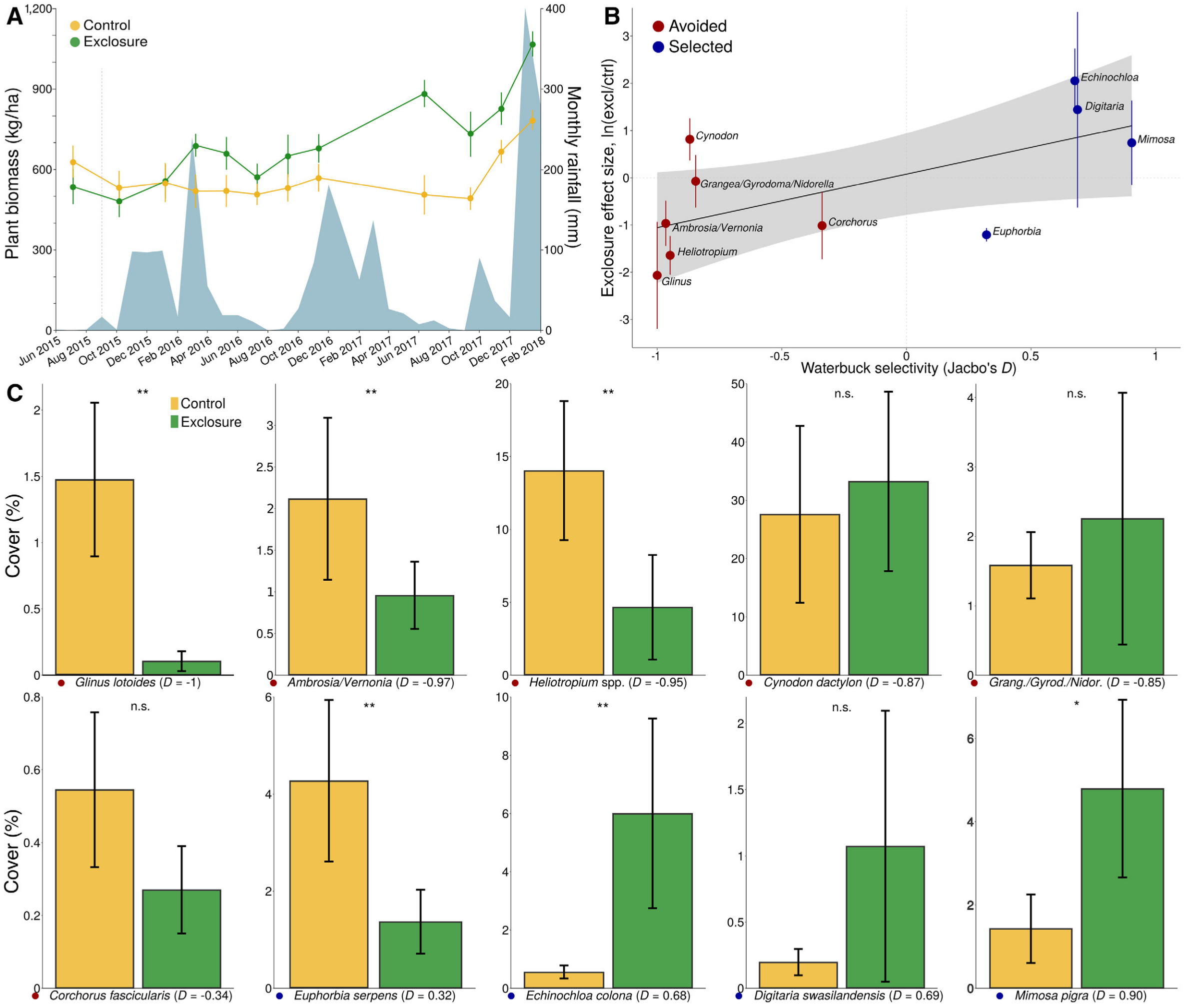

FIG. 1. Ungulates suppressed food availability in the floodplain. (A) Plant biomass (mean ± SE; left y-axis) in exclosure and control plots from 2015–2018, with monthly rainfall (right y-axis) in blue. Dashed vertical line denotes exclosure establishment in September 2015. Ungulate exclusion increased plant biomass, with the treatment effect emerging within a year of exclosure establishment (mixed-effects model: treatment $F_{1,129} = 1.19$, $P = 0.28$; time $F_{1,129} = 41.06$, $P < 0.0001$; treatment × time $F_{1,129} = 25.94$, $P < 0.0001$). Rainfall had a significant main effect on biomass ($F_{1,129} = 23.65$, $P < 0.0001$) but did not modulate the effect of herbivory (treatment × rainfall $F_{1,129} = 0.12$, $P = 0.74$). (B) The effect size (mean ± SE) of ungulate exclusion on the percent cover of 10 common plant taxa (where negative values indicate greater abundance in controls and positive values indicate greater abundance in exclosures) was an increasing function of waterbuck selectivity (D, where negative values indicate avoidance relative to availability and positive values indicate selection relative to availability; $r = 0.65$, $F_{1,8} = 5.73$, $P = 0.04$). (C) Percent cover (mean ± SE) of the same 10 plant taxa in exclosure and control plots (left–right and top–bottom in order of increasing waterbuck selectivity, with colors next to plant names denoting avoidance/selection as in panel B. Asterisks denote significant differences between treatments ($^{*}P < 0.05$, $^{**}P < 0.01$) in Wilcoxon tests with $n = 12$ plots.

RESULTS

Floodplain forage availability

In accordance with our prediction, ungulates substantially depleted forage availability in the floodplain, and this effect was most pronounced among food plants selected by waterbuck (Fig. 1). Mean aboveground plant biomass was roughly equivalent across plots at the start of the experiment in 2015 but was 75% greater in exclosures than in controls in July 2017 (a dry period) and 36% greater in February 2018 (a wet period; Fig. 1A). By mid-dry season, the depletion of biomass outside of exclosures was often visually dramatic (Appendix S2: Fig. S1). Moreover, food plants selected ($D > 0$) by waterbuck tended to be more abundant in exclosures than controls, whereas the reverse was true for plants avoided ($D < 0$) by waterbuck (Fig. 1B, C). The most conspicuous outlier in Fig. 1B is an exception that reinforces the general rule. The forb *Euphorbia serpens* was (weakly) selected by waterbuck in 2016, yet was significantly more abundant in control plots than in exclosures (Fig. 1C). The selection

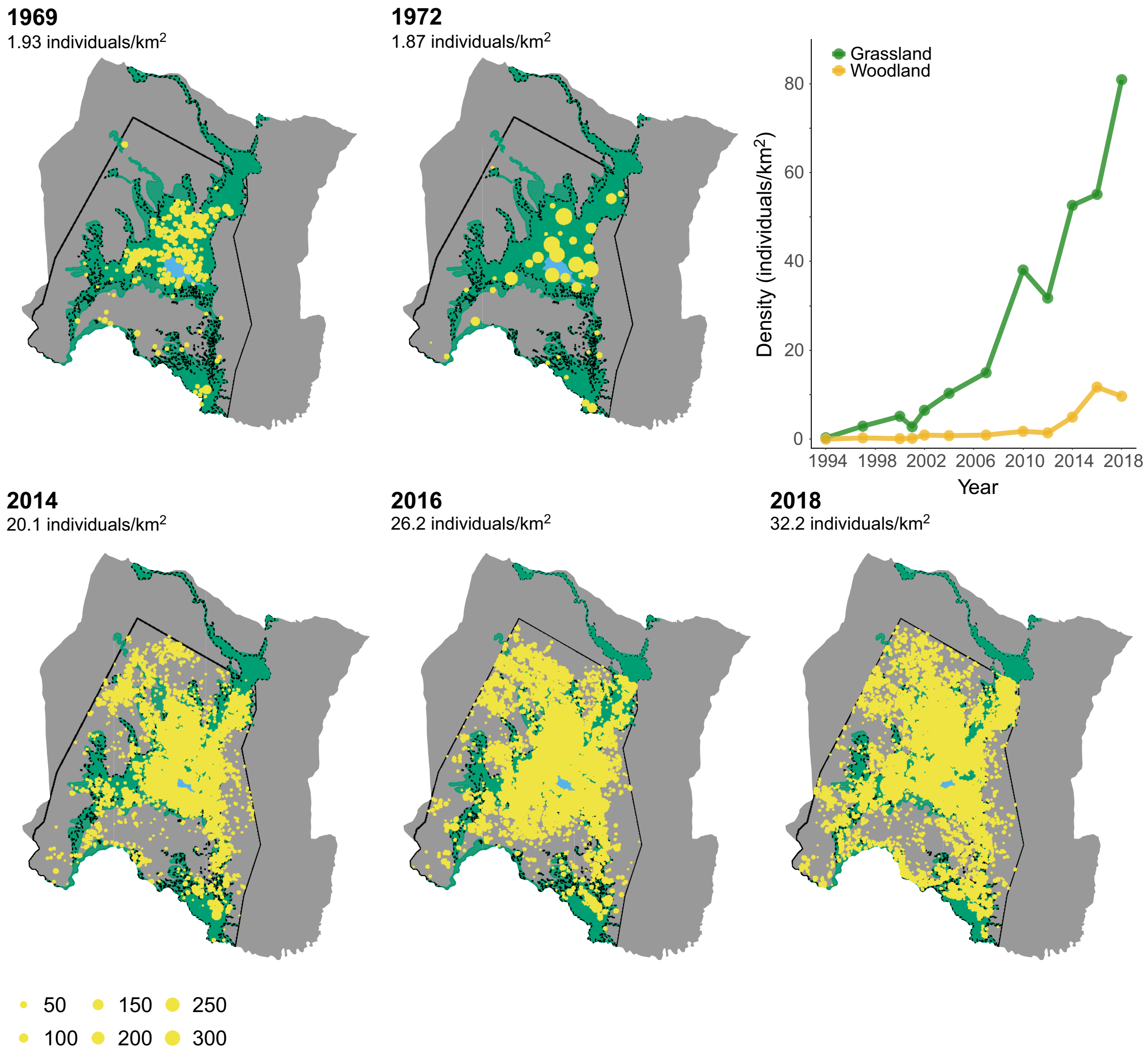

FIG. 2. Distribution and density of waterbuck in Gorongosa through time. Maps show pre-war (1969, 1972) and post-war (2014, 2016, 2018) distributions of waterbuck (yellow circles, scaled by the group size counted at each location) from aerial surveys during the late dry season (October) when visibility is highest. Overall waterbuck density throughout the surveyed area is shown beneath each year. Solid black outline delineates the aerial-survey block. Savanna habitat is shown in gray, Lake Urema in blue, and floodplain in green (dashed black line denotes the transition between the interior treeless grassland and the sparsely wooded floodplain margin). Graph (top right) shows post-war waterbuck densities in floodplain and savanna habitats.

for *Euphorbia* was surprising because members of this genus are typically rich in toxic secondary compounds (Seigler 1994). However, 2016 was the only year that we detected this species in waterbuck diets; in any other year, it would have been assigned a selectivity index of $D = -1$ and clustered with the strongly avoided plant taxa in the lower-left of Fig. 1B. Altogether, these results accord both with our assumption that the net effects of herbivore exclusion would be driven by waterbuck and with our hypothesis that intraspecific competition among waterbuck has contributed to food limitations in the floodplain.

Waterbuck density and distribution

Gorongosa's waterbuck were found exclusively on the floodplain before and immediately after the civil war; since 2012, however, the population has expanded into the adjoining savanna, even as proportional use of the floodplain continued to increase (Fig. 2). Waterbuck density in savanna dipped somewhat in 2018 (a >90th percentile rainfall year, 1,389 mm) after peaking at 12 individuals/km² in 2016 (a below-average rainfall year, 755 mm). In 2018, waterbuck density in the floodplain was 80.9 individuals/km² (~16,000 kg/km²), which

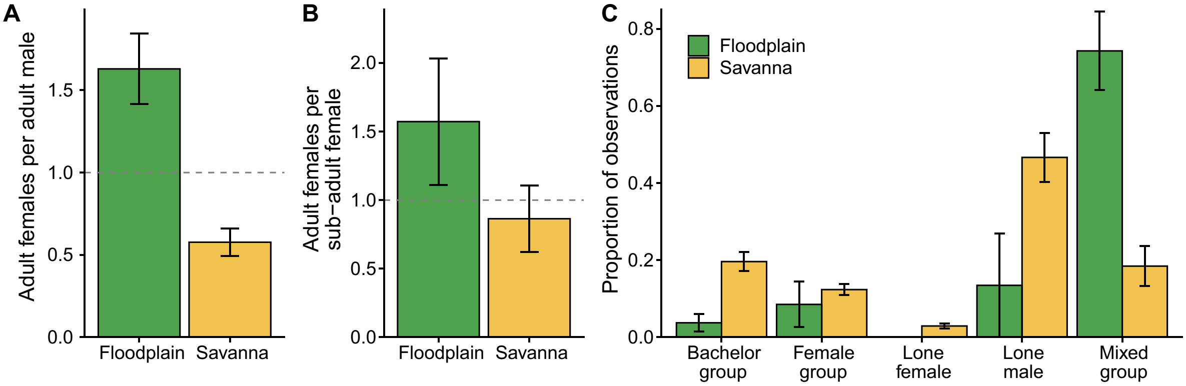

Fig. 3. Prime-age breeding waterbuck were concentrated in the floodplain. (A, B) Mean (±SE) across surveys of waterbuck sex and age ratios in 2019, with dashed horizontal lines at unity (i.e., equivalent numbers of each category). (A) In the floodplain, there were more adult females than adult males, whereas this pattern was reversed in savanna (ANOVA: $F_{1,7} = 24.96$, $P = 0.002$). (B) Female waterbuck in the floodplain were predominantly adults, whereas subadult females were relatively more common in savanna, although there was not strong statistical support for this difference with the small sample size available (ANOVA: $F_{1,7} = 2.09$, $P = 0.19$). (C) Mean proportional representation (±1 SE) of social-group types in each habitat suggests that breeding individuals were disproportionately common in the floodplain, where mixed groups accounted for 75% of observations (compared with just 19% in savanna); in contrast, lone individuals and bachelor groups were more frequent in savanna (perMANOVA of habitat effect on social-group structure: pseudo-$F_{1,7} = 14.15$, $P = 0.02$, $R^2 = 0.67$).

almost precisely matches the “high” estimate of park-wide carrying capacity (81 individuals/km^2) postulated by Stalmans et al. (2019). This number is extraordinary: a density of 30 individuals/km^2 in Kenya’s Lake Nakuru National Park (Kutilek 1974) was previously described as “by far the highest density recorded for waterbuck” (Wirtz and Kaiser 1988:162).

The average number of females per male in 2019 was roughly threefold higher in the floodplain (~1.5) than in savanna (~0.5; Fig. 3A). The average number of females per male observed in seven other waterbuck populations across eastern and southern Africa was ~1.78 (range 1.00–3.45; Spinage 1970), which is similar to what we observed in the floodplain and much higher than what we observed in savanna. The number of adult females per subadult female trended roughly 80% higher on average in the floodplain than in savanna (where the ratio was close to 1:1), although this difference was not statistically significant (Fig. 3B). Among social-group types, bachelors and lone individuals occurred more frequently in savanna, whereas mixed groups predominated in the floodplain (Fig. 3C). Collectively, these patterns are consistent with our prediction that the floodplain is disproportionately occupied by the individuals most likely to breed.

Waterbuck diet composition and quality

In the 111 fecal samples analyzed, we detected 83 mOTUs representing 28 plant families. Each year from 2016 to 2019, dietary richness and diversity were higher in savanna than in the floodplain, with savanna waterbuck eating ~50% more plant mOTUs on average (Appendix S2: Fig. S2). In line with our prediction, floodplain and savanna waterbuck diets were compositionally distinct and consistently formed minimally overlapping clusters in NMDS ordinations (Fig. 4). This dietary dissimilarity was reflected in the proportional representation of the six predominant food-plant families in each year. In savanna, waterbuck diets were dominated by Poaceae (grasses, 10–17 mOTUs accounting for 56–81% of mean RRA per year, vs. 5–12 mOTUs and 17–60% of RRA in the floodplain) and tended to contain higher proportions of Arecaceae (lala palm, *Hyphaene coriacea*) and Sapindaceae (river-litchi, *Lecaniodiscus fraxinifolius*). Floodplain waterbuck ate more Fabaceae (legumes, 2–7 mOTUs accounting for 22–49% of mean RRA per year, vs. 7–10 mOTUs and 8–21% of RRA in savanna) and higher (albeit annually variable) proportions of Elatinaceae (waterwort, *Bergia mossambicensis*), Euphorbiaceae (matted sandmat, *Euphorbia serpens*), and Pontederiaceae (water hyacinth, *Eichhornia crassipes*; Fig. 4).

Waterbuck diet quality was higher in the floodplain, especially in 2016–2017; however, most indicators of diet quality deteriorated through time in the floodplain while staying relatively consistent in savanna. Digestibility and digestible-protein content, two key components of diet quality, were greater in the floodplain than in savanna in every year, although the difference in digestibility shrank with time (Fig. 5A,B). Initially, floodplain diets were also higher in water content, lower in toughness (tensile strength), and composed of shorter (more accessible) plants, but each of these metrics converged across habitats over time owing to monotonic changes in the floodplain: from 2016 to 2019, the average floodplain diet decreased in percent water content by 18%, roughly doubled in leaf toughness, and increased roughly 11-fold in plant height (Fig. 5C-E). Dietary sodium, often a limiting nutrient for herbivores (Kaspari 2020), was the only measured quality metric that was higher in savanna (Fig. 5F). The generally higher quality of floodplain diets (especially in terms of digestibility and protein) aligns with our prediction that the historically avoided savanna is a lower-quality habitat for waterbuck. Moreover, the monotonic declines of several diet-quality indicators in the floodplain through time, coupled with the depletion of preferred food plants in the floodplain (Fig. 1, Appendix S2: Figs. S1, S2), are consistent with our prediction that the floodplain became increasingly resource-limited as waterbuck density monotonically increased (Fig. 2). Although these temporal trends are to some degree confounded by interannual variation in rainfall, the rainfall pattern was not monotonic (driest in 2017, wettest in 2019) and is therefore unlikely to explain the trends in diet-quality indicators in the floodplain.

Waterbuck parasite burdens

Savanna waterbuck had more ticks and lice on their faces, necks, and ears; these ectoparasites were completely absent from the floodplain waterbuck that we evaluated (Fig. 6A). Strongyle nematode egg counts increased from 2017–2019 in both habitats, but did not differ significantly between habitats (Fig. 6B).

Waterbuck movement and space use

The mean utilization distribution (UD) areas and movement rates of waterbuck did not differ significantly as a function of proportional grassland use (where high values correspond to floodplain individuals and low values correspond to savanna individuals), suggesting that these fundamental movement characteristics were similar regardless of habitat affiliation (Fig. 7A,B). Waterbuck in both habitats spent most of their time either eating or resting (mean ± SE: 93% ± 0.01%). However, waterbuck in the floodplain spent more time eating than those in savanna (Fig. 7C, Appendix S1: Fig. S4). There was no significant correlation between floodplain occupancy and any of the other behavioral states (resting, walking, running), thus increased time spent eating resulted in similar reductions in time spent in each of the three alternative states. Use of surface-water sources also differed as a function of habitat affiliation: waterbuck in the floodplain made more frequent visits to Lake Urema (which is perennial), whereas waterbuck in savanna primarily utilized pans (most of which are small and seasonal) (Appendix S2: Fig. S3A, B). Both the mean and maximum number of revisitations to any one water source were highest for pans (Appendix S2: Fig. S3C, D), suggesting that savanna waterbuck may have had access to fewer water sources and/or obtained less water per drinking bout. The floodplain also contains many drainage channels that may provide supplementary surface water sources for waterbuck and result in fewer visits to Lake Urema. These results, together with the lower dietary water content of savanna waterbuck, further support our prediction that savanna is a lower-quality resource environment for waterbuck.

Waterbuck energetics

Mean bite rate was significantly higher in the floodplain (Fig. 8A; $t = 3.92$, df = 34.22, $P < 0.001$), whereas estimated bite size and intake rate were higher in savanna (Fig. 8B). Estimated energetic costs were similar across habitats; however, the lower digestibility of savanna waterbuck diets and the lesser time they spent eating per day resulted in ~30% higher daily net energy balance for floodplain waterbuck (Fig. 8B). Daily energy balance was largely insensitive to variation in estimates of body mass and bite rate (i.e., small effect sizes) but was strongly correlated with handling time and bite size (negatively and positively, respectively) (Appendix S2: Fig. S4). The qualitative result that floodplain waterbuck had higher daily net energy balance than savanna waterbuck was robust to sensitivity analyses on our bite-size estimates (Appendix S2: Fig. S4). However, when we assumed higher handling times in both habitats (>1.2 s/bite), our sensitivity analyses showed that savanna waterbuck could achieve similar or even greater net energy balance (Appendix S2: Fig. S4). Our calculations suggest that waterbuck ate between 3.2% (savanna) and 3.4% (floodplain) of their body mass daily, which aligns with estimates from both captive and field-based feeding trials of female North American cervids (Berry et al. 2019, Ulappa et al. 2020). Waterbuck in the floodplain also consumed more protein per day than those in savanna (Fig. 8B). Waterbuck in both habitats appear able to meet daily energy requirements for basal metabolic maintenance and movement, although our analyses did not include the costs of thermoregulation or other activities beyond locomotion.

Waterbuck body condition

Despite the differences between habitats in diet composition and quality, ectoparasite loads, movement behavior, and energetics, we found no clear differences in body condition between floodplain and savanna waterbuck (Fig. 8C, D). Individual scores for principal components 1 (most highly associated and positively correlated with measurements of fat deposition) and 2 (most highly associated and negatively correlated with size-related measurements such as body and hind foot length) were slightly (nonsignificantly) higher among waterbuck in savanna, suggesting that these individuals tended to be smaller but to have more body fat than individuals in the floodplain (perhaps reflecting the skewed distribution of age classes between the two habitats; Fig. 2B).

Discussion

The release of a population from ecological limiting factors can precipitate both rapid population growth

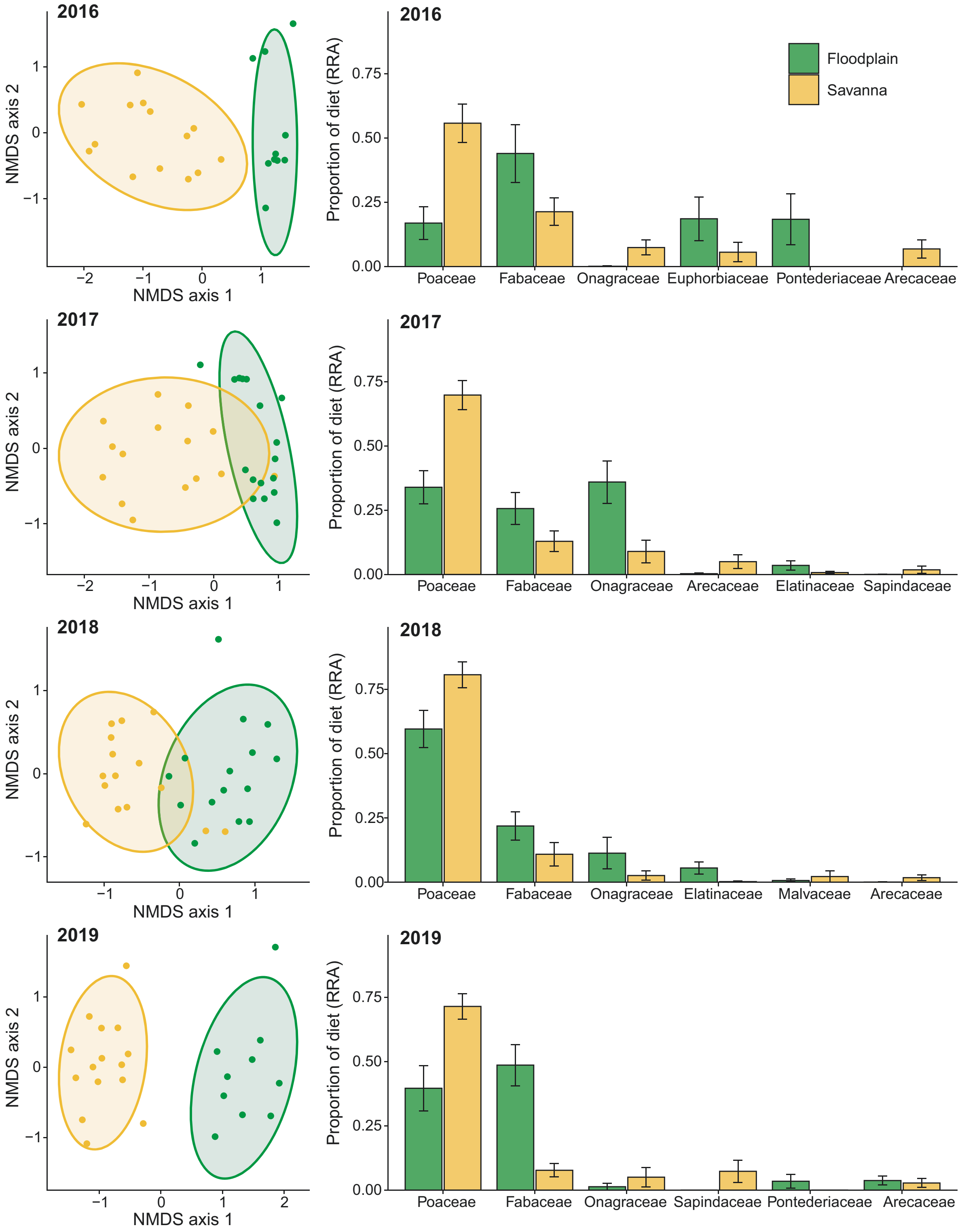

FIG. 4. Waterbuck diets differed in floodplain and savanna habitats. At left, nonmetric multidmensional scaling (NMDS) ordinations illustrate the dietary dissimilarity (at the level of plant molecular operational taxonomic units [mOTUs]) among waterbuck fecal samples collected in floodplain and savanna in each year from 2016 to 2019 (stress = 0.10, 0.16, 0.14, 0.12, respectively). Points in each plot represent individual fecal samples, with points farther apart being more dissimilar; 90% confidence ellipses are shown for each habitat (perMANOVA testing the effect of habitat type, 9999 permutations: 2016 pseudo-$F_{1,22}$ = 8.29, $P < 0.001$,

(FIG. 4. *Continued*)

$R^2 = 0.27$; 2017 pseudo-$F_{1,30} = 7.64$, $P < 0.001$, $R^2 = 0.20$; 2018 pseudo-$F_{1,28} = 8.22$, $P < 0.001$, $R^2 = 0.23$; 2019 pseudo-$F_{1,23} = 10.95$, $P < 0.001$, $R^2 = 0.32$). At right, the proportional representation (RRA; ±SE) of the six plant families that contributed most to waterbuck diets in each year (which always included all families that accounted for ≥1% of RRA on average across all samples). Composition of these plant families likewise differed significantly between habitats in each year (perMANOVA of habitat effect, 9,999 permutations: 2016 pseudo-$F_{1,22} = 6.31$, $P = 0.001$, $R^2 = 0.22$; 2017 pseudo-$F_{1,30} = 9.31$, $P < 0.001$, $R^2 = 0.24$; 2018 pseudo-$F_{1,28} = 3.64$, $P = 0.02$, $R^2 = 0.12$; 2019 pseudo-$F_{1,23} = 12.83$, $P < 0.001$, $R^2 = 0.36$). Floodplain waterbuck ate more legumes (mean 35% RRA, mostly the shrub *Mimosa pigra*) than savanna waterbuck (mean 13% RRA, mostly *Acacia* syn. *Vachellia* spp.), whereas savanna waterbuck ate substantially more grass (mean 69% RRA, mostly *Urochloa mosambicensis* and *Panicum* spp.) than floodplain waterbuck (mean 38% RRA, predominantly *Digitaria swazilandensis* and *Cynodon dactylon*).

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and niche expansion. We tested the hypothesis that unchecked population growth in a territorial ungulate (and consequent depletion of resources in the preferred habitat) leads to demographically skewed expansion into lower-quality habitat and accompanying expansion of the population-level dietary niche. We expected that this niche expansion would occur primarily through individual differentiation rather than increased individual generalization—i.e., that the population would segregate into floodplain- and savanna-affiliated individuals with correspondingly different diets—and the data were consistent with this notion (with some caveats discussed below). Recent theory holds that niche expansion should occur via this route only when individual generalization is costly (Sjödin et al. 2018). Our results suggest that the costs of savanna occupancy include fewer reproductive opportunities and reduced diet quality. The fitness implications of these costs should be greatest for prime-age potential breeders with high energetic demands, consistent with the observed demographic skew in habitat use. Individuals in the poorer habitat may be able to mitigate these costs if behavioral flexibility is sufficient to compensate for the differences in diet quality, potentially enabling them to trade off current for future reproduction.

In agreement with our predictions 1 and 2, we found that Gorongosa's waterbuck have increasingly expanded out of the historically preferred but currently food-limited floodplain and into the historically avoided savanna. Notably however, proportional use of the floodplain increased through time despite resource depletion, underscoring the continuing value of floodplain habitat and suggesting a difference between habitats in the relationship between density and fitness. In accordance with prediction 3, breeding individuals predominantly remained in the floodplain, whereas savanna occupancy was biased toward pre-reproductive individuals and solitary (perhaps senescent) males that are less likely to attain mating opportunities in the floodplain. Waterbuck in savanna ate a taxonomically and functionally distinct (and more diverse) suite of plants (prediction 4), reflecting differences in plant community composition across habitats, yet their diets were less digestible and protein rich than those of waterbuck in the floodplain; floodplain waterbuck also had a more seasonally reliable source of drinking water and fewer ectoparasites than savanna waterbuck, all of which supports the prediction (5) that savanna is the lower-quality habitat. Nevertheless, our results suggest that waterbuck are able to compensate for the costs of density-dependent spillover, at least in the short term, and that the difference in diet quality between habitats is dissipating as intraspecific density in the floodplain continues to increase; although waterbuck in the floodplain achieved higher net energy balance (limited support for prediction 6), body condition was similar in both habitats (prediction 7). Collectively, our results provide evidence of despotic density-dependent habitat selection, enabled by individual behavioral flexibility that dampens the fitness costs of occupying low-quality (but also lower density) habitat.

Although we acknowledge some uncertainty in the energetic and body-condition results, as several of our energetic parameters were approximations derived from research in other systems and our body-condition metrics have not been formally validated for waterbuck, the results withstood sensitivity analysis and are consistent with predictions of life-history theory. Our sensitivity analysis showed that savanna waterbuck could achieve equal or greater energy balance if handling times were high in both habitats (Appendix S2: Fig. S4). We consider this scenario unlikely—the greater toughness and height of savanna food plants (Fig. 5C,D) suggest that handling time is probably higher in savanna—but it is possible that depletion of high-quality food in the floodplain (Figs. 1, 5) has increased handling time there, which could reduce the energy-balance differential and contribute to convergence in body condition across habitats. We also note that our estimates of energy expenditure captured only the costs of basal metabolism and locomotion. We hypothesize that females in the floodplain (biased toward breeding-age individuals) expend more energy on reproduction (higher pregnancy and lactation rates, fewer reproductive pauses, larger calves), which could prevent these individuals from subsisting on lower-quality savanna diets and might likewise promote convergence in body condition across habitats. Future work on the relative reproductive investment and lifetime fitness of floodplain and savanna waterbuck would be a useful next step.

Behavioral and ecological signatures of density-dependent habitat expansion

Our results suggest that flexibility in fine-scale foraging behavior plays an important role in how ungulate

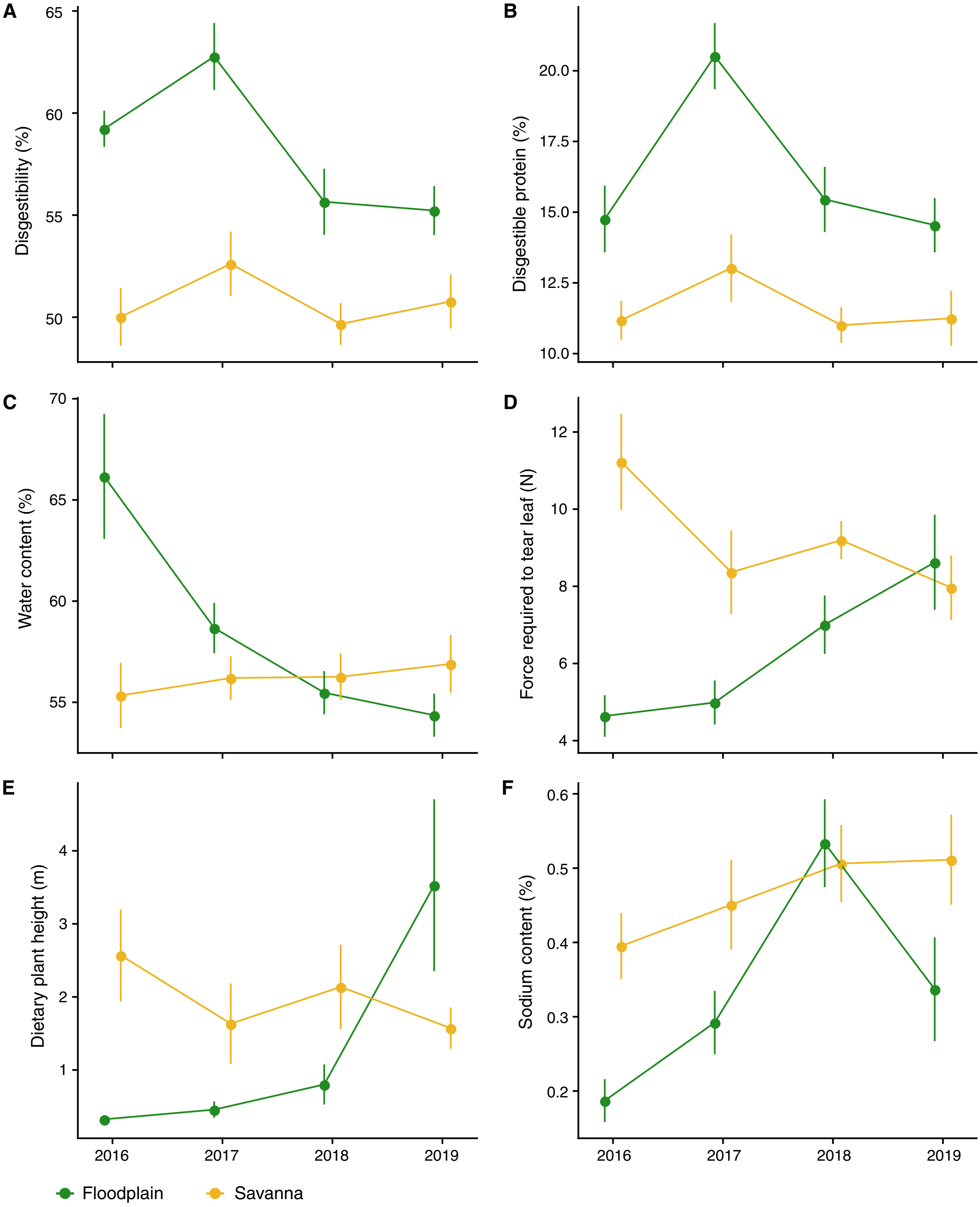


Fig. 5. Waterbuck diet quality was generally higher, but declining, in the floodplain. (A) Digestibility was higher on average but declined over time in the floodplain (linear model: habitat $F_{1,105} = 55.56$, $P < 0.001$; year $F_{1,105} = 3.91$, $P = 0.05$; habitat × year $F_{1,105} = 4.71$, $P = 0.03$). (B) Digestible-protein content was consistently higher in the floodplain, with no directional temporal trend in either habitat (habitat $F_{1,105} = 43.36$, $P < 0.001$; year $F_{1,105} = 1.56$, $P = 0.21$; habitat × year $F_{1,105} = 0.80$, $P = 0.37$). (C) Dietary water content was initially higher but declined monotonically in the floodplain over time, leading to convergence across habitats (habitat $F_{1,105} = 4.34$, $P = 0.04$; year $F_{1,105} = 7.54$, $P = 0.007$; habitat × year, $F_{1,105} = 18.90$, $P < 0.001$). (D) Leaf toughness was initially lower but increased monotonically in the floodplain, leading to convergence across habitats (habitat $F_{1,105} = 23.57$, $P < 0.001$; year $F_{1,105} = 0.10$, $P = 0.75$; habitat × year $F_{1,105} = 16.27$, $P < 0.001$). (E) Plant height was initially lower but increased

(Fig. 5. *Continued*)
through time in the floodplain, leading to convergence across habitats (habitat $F_{1,105} = 30.12$, $P < 0.001$; year $F_{1,105} = 7.30$, $P = 0.008$; habitat × year $F_{1,105} = 17.25$, $P < 0.001$). (F) Sodium content was generally higher in savanna (habitat $F_{1,105} = 8.69$, $P = 0.004$; year $F_{1,105} = 9.13$, $P = 0.003$; habitat × year $F_{1,105} = 0.99$, $P = 0.32$). Quality indicators (mean ± SE) were calculated by averaging the trait values of food-plant taxa (weighted by their RRA) in each waterbuck fecal sample.

populations mitigate the effects of density dependence and intraspecific competition more broadly (Morris 2003). Despite the reduced diet quality associated with habitat expansion, individual flexibility in the types of plants eaten and the amount of time spent eating enabled females to maintain positive energy balance in savanna. Part of this response may reflect a unique feature of ruminant physiology: the rate of food intake is limited by the time required to process food in the rumen, which is negatively correlated with food quality (Wirtz and Oldekop 1991). Spending less time eating while taking larger bites might allow savanna waterbuck to increase gut-processing time to accommodate low-quality food while still meeting daily energy requirements. Indeed, such fine-scale adjustments to activity budgets have been observed in waterbuck elsewhere when individuals were restricted to nutritionally poor habitats. In Kenya, bachelor males that were excluded from high-quality territories spent less time foraging than territory holders, and females within these high-quality areas spent more time eating than those outside (Wirtz and Oldekop 1991). Ultimately, this behavioral flexibility and the positive energy balance of individuals in both habitats may be enabling continued population growth, despite the increasing saturation of the floodplain. Yet, the lower energy and protein intake of savanna individuals suggests that savanna may only be a viable refuge so long as interspecific competition and predation pressure remain low, plants remain sufficiently abundant to allow large bite sizes, and the floodplain remains a source habitat.

Behavioral flexibility enables animals to rapidly adjust to shifting environmental conditions, thereby promoting the maintenance of individual condition, reproductive success, and population persistence (Huey et al. 2003, Kearney et al. 2009, Long et al. 2014). Individual differentiation in behavior and diet is often observed in populations responding to biotic stressors that limit resource availability, such as competition (Svanbäck and Bolnick 2007). In this regard, our results accord with predictions of foraging theory (Stephens and Krebs 1986) and theories of niche expansion (Sjödin et al. 2018). Consistent

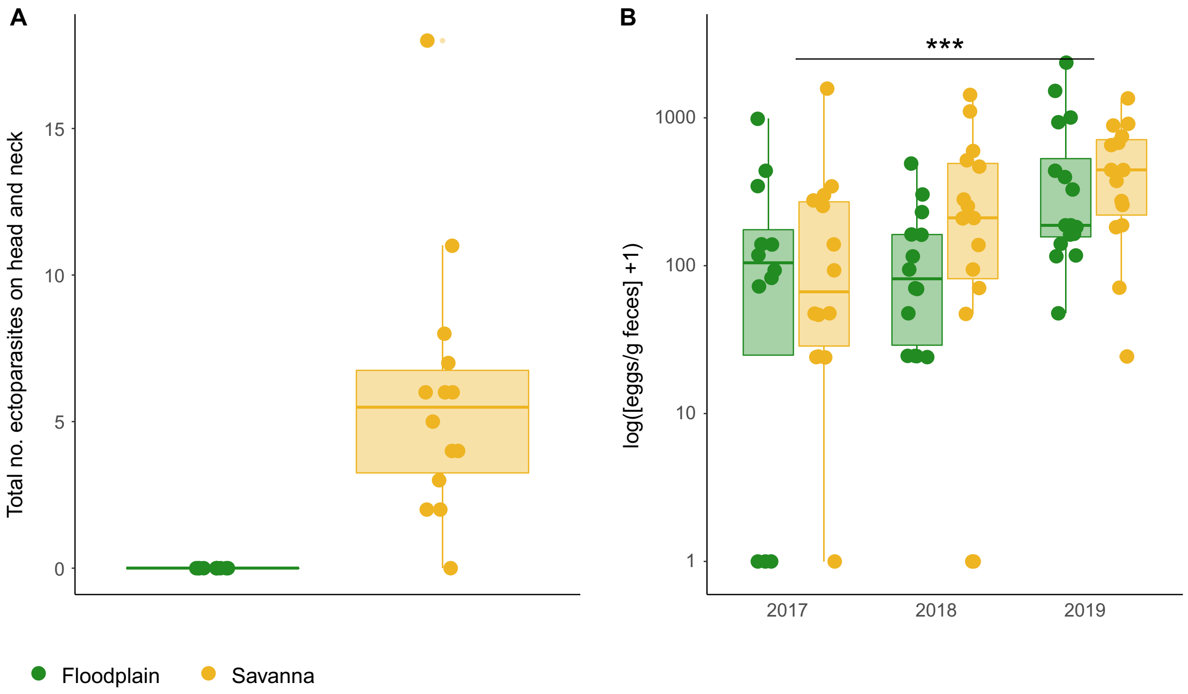


Fig. 6. Ectoparasite burdens were higher in savanna waterbuck, whereas endoparasite loads were similar across habitats. (A) No ticks or lice were counted on the ears, faces, or necks of waterbuck collared in the floodplain in 2016 ($n = 10$) whereas those collared in savanna ($n = 15$) had more. (B) Numbers of strongyle nematode eggs per gram of feces ($n = 26$, 29, and 31 in 2017, 2018, and 2019, respectively) did not differ significantly between habitats (negative-binomial GLM: habitat = 0.29 ± 0.27, $Z = 1.06$, $P = 0.29$) but did increase significantly from 2017–2019 (year = 0.45 ± 0.17, $Z = 2.73$, $P = 0.01$). Box plot components are mid line, median; box edges, interquartile range; and whiskers, 1.5 x interquartile range.

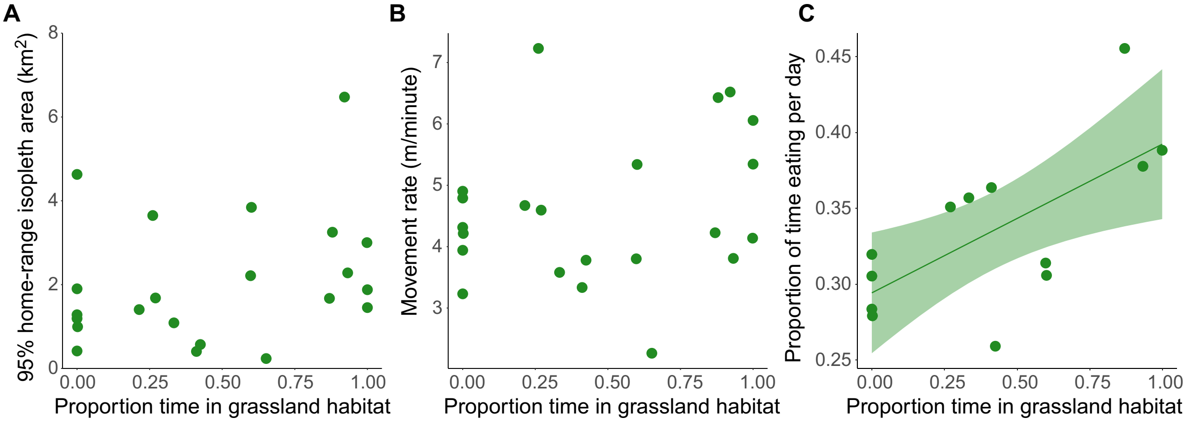
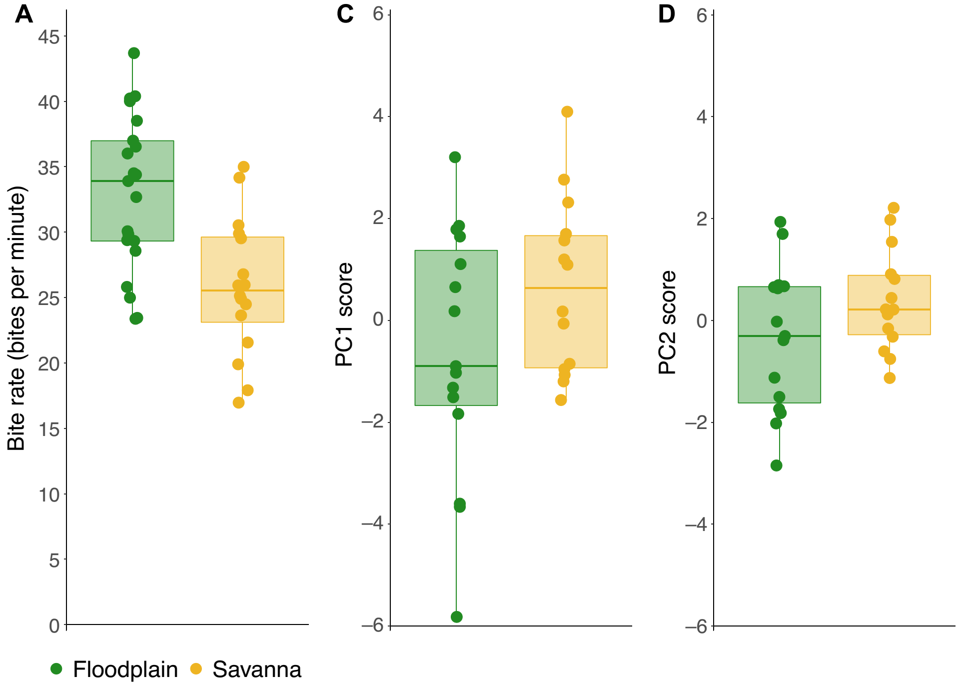


FIG. 7. Savanna waterbuck spent less time eating than floodplain waterbuck. (A) Area of each individual's 95% home-range isopleth (derived from the utilization distribution, i.e., the relative intensity of space use; $R^2 = 0.03$, $F_{1,20} = 1.56$, $P = 0.23$). (B) Individual movement rate in m/min ($R^2 < 0.01$, $F_{1,20} = 1.19$, $P = 0.29$). (C) The proportion of time that individuals spent eating ($R^2 = 0.39$, $F_{1,11} = 8.79$, $P = 0.01$). One outlier was removed from the data set before fitting the regression in panel C owing to implausibly low activity levels (resting >75% of the time) suggesting accelerometer malfunction (Appendix S1); the full data set is plotted in Appendix S1: Fig. S4. The behavioral states used in panel C were determined using classification algorithms trained on the accelerometry data and verified using high-definition animal-borne video data (Park et al. 2019; Appendix S1). Behavioral attributes were assessed using linear regression as a function of the proportion of time each individual spent in the interior of the floodplain.

with the niche variation hypothesis (Van Valen 1965), total dietary niche width of the population expanded mainly through inter-individual differentiation in diet composition that occurred when intraspecific competition forced some waterbuck to move from floodplain into the floristically distinct savanna (where dietary niche width was also greater than in the floodplain: Appendix S2: Fig. S2). Niche expansion through the alternative pathway of individual generalization (parallel release) would entail costs of travel, nutrition, reproduction, parasite load, and water availability, which reflect the scale-dependence of habitat selection and help to explain the observed pattern of niche differentiation (Morris 1992, Sjödin et al. 2018). One caveat to this interpretation is that owing to the short duration of our movement data, we could not conclusively determine whether this individual differentiation arose from fixed phenotypic differences among individuals or within-individual plasticity over timescales longer than our measurements (e.g., frequent movement across habitat boundaries with facultative behavioral adjustments to the habitat occupied at any given time). Our demographic data suggest that individuals may move between savanna and floodplain depending on age and reproductive stage; however, the GPS data did show that most individuals remained either in the floodplain or in savanna for at least two consecutive weeks, and we consider it likely that habitat affiliations are relatively stable on seasonal or annual timescales.

Our findings from a naturally occurring tropical antelope population contribute to a larger body of research on density-dependent processes in ungulates, much of which has focused on high-latitude species (often cervids) and on insular populations (often introduced). In those cases, similar patterns of density-dependent habitat and diet expansion typically follow a period of irruptive growth after populations are introduced or after predators are removed (Caughley 1970, Coulson et al. 2001, Forsyth and Caley 2006, White et al. 2007). Multigenerational data sets from these systems show that such dynamics often result in population crashes if habitat expansion delays the effects of density-dependent regulation (Caughley 1970, Coulson et al. 2001, Forsyth and Caley 2006, White et al. 2007). Our focus on the proximate mechanisms underpinning the expansion of ungulates into new habitats provides a complementary perspective on how density-dependent habitat selection and niche expansion occur at the individual level. Previous studies have also found that ungulates often violate the assumptions of the ideal free distribution (van Beest et al. 2014). Although not designed to test such models, our study suggests that waterbuck conform broadly to the ideal despotic distribution or the preemptive model of habitat selection (Fretwell and Lucas 1969, Pulliam and Danielson 1991, Beckmann and Berger 2003). Individuals do not move into savanna at random; rather, pre-reproductive females, lone males, and bachelors were more likely to occupy savanna, perhaps because they are competitively excluded from the higher-quality floodplain. These individuals may incur fitness costs by virtue of occupying a lower-quality habitat during development and/or by having fewer breeding opportunities outside of the high-quality floodplain territories—but may also be making the best of a bad situation by trading short-term reproductive opportunities for future ones.



B

Energetics parameter	**Unit**	**Floodplain**	**Savanna**
Body mass (M)	kg	200	200
Energy gain			
Max. processing rate ($R_{\max}$)	g/minute	28.97	28.97
Handling time (h)	minute/bite	0.015	0.015
Gross energy content (GE)	kcal/g	4.58	4.58
Digestibility (DG)	%	58.46	51.08
Digestible protein (DP)	%	16.76	11.57
Bite rate (B)	bites/minute	33.0	25.8
Bite size (S)	g/bite	0.44	0.69
Intake rate (I)	g/minute	14.64	17.77
Foraging time (F)	minute/d	467.40	361.78
Daily protein intake	**g/d**	**1,147.03**	**743.62**
Daily energy intake	**kcal/d**	**18,318.95**	**15,042.05**
Energy loss			
Distance moved (DM)	km/d	5.90	5.75
Costs of locomotion (L)	kcal/kg/km	0.49	0.49
Energy expenditure from movement	**kcal/d**	**578.48**	**563.38**
Basal metabolic rate (BMR)	kcal/d	3,722.81	3,722.81
Net energy balance	**kcal/d**	**14,017.66**	**10,755.86**

FIG. 8. Body condition and energetics of floodplain and savanna waterbuck. (A) Bite rate (cropping bites per minute), estimated from videos of waterbuck recorded in each habitat in 2017 (see Video S2), was significantly higher in the floodplain (t = 3.92, df = 34.22, P < 0.001; n = 22 in the floodplain, n = 17 in savanna). (B) Parameter estimates used to calculate waterbuck energy balance in savanna and floodplain; values in this table are rounded to a standardized number of significant digits for ease of presentation, but we used unrounded values in our energetic calculations. (C, D) Eleven individual body-condition metrics were aggregated into two condition scores using principal component analysis (Appendix S1: Fig. S2; Tables S1, S2). Plots show the scores for principal components 1 (C, a proxy for body fat) and 2 (D, a proxy for body size), which together explained 59% of the variance in the body-condition metrics, for 29 female waterbuck collared in 2015 and 2016 (n = 15 floodplain and 14 savanna). Neither condition score differed significantly between the two habitats (A, t = −1.62, df = 25.06, P = 0.12; B, t = −1.65, df = 25.16, P = 0.11). Box plot components are mid line, median; box edges, interquartile range; and whiskers, 1.5 x interquartile range.

Comparative ecology of waterbuck across systems

The behavioral plasticity observed in response to density-dependent resource limitation in the floodplain align with the responses of waterbuck to resource scarcity elsewhere. In Zimbabwe, waterbuck ate more browse species and spent more time in wooded habitats during the dry season (Tomlinson 1980, 1981). In Kenya, waterbuck moved into shrubland during periods of low rainfall, while open grasslands were favored during wetter periods (Wirtz and Kaiser 1988). Although these patterns represent temporary seasonal shifts rather than the multi-annual process of niche expansion in the Gorongosa population, they are consistent with our findings that resource limitation prompts waterbuck to use less preferred woody habitat and eat more diverse diets. A study in Uganda found that females may be less flexible in their dietary choices under seasonal resource limitation, as they consistently avoided areas of tough, unpalatable grass (Spinage 1982). We observed a similar pattern, finding more males per female in savanna, where the food was tougher and less nutritious than in the floodplain (Fig. 5). In Zimbabwe, territorial males tended to remain in the highest-quality grassland habitat year-round, whereas bachelors and females increased their use of grassland from the wet to the dry season as food availability in alternative areas declined (Tomlinson 1981). There may be limits to dietary flexibility that constrain further habitat expansion by the Gorongosa waterbuck. For example, the supplementation of the diet with browse requires ready access to water, as the higher protein content of these food plants necessitates increased water intake for the excretion of nitrogenous waste (Spinage 1970).

Despite their extensive distribution, waterbuck are rarely numerically dominant in historically intact African ungulate assemblages. Due to their non-migratory nature, strong water-dependence, and high protein requirements, waterbuck are typically restricted to a narrow range of habitats and may be highly susceptible to interspecific competition from larger, herd-forming grazers such as buffalo and zebra (Taylor et al. 1969, Spinage 1982, Ogutu et al. 2012, Kihwele et al. 2020). In pre-war Gorongosa, waterbuck numbers were thought to be limited by interspecific competition; buffalo were numerically dominant, and the waterbuck population in the floodplain fluctuated with the seasonal zebra migration (Tinley 1977). The war caused collapses in all ungulate populations, and buffalo and zebra remain at very low densities (Stalmans et al. 2019), whereas waterbuck have reached extraordinary densities and now overlap extensively in habitat use and diet with more than a dozen other ungulate species that have lagged in their recovery (Pansu et al. 2019).

This scenario is consistent with the idea that interspecific competition limited the pre-war Gorongosa waterbuck population but does not explain why waterbuck seem to have won the post-war lottery. The physiological and life-history traits of waterbuck do not obviously suggest a propensity for explosive population growth, as waterbuck have exceptionally high resource requirements (Spinage 1982) and occupy the “slower” half of Gorongosa’s ungulate species in terms of gestation length, interbirth interval, weaning age, and number of births per year (Jones et al. 2009). Although zebra and buffalo have even slower life-histories than waterbuck, species such as impala and wildebeest have similar life-histories and are more often locally abundant in other systems, but have not risen to dominance in Gorongosa. We propose that the disproportionate increase in the waterbuck population occurred because they had a head start in the low-competition, low-predation post-war environment (see also Morris et al. 2000). Although the very first post-war aerial survey gave no clear indication of such an advantage (6 of 32 individual animals spotted in 1994 were waterbuck), later surveys suggest that this first count significantly underestimated the number of waterbuck that survived the war (151 were recorded in 1997, more than threefold higher than the next-most abundant species, and 408 were recorded in 2000; Stalmans et al. 2019). Waterbuck are likely to have survived the war in higher numbers owing to some combination of their year-round occupation of the floodplain (which is swampy, has high visibility, and lacks trees for anchoring snares) and their allegedly disfavored status as bushmeat (Martin et al. 2013). A crucial management question for Gorongosa is whether the historically dominant larger-bodied grazers such as buffalo, zebra, and wildebeest will competitively displace waterbuck, or whether priority effects will enable waterbuck to maintain dominance (Chase 2003).

For insight into the long-term dynamics of waterbuck in Gorongosa, other systems may be instructive. The early history of Kenya’s Lake Nakuru National Park offers a striking parallel to the recent history of Gorongosa. Nakuru was established in 1961 as a tiny park (63.5 km^2, two-thirds of which was lake) and expanded in 1974 with the acquisition of 150 km^2 of largely wildlife-free adjacent land, which dramatically reduced ungulate densities (Kutilek 1974, Ogutu et al. 2012). From 1970 to 1988, the Nakuru waterbuck population increased from ~900 to ~5,000 individuals (Wirtz and Kaiser 1988, Ogutu et al. 2012, 2017), accounting for >75% of ungulate biomass throughout the 1970s and nearly 60% into the mid-1980s (Kutilek 1974, Ogutu et al. 2012, 2017), similar to their dominance in post-war Gorongosa. The subsequent crash of the waterbuck population to an average of ~200 individuals in the 2010s has been attributed to competitive displacement by zebra and buffalo, both of which steadily increased from small initial populations until they reached density-dependent limitation in the mid-2000s (Ogutu et al. 2012, 2017). During this time, top carnivores were scarce, as lion and spotted hyena were not introduced until the mid-1980s (Ogutu et al. 2012). Nakuru thus was initially a similar environment to post-war

Gorongosa for waterbuck, with weak competition, minimal predation, and high availability of favorable lakefront habitat (Kutilek 1974). Likewise, the history of Nakuru suggests a possible future trajectory for Gorongosa: a precipitous drop in waterbuck numbers as buffalo, zebra, wildebeest, and carnivore numbers climb, associated with a contraction of the dietary niche and habitat use among waterbuck.

Behavior as an indicator of population status

Individual adaptive behaviors, and changes in these behaviors, can reveal information about the status of a population prior to numerical signals such as a decline in population growth rate. In particular, habitat selection, foraging behavior, and diet choice may be reliable indicators of population status because of their direct links to energy gain, survival, and reproductive success (Morris et al. 2009). This connection should be especially pronounced for large herbivores, in which these behaviors are density- and/or frequency-dependent (Kotler et al. 2007). Our study is consistent with the proposition that behavior serves as a leading indicator of population trends. However, interpreting behavioral plasticity for conservation and management requires an understanding of the underlying ecological mechanisms. Niche expansion in Gorongosa's waterbuck appeared to stem directly from resource depletion in the floodplain (Fig. 1, Appendix S2: Fig. S1), and the tenuous energetic balance of waterbuck in savanna (Fig. 8C,D) suggests an incipient decline in population growth rate. Yet, similar behavioral changes in habitat use and diet can also result from non-regulatory processes and ecological opportunity. The relaxation of predation risk following the collapse of carnivores in Gorongosa enabled bushbuck, a small forest antelope, to expand out of savanna and into the floodplain, where they ate better diets and attained larger sizes (Atkins et al. 2019). That different processes can produce superficially similar habitat shifts underscores the necessity of understanding the mechanistic bases of habitat use for making reliable inferences about population dynamics and management.

The continuing disruption of natural systems and the rise of large-scale restoration initiatives add urgency to the goal of clarifying behavioral indicators of population status. Large-mammal populations are particularly susceptible to variation in hunting pressure, habitat change, and movement restrictions (Morris et al. 2009, Tucker et al. 2018). These species also present challenges for population assessment given their wide ranges, extensive movements, and slow intrinsic rates of increase (Purvis et al. 2000, Morris et al. 2009). Our results suggest that investment in behavioral monitoring is worthwhile in general, and particularly in the context of trophic rewilding, where strategies for benchmarking progress are needed (Bakker and Svenning 2018, Torres et al. 2018). In addition to providing signals about current waterbuck population status, behavioral indicators such as shifting patterns of space use may foreshadow a decline in the population as competitors such as buffalo and zebra recover in Gorongosa. Our work suggests that behavioral indicators may be useful for determining whether, when, and how to use intervention to achieve specific conservation goals. The use of behavioral indicators to forecast future community states may be particularly valuable in large-mammal communities, which may take decades to reach a stable composition (Purvis et al. 2000). We highlight two key general questions for future research. At what point do behavioral responses to ecological limiting factors reflect a concurrent decline in demographic performance and vital rates? And, by tracking behavioral changes in rapidly growing populations, can ecologists identify the optimal time for management interventions (e.g., removal of some individuals) to stabilize population dynamics and increase community diversity? Given that multiple stable states are possible in diverse ecological circumstances (Chase 2003, Suding et al. 2004), focusing on behavioral responses in addition to numerical indicators may be essential for forecasting the dynamics of reassembling communities.

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SUPPORTING INFORMATION

Additional supporting information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/ecm.1476/full

OPEN RESEARCH

Data (Becker et al. 2021) are available in the Dryad digital repository at https://doi.org/10.5061/dryad.qfttdz0h4.

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Appendix S1. Comprehensive description of the study methodology

METHODS

Study system

Gorongosa National Park is a floodplain savanna ecosystem in central Mozambique, occupying roughly 4000 km^2 at the southern end of the Great Rift Valley (-18.96, 34.36). Our study area is located near the center of the park and is bounded in the north by Lake Urema. This region has a mean annual rainfall of approximately 850 mm (interquartile range 644–1079 mm between 1957 and 2018), most of which falls between November and March (Tinley 1977). During a typical rainy season, Lake Urema expands to cover most of the ≈780-km^2 floodplain; during the dry season, the floodplain is a near-treeless expanse of grasses, forbs, subshrubs, and mudflats, dissected by drainage channels. Moving south from the lake, the habitat transitions into intermittently flooded savanna dominated by fever trees (*Acacia* syn. *Vachellia xanthophloea*) and lala palms (*Hyphaene coriacea*), and still further south into savanna woodland (mixed acacia-*Combretum*, sand forest, termitaria thicket).

Gorongosa was historically home to dense populations of ungulates (27 species; Tinley 1977) and large carnivores, but populations crashed during the Mozambican Civil War. Large-herbivore biomass declined by >90%, and leopard, African wild dog, and hyena were extirpated, while lion barely persisted (Stalmans et al. 2019). In 2007, the Gorongosa Project was founded as a public-private partnership to restore wildlife and support human development and scientific research in the park and surrounding communities (Pringle 2017). Owing to a combination of 'active' and 'passive' rewilding approaches (*sensu* Svenning et al. 2019)—involving targeted translocations, snare removal, and enforcement of anti-hunting laws—large-herbivore biomass has recovered to ≈80% of estimated pre-war levels in our study area (Stalmans et al. 2019). This recovery has been dominated by waterbuck, in contrast to the megaherbivore-dominated pre-war assemblage (Stalmans et al. 2019; Guyton et al. 2020). Predator recovery has lagged behind that of waterbuck and other ungulates. As of 2018, ≈80 lions were known to occur in the park (relative to a rough pre-war estimate of 200; Bouley et al. 2018), and leopards and wild dogs remained absent. In mid-2018, 14 wild dogs were reintroduced and scattered leopard sightings were confirmed; only sporadic sightings of hyena have occurred since 1977. The abundance of vegetation in the Urema floodplain and elsewhere in Gorongosa increased considerably between the 1970s and 2010s, when herbivore densities were low (Daskin et al. 2016; Guyton et al. 2020). Thus, as intensive restoration activity got underway in Gorongosa, ungulate populations were effectively released from bottom-up and top-down limiting factors, with abundant forage, few competitors or native predators, and curtailed human hunting (Stalmans et al. 2019; Gaynor et al. 2020).

Study species

Waterbuck are medium-sized (150–300 kg) antelopes that occur throughout Africa, but only "at or near water" owing to their high susceptibility to dehydration and overheating relative to other African bovids (Taylor et al. 1969, p. 630; see also Spinage 1982; Kihwele et al. 2020). Typical habitats include lakeshores, riverine woodlands, and open grasslands (Wirtz and Kaiser 1988). The typical diet is dominated by grasses and other graminoids (Tomlinson 1980; Cerling et al. 2003; Codron et al. 2007); individuals may also browse, especially during the dry season (Kassa et al. 2008; Pansu et al. 2019), which has been attributed to the high protein requirements of waterbuck (Taylor et al. 1969). Waterbuck exhibit strong territorial behavior. Prime-age males establish and defend year-round territories in areas of abundant, high-quality resources, often in close proximity to water sources such as lakes and rivers (Spinage 1982); females form fluid groups that share common home ranges overlapping male territories (Spinage 1982). Young bachelor males and older males are effectively excluded from the most resource-rich areas by territory-holding males (Tomlinson 1981) and therefore have fewer breeding opportunities (Wirtz 1982). Fewer than 10% of adult males maintain a territory at any one time, although territorial males occasionally tolerate satellite males (Wirtz 1981, 1982).

Historically, waterbuck in Gorongosa had "the most restricted dispersion of all the ungulates in the system" and were largely "confined to the green zone pastures [floodplains] which expand and contract with flood and ebb of the Urema Lake" (Tinley 1977, p. 140). In the peak dry season, "almost the entire waterbuck population" occurred in this area (Tinley 1977, p. 147). Waterbuck were the only ungulate species that stayed in the floodplain both day and night and throughout the dry and wet seasons (Tinley 1977). Pre-war aerial surveys estimated waterbuck density at 1.7 individuals km^{-2}, representing 4% of biomass among the 9 largest-bodied herbivore species; in 2018, parkwide waterbuck density was 32 individuals km^{-2}, representing 74% of the biomass of these 9 species, 75% of all large-herbivore biomass in the floodplain, and 64% of large-herbivore biomass park-wide (Stalmans et al. 2019; Guyton et al. 2020). As such, by 2018 waterbuck were approaching or perhaps already exceeding plausible estimates of carrying capacity (low, medium, and high estimates of 23, 41, and 81 individuals km^{-2}, respectively), which were derived by regressing the total large-herbivore biomass of 30 African savannas against rainfall (Coe et al. 1976) and calculating the 10th quantile, mean, and 90th quantile (respectively) for a system with Gorongosa's rainfall (Stalmans et al. 2019). In sum, all indications are that waterbuck population recovery has thus far been unimpeded by predation or interspecific competition, but that intraspecific competition and density-dependent limitation should be intensifying.

Forage availability in the floodplain

In September 2015, we built six herbivore exclosures (hexagonal, 260-m^2, >2-m tall) in the floodplain, each paired with an adjacent unmanipulated control plot of the same size (see Guyton et al. 2020 for details). We assumed that any effects of herbivore exclusion would be driven primarily by waterbuck, given their disproportionate abundance in the floodplain. We surveyed plant communities 12 times between August 2015 (immediately prior to exclosure construction) and February 2018 by placing 19 evenly spaced 1-m^2 quadrats per plot and measuring the aboveground plant biomass (using a disc pasture meter, Trollope and Potgieter 1986, which we calibrated locally; Fig. S1) and the percent cover of each plant species (using the cover-abundance scale of Braun-Blanquet 1932 and extracting the midpoint of each bin for analysis; see also Pansu et al. 2019). To test the prediction that waterbuck have reduced food availability in the floodplain, we first averaged the 19 biomass measurements from each plot in each survey and then analyzed these plot-level values in R (R Development Core Team 2019) using a linear mixed-effects model [*lmer* in package *lme4* (Bates et al. 2020), *anova* and *rand* in package *lmerTest* (Kuznetsova et al. 2020)] with treatment, time, rainfall during the prior month, treatment×time, and treatment×rainfall as fixed effects, and with exclosure-control pair (i.e., block) as a random effect (intercept) to account for the repeated measurements within plots and any baseline differences among them. Because the data spanned pre- and post-treatment surveys, we expected a significant treatment×time interaction.

To test whether food plants favored by waterbuck have been especially depleted, we used only the six surveys conducted between October 2016 (1 year after exclosure establishment) and February

2018. We first reduced data to the plot level (*n* = 12) by averaging the percent cover of each taxon across the 19 quadrats per plot and averaging those values across all surveys of each plot; we then calculated a standardized measure of experimental effect size [log-response ratio, ln(exclosure/control)] for each plant taxon in each block where the taxon was present in both plots. We regressed these mean effect sizes against previously published data on the selectivity (Jacobs' *D* index) of waterbuck for/against the 14 floodplain plant taxa that were most abundant (>1% of areal cover) in control plots in August 2016 (Pansu et al. 2019). In three cases where the selectivity measure lumped two or three closely related species (due to taxonomic ambiguities in dietary records), we summed the percent cover of those species before calculating effect size; we excluded one taxon that was identified only to family level and for which we considered the selectivity datum unreliable (Cyperaceae) and three for which we were unable to obtain effect sizes in at least two exclosure-control pairs (*Abutilon* sp., *Sida* sp., *Tephrosia* sp.), leaving *n* = 10 taxa for analysis. For each of these 10 taxa, we also tested whether percent cover differed between treatments by using Wilcoxon tests on the non-normally distributed data, with exclosure-control pair as a blocking factor, in JMP® Pro (Version 14, SAS Institute Inc., Cary, NC, 1989-2019).

Waterbuck population distribution

To assess shifts in waterbuck distribution and population structure, we used data from 12 aerial wildlife counts conducted between 1994 and 2018, along with ground-based surveys of waterbuck age and sex composition in 2019. Synoptic data from the aerial wildlife counts were previously published (Stalmans et al. 2019 contains full methodological details and summary data for all species); here, we used spatial data associated with the counts to quantify the relative densities of waterbuck in floodplain and savanna habitats. Briefly, the 1994, 1997, and 2004 surveys were conducted from a fixed-wing aircraft along parallel 250–300-m wide strips. The 2000–2002, 2007, and all subsequent surveys were conducted by helicopter along parallel 500-m wide strips. While surveys conducted from fixed-wing aircraft and helicopters can produce differing results (Gosse et al. 2002; Udevitz et al. 2006), the magnitude of such differences is unlikely to influence our results because waterbuck densities increased most rapidly after fixed-wing surveys were abandoned (Stalmans et al. 2019). Moreover, the three fixed-wing surveys (1994, 1997, 2004) and the three closest (in time) helicopter surveys (2000-2002) produced similar estimates of mean (± 1 SEM) waterbuck densities within the counting block (fixed-wing = 1.62 ± 1.05, helicopter = 1.75 ± 0.47; Stalmans et al. 2019). All counts were conducted in the late dry season (October–November), when visibility is highest, except in 2012 (May, early dry season). Animals were individually counted in flight, except in 2014 and 2018 when photographs were taken of waterbuck groups that were too dense or large to allow accurate in-flight counting. For all surveys, we used only observations recorded within a standardized 183,163-ha count block (representing 50% of the park and 72% of the Rift Valley landscape within it), which was comprehensively (i.e., 100% of count block) surveyed three times from 2014–2018 (Stalmans et al. 2019). Waterbuck counted during the surveys were classified as occupying either floodplain or savanna habitat on the basis of a pre-existing habitat classification map (Stalmans and Beilfuss 2008). Density estimates were calculated for each habitat in each survey by dividing the number of waterbuck by the total area surveyed in that habitat (Stalmans et al. 2019; see also Atkins et al. 2019; Guyton et al. 2020).

Waterbuck age and sex ratios were recorded during monthly surveys (*n* = 4 in floodplain and 5 in savanna) along the park's road network between May and September (early to mid dry season) in 2019. Animals were counted using 10×40-mm binoculars from a vehicle travelling a maximum of

25 km hr^{-1} during early morning (07:00–12:00) and late afternoon (14:00–16:30). For each sighting, we recorded the number of individuals, sex and age composition, group structure, GPS location, and habitat (floodplain or savanna). Sex was determined based on the presence of horns. Age was classified as juvenile, yearling, or adult (Owen-Smith and Mason 2005; Decesare et al. 2012) on the basis of body size and (for males) the presence, size, and shape of horns (Lundrigan 1996; Decesare et al. 2012). Group structure was classified in five categories: lone male, lone female, bachelor group, female group, or breeding/mixed group. Individuals were considered part of the same group when they were <50 m apart (Marealle et al. 2010; Blank et al. 2012). To evaluate our prediction that habitat expansion is biased by reproductive stage and that the floodplain is the prime breeding ground, we tested whether the ratios of adult females to adult males and adult females to subadult females were greater in the floodplain, and whether male-female associations (i.e., mixed groups) were more common in the floodplain, all of which would be consistent with the territorial social system of waterbuck and with the best territories being in the floodplain. We compared female-male and adult-subadult ratios between habitats using analysis of variance (ANOVA), verifying that the residuals were normally distributed and the variances homogeneous. We analyzed social-group composition in R using permutational multivariate ANOVA (perMANOVA) with *adonis2* in *vegan* v2.5-6 (Oksanen et al. 2019).

Body condition

In 2015 and 2016, we chemically immobilized a total of 30 female waterbuck from savanna (n = 15) and floodplain (n = 15) and fit them with custom-built collars (Park et al. 2019) that included GPS units, video recorders (National Geographic Crittercam), and tri-axial accelerometers (see *Movements and activity patterns*) in June–August 2015 (n = 5 in floodplain) and August 2016 (n = 10 in floodplain, 15 in savanna); we present data from both years in the main text, but the results were equivalent when we analyzed the 2016 data only. Animals were darted (thiafentanil, medetomidine, azaperone) from a helicopter. Handling procedures were approved by the Institutional Animal Care and Use Committee of Princeton University (protocol 2075F-16) and accorded with American Society of Mammalogists guidelines (Sikes et al. 2011). We collected a suite of measurements and samples from anaesthetized individuals before fitting them with the custom-built collars, which were also pre-programmed to release without recapturing animals.

Body-condition measurements included chest girth, body length, and hind-foot length (measured with a tape); thickness of the biceps femoris and longissimus dorsi and the maximum depth of rump fat (measured using ultrasonography); and standardized palpation scores of fat deposition at the sacrosciatic ligament, lumbar vertebrae, sacrum, base of the tail, and caudal vertebrae. Equations for converting these measurements into an estimate of ingesta-free body fat have been validated only for a subset of North American cervids (Cook et al. 2010); in the absence of a validated model for tropical antelopes, we followed Atkins et al. (2019) in developing a body-condition index by using a principal component analysis, of which the first two components (i.e., linear combinations of condition metrics) together explained 59% of the variation in the metrics among 29 of the waterbuck (one savanna individual was excluded because an erroneous measurement was recorded for hind-foot length) (Fig. S2; Tables S1, S2). Principal component 1 was most strongly associated with the measurement of maximum rump-fat depth, palpation scores, and chest girth; principal component 2 was most strongly associated with body length and hind-foot length. We compared the scores for each of the first two components across habitats using two-sample t-tests. In the absence of information on habitat-use patterns prior to collaring, we assessed habitat affiliation based on capture location; however, our conclusions were qualitatively unaltered when we instead assessed habitat affiliation based on subsequent GPS locations of collared animals.

Movements and activity patterns

We analyzed collar-derived data from 22 of the 30 captured waterbuck (n = 10 captured in the floodplain, 5 each in 2015 and 2016; n = 12 captured in savanna in 2016); eight individuals were excluded from these analyses owing to collar malfunctions. The custom collars that we used are described in detail by Park et al. (2019). Collar-mounted GPS units, accelerometers, and Crittercams were programmed using algorithms to regulate the frequency of data collection, enabling a high temporal resolution of activity information while also conserving battery life to maximize the number of days of tracking (mean 12.8 d; range 2.9–22.8 d). These algorithms were used to switch the devices between four modes: *High, Alert, Ready*, and *Sleep* (Park et al. 2019). Sampling mode was determined by a combination of the predicted behavioral state of the animal (resting, walking, eating, running; see below) and the proximity of other collared animals. Devices were placed in *Sleep* mode when the activity state was classified as resting and in *Ready* mode when the activity state was classified as walking, eating, or running; *Alert* and *High* modes were only activated in the presence of other collared individuals. In all modes, acceleration data were collected at 50-Hz (these data were not stored by devices in *Sleep* mode but were still collected to allow the sampling mode to switch when the animal's activity changed). GPS fixes were recorded every 600-s in *Sleep* mode, every 400-s in *Ready* mode, and every 20-s in *Alert* and *High* modes. Video recording was triggered using a combination of time-based initiation (to ensure that approximately five 5-min videos were recorded by each device every day, independent of sampling mode) and proximity-based initiation (triggered by devices switching from *Alert* to *High* mode to record potential interactions between collared individuals and use of specific points of interest on the landscape such as vegetation plots). Here, we used GPS data to assess movement patterns (rarefied to an average fix-rate between 5–10-min), accelerometry data to assess activity patterns (as described in the following paragraphs), and video data to validate energetic attributes (i.e., periods of continuous cropping; see *Energetics* and Video S1).

Although Gorongosa's floodplain and savanna are distinct habitat types, each is spatially heterogeneous; in particular, the floodplain comprises a broad treeless ring around Lake Urema that grades into sparsely wooded grassland towards the floodplain-savanna boundary (Fig. S3). Moreover, although habitat affiliation was classified *a priori* based on capture location (per the habitat map of Stalmans and Beilfuss 2008), individuals move between habitat types, and thus capture location might not be representative of subsequent habitat use. Therefore, for analyses of movement and activity patterns, we compared waterbuck using a continuous measure of habitat affiliation—specifically, the proportion of time that each individual spent in the treeless grassland around Lake Urema (the interior floodplain, henceforth 'grassland'; see Fig. S3 and Atkins et al. 2019). Proportional use of grassland was measured by calculating the 95% utilization distribution (UD)—a spatially explicit representation of the relative intensity of space use by an animal within its home range (Millspaugh et al. 2006)—for each individual's daytime and nighttime GPS locations using the Dynamic Brownian Bridge kernel estimation method in the *move* package (v.3.2.0; Kranstauber and Smolla 2020) in R v.3.6.1. We overlaid each individual's UD on the habitat map of Stalmans & Beilfuss (2008), assigning values of 1 to grassland and 0 to all other habitats. We then calculated the proportional volume of the UD that overlapped with grassland habitat for each individual. In the *Results*, for simplicity, we present the average proportional use of grassland for each individual across both day and night; treating day and night separately yielded qualitatively equivalent inferences (Fig. S4).

We used the GPS data to quantify two characteristics of individual movement patterns, 95% home-range isopleth and movement rate. The areas of the 95% home-range isopleths were extracted from the UDs and averaged across day and night measurements. Despite variation in the number of GPS fixes collected for each individual, there was no correlation between the length of time each individual was collared and the area of the isopleth (Fig. S5). Movement rate was measured by calculating the distance that each individual moved during a given period of time. Owing to a small difference in the average fix rate between 2015 and 2016 (2015, 8.9 ± 0.03 min; 2016, 5.8 ± 0.5 min), we calculated a standardized measure of individual movement rate (in m min^{-1}) by dividing individual step lengths by the average time lag between GPS fixes within each year. Step lengths were quantified using the *move* package as the Euclidean distance between two successive GPS locations. We used linear regressions to examine how the area of the 95% home-range isopleth (log-transformed owing to non-normality) and movement rate varied as a function of proportional grassland use.

Given the exceptionally high water dependence of waterbuck, we also used GPS data to assess how waterbuck used water sources—Lake Urema, rivers, and pans (seasonal or perennial ponds)—in floodplain and savanna. We estimated the recursive movement of waterbuck around these water sources using two measures: the average number of times an individual visited each type of water source (i.e., lake, rivers, pans), and the maximum number of times an individual visited any single water source. Recursion was quantified using the R package *recurse* (v.1.1.2, Bracis et al. 2018). A visit to a given location was counted whenever a waterbuck entered a circular buffer of 100-m radius around the centroid of each pan (425 locations in total), and at random locations along the edges of Lake Urema (194 locations in total) and rivers (439 locations in total) based on remotely-sensed maps of the lake and river boundaries. This buffer was used to account for potential error in both the classification of water sources and the GPS location data. A visit to a location was counted as a revisit only if it was separated from the previous visit by ≥30-min. The locations of Lake Urema and the two permanent rivers were derived from Stalmans & Beilfuss (2008). Pan locations were manually digitized using ArcGIS Online and Google Earth satellite imagery.

Waterbuck activity was classified into one of four behavioral states using triaxial acceleration and velocity profiles. Resting, walking, and running have well-defined acceleration signatures, and placement of the device around the neck enabled us to distinguish between walking and eating (via the relative accelerometry along the *z*- and *x*-axes when animals bent their necks down and moved their heads to crop vegetation; see Appendix C of Park et al. 2019). The algorithm used to assign behavioral states was trained via supervised classification of contemporaneous acceleration and video data segments collected in 2016. The standard deviation along each axis of the triaxial acceleration data was then computed for each of the classified segments, and supervised learning was applied to find partitions in these standard deviations that delineated each activity state (Park et al. 2019). Performance of this algorithm was previously assessed using the data collected from waterbuck in 2015 (Park et al. 2019). Algorithm-based classifications were compared to known behaviors recorded by the animal-borne video cameras for contemporaneous segments of accelerometer and video data; this validation indicated an accuracy rate of 88–97% across individuals (Park et al. 2019). We present activity data for the 14 waterbuck collared in 2016 (but we used GPS location data from both years). Three additional individuals collared in 2016 were excluded owing to errors in the activity-data collection process. To evaluate activity budgets, we used the behavioral-state classifications to calculate the proportion of all accelerometer data points (at 50-Hz) in which each individual was resting, walking, eating, or running. We then used linear regressions to examine how the proportion of time spent eating, walking, running, and resting varied as functions of proportional grassland use. One waterbuck was flagged in these analyses owing to anomalously and suspiciously low activity levels throughout the collaring period (i.e., in the resting state >75% of the time). We present results of the regression without this outlying individual in the main text; results with this individual included are in Fig. S4E,F.

Diet composition

We used DNA metabarcoding to identify food plants and quantify the relative abundance of plant DNA sequences amplified from individual fecal samples. Sample-collection and metabarcoding protocols broadly followed those used in our previous studies of large-herbivore diets in Gorongosa (Pansu et al. 2019; Atkins et al. 2019; Branco et al. 2019; Guyton et al. 2020). In 2016, we collected fecal samples (*n* = 10 floodplain, 15 savanna) from anaesthetized individuals at the time of collaring; we interpreted the capture location as reflecting the habitat affiliation for the purpose of diet analysis, as fecal samples reflect consumption over the preceding few days, and the data supported this assumption (see *Results: Waterbuck diet composition and quality*). In subsequent years (2017–2019), we opportunistically collected samples by driving roads in the floodplain and savanna in June–July of each year (mid-dry season, similar to 2016) and collecting samples from waterbuck that we observed defecating (approximately *n* = 15 per habitat per year). We placed samples on ice for transport to the field laboratory, where we homogenized them and transferred pea-sized subsamples into tubes containing silica beads and DNA lysis and conservation buffer (Zymo Xpedition Stabilization/Lysis Solution, Zymo Research, CA). Tubes were vortexed, subjected to an antiviral heat treatment of 72°C for 30 min (per United States Department of Agriculture permit 130123 to R.M.P.), and frozen at -20°C until transport to Princeton University where they were stored at -80°C. DNA was extracted in batches of 29 samples and 1 negative control using Zymo Soil/Fecal DNA Miniprep extraction kits according to the manufacturer's protocol. In 2018 and 2019, DNA concentrations were standardized between samples prior to PCR. We amplified plant DNA from each fecal sample using established PCR methods targeting the P6-loop of the chloroplast *trn*L intron, a widely used metabarcode for vascular plants (Taberlet et al. 2007; Kartzinel et al. 2015). Details on PCR protocols can be found in Pansu et al. (2019). We conducted three replicate PCRs for each sample, as well as for negative extraction controls, positive PCR controls (in 2016 and 2017 only) and negative PCR controls. We used gel electrophoresis to confirm amplification of the P6 barcode and purified the PCR products using Qiagen MinElute kits (Qiagen, MD, USA). We prepared purified products for sequencing (Illumina Hi-Seq, 2×150 bp paired-end reads) using PCR-free (2016-2017) and PCR-based library preparations (2018-2019).

We filtered sequence data using the OBITools pipeline (Boyer et al. 2016) following the order of operations described in Pansu et al. (2019). First, paired-end DNA reads were assembled and assigned to the fecal sample they came from. Next, we discarded low-quality sequences, those resulting from PCR errors, and those with low abundance over the entire dataset ($n \leq 10$ reads). Remaining sequences were preferentially assigned to plant taxa based on a local reference library of DNA sequences for 243 common Gorongosa plant species (Pansu et al. 2019); if the match in this local database was <98% similarity, the sequence was assigned to a global reference set of DNA sequences from the European Molecular Biology Laboratory database (Release 134; Baker et al. 2000). We discarded sequences that were variants of abundant sequences, had low similarity (<80%) with the closest reference sequence, or were putative contaminants (i.e., had the highest relative abundance in negative controls). The remaining sequences, with taxonomic information attached, were considered molecular operational taxonomic units (mOTUs) representing distinct taxa. We assessed the repeatability of mOTU composition between PCR replicates using the Bray-Curtis distances between replicates. We discarded a sample replicate if its distance to other replicates was above the 95th quantile of the distances for all intra-sample comparisons or if it fell within the distribution of inter-sample distances (Taberlet et al. 2018). PCR replicates were then merged using the average number of reads across all retained replicates for a sample (discarding samples with only one retained replicate); sequences were considered to be present in a sample only if they represented ≥1% of a sample's reads. As a final step, we rarefied the data to 1250 reads per sample (to facilitate compositional comparisons) and converted them into relative read abundance (RRA), the proportional representation of each sequence in a sample. Previous studies indicate that RRA of the *trn*L-P6 barcode provides a reasonable proxy for diet composition in large herbivores (Willerslev et al. 2014; Craine et al. 2015; Kartzinel et al. 2015; see also Deagle et al. 2019); accordingly, we used RRA for our analyses of diet composition. In total, we present dietary data from 111 waterbuck samples collected between 2016 and 2019. Owing to the subtle differences in laboratory procedures between years, we focus primarily on within-year comparisons of diet composition.

To visually compare diet compositions of floodplain and savanna waterbuck, we used non-metric multidimensional scaling (NMDS) ordinations based on Bray-Curtis dissimilarities; we tested whether floodplain and savanna waterbuck diets were compositionally distinct in each year using perMANOVA with the *adonis2* function of *vegan*. At a coarser taxonomic grain, we assessed the contribution of different plant families to waterbuck diets in each habitat using perMANOVA. We also compared waterbuck dietary richness between habitats in each year using sample-based rarefaction (*specaccum* function in *vegan*) and calculated the Shannon diversity index (total niche width; Roughgarden 1972) of diets in each habitat and year (*diversity* function in *vegan*).

Diet quality

We combined the dietary data with local measurements of food-plant functional traits to estimate the quality of waterbuck diets in each habitat. We measured eight physical and chemical traits for 204 plant species, including most of those expected to occur in waterbuck diets. Physical traits (height, leaf dry-matter content, leaf tensile strength) were measured for 1–6 focal individuals per plant species (mean ± 1 SEM: height = 2.58 ± 0.06; leaf dry-matter content = 2.55 ± 0.06; leaf tensile strength = 2.55 ± 0.06). Leaf traits (dry-matter content and tensile strength) were also measured for multiple leaves per individual (mean ± 1 SEM: dry-matter content = 4.92 ± 0.02, tensile strength = 1.05 ± 0.01). Plant height was measured in the field. Stems with mature, sun-exposed leaves from each focal individual were transported in coolers to the field laboratory and processed the same day; we measured leaf dry-matter content (dry mass as a percentage of wet mass) and tensile strength (longitudinal force required to tear leaf, corrected for leaf cross-sectional area, using a 50-N Compact Force Gauge, Mecmesin Corporation, West Sussex, UK) for up to five sequential green leaves on each stem, starting from the youngest fully open leaf. We estimated percent water content for each plant by subtracting the mean percent leaf dry-matter content from 100. For leaf chemistry (crude protein, total ash, acid detergent lignin, neutral detergent fiber, percent sodium), we collected >5-g of the youngest fully open leaves in roughly equal amounts from each of ≥3 individuals per species, which were oven dried at 55°C and analyzed by Dairy One Cooperative (Ithaca, NY). We calculated percent digestibility and digestible-protein content for each plant using the summative equations of Robbins et al. (1987*a,* 1987*b*). Trait values for each species were averaged across replicate individuals for analysis. Sampling of three individuals is considered a minimum for capturing intra-specific variation in plant traits (Perez-Harguindeguy et al. 2013). However our priority was to measure trait values for a maximum number of dietary plant species, which occasionally came at the expense of intra-specific replication for scarce taxa.

Plant species in the traits dataset were assigned to dietary mOTUs using a systematic process that accounted for minor differences in taxonomic assignment. First, we paired all mOTUs identified to species in the diet data with perfectly matched species in the traits data. Second, the identities of some mOTUs that were identified to levels between genus and family were inferred by using BLAST (Sayers et al. 2020) in conjunction with our knowledge of the local flora. Using these identifications, we paired remaining higher taxonomic-level mOTUs (genus through family) with the average trait values of all remaining species in that higher taxon. Last, we removed all mOTUs left without a match in the traits dataset and calculated the remaining proportion of the diet (RRA) represented by traits-matched mOTUs. If this value was less than 0.8 (i.e., <80% of the diet was matched to plant traits), we excluded those fecal samples from analysis; all but two samples met this threshold, and the mean RRA of traits-matched mOTUs in the remaining 109 samples was 0.98. We then rescaled the data so that RRA again summed to 1 for each sample and used the RRA-weighted averages of trait values to estimate the digestibility, digestible-protein content, water content, tensile strength, plant height, and sodium content of each diet (Atkins et al. 2019; Branco et al. 2019). We analyzed these data for samples collected from 2016–2019 using a linear model (*aov* in R) with habitat type, year, and their interaction as factors. Plant height was log-transformed to meet model assumptions.

Energetics

Waterbuck bite rates (cropping bites per minute) were estimated using videos of foraging female waterbuck recorded by camera traps (Bushnell Aggressor No Glow) in June–July 2017 (Video S2). All cameras were set to record 1-min videos with a 10-sec delay between triggers. Each camera was strapped to a tree or steel rod at ≈1-m off the ground. The area in front of each camera was cleared of tall grass, branches, and debris. We set up 32 camera traps across two grids, one in the floodplain and one in savanna, with cameras ≈500-m apart (Fig. S6). Each camera was set up for approximately 3 weeks during the dry season. We then extracted a subset of the videos based on video quality; we only used videos in which individual cropping bites could be discerned. Each video was scored by one or two observers. Observers first trained on a subset of videos from each habitat type to ensure concordance in their bite rate estimates. Half of the videos (n = 12 savanna, n = 8 floodplain) were scored independently by two observers. The remaining videos (n = 5 savanna, n = 14 floodplain) were scored by just one observer; due to strong agreement in the recorded bite rates for each habitat using videos scored by either one or two observers, both sets of videos were included in the analysis. This resulted in n = 22 videos in the floodplain and n = 17 videos in savanna. A cropping bite was scored whenever the waterbuck had its head down and tugged its head to tear vegetation. We also scored the total time continuously foraging (i.e., actively eating or chewing) in each video to ensure the accuracy of our bite rate estimates. Bite rate was equal to the number of cropping bites divided by the total time spent foraging per video and was averaged across estimates when there were two observers.

We used these data to estimate the energetic balance of waterbuck in each habitat. We first rearranged equation 4 from Gross et al. (1993) to estimate average bite size (S, in g bite^{-1}) for each habitat

$$S = \mathrm{Rmax} \times (1/\mathrm{B} - \mathrm{h}) \qquad \text{(Eq. S1)}$$

where B is bite rate (bites min^{-1}); R_{max} is maximum processing rate per bite (g min^{-1}) and was estimated as $0.71 \times M^{0.7}$ (M, body mass, was assumed to be 200kg for all individuals; Shipley et al. 1994); and h is handling time (min bite^{-1}) needed to process a bite, assumed to be 0.015, the average value across all mammalian herbivores (Shipley et al. 1994). We similarly calculated food intake rate (I, in g min^{-1}), using equation 5 from Gross et al. (1993)

$$I = [(R_{max} \times S) / (R_{max} \times h + S)] \qquad \text{(Eq. S2)}$$

We then estimated daily energy and protein intake for individuals in each habitat as

$$\text{energy intake} = I \times F \times DG \times GE \qquad \text{(Eq. S3)}$$

$$\text{protein intake} = I \times F \times DP \qquad \text{(Eq. S4)}$$

where F is total time per day spent foraging (estimated as a proportion using the behavioral-state classifications), GE is the gross energy content (kcal g^{-1}), DG is digestibility (%), and DP is digestible protein (%). In this framework, F must be limited to periods of continuous foraging/cropping; to estimate F, we calculated the time spent eating per day using the activity classifications and corrected this value to time spent continuously cropping by comparing contemporaneous activity classifications with the observed behavior in a subset of video data collected from the animal-borne Crittercams (n = 3 individuals for both savanna and floodplain waterbuck). Nutrient values were estimated using the same methods for plant traits described above. For DG and DP, the mean for each quality metric was calculated using diet-weighted trait averages for each habitat type. We used a constant value for GE (mean across all plants) because we expected this value to be similar across plant taxa (Barboza et al. 2009) and because GE data were available only for a subset of the plant species measured (39 of 204). To quantify energy expenditures, we estimated the mass-specific energetic cost of locomotion (L, in kcal kg^{-1} km^{-1}) using the equation from Parker et al. for cervids on horizontal ground (1984)

$$L = 2.97 \times M^{-0.34} \qquad \text{(Eq. S5)}$$

and multiplied this value by the total distance moved per day (in km) and by M (200 kg, as above) to obtain the energy expended in movement by each individual. We estimated basal metabolic rate using Kleiber's rule ($70 \times M^{0.75}$). Net energy balance was then calculated as the total energy intake minus the total energy expended per day (i.e., $I - L -$ BMR; Eq. S6).

Owing to the uncertainty in some of our parameter estimates, we used Latin hypercube sampling (McKay et al. 1979) to investigate the sensitivity of our net-energy-balance estimates to variation in the values for handling time (h), body mass (M), and bite rate (B). Because bite size (S) was estimated as a function of B, this analysis also allowed us to assess the sensitivity of our results to variation in S. We allowed h to vary between a minimum of 0.012 and a maximum of 0.025 min bite^{-1}, M between 180 and 220 kg, and B within ±15% of the mean values estimated from the videos. We selected 1,000 random samples of each of these three parameters for both the floodplain and savanna waterbuck, assuming a uniform distribution for each parameter within the chosen ranges. We then repeated our calculations of daily energy balance using these sampled values while holding all other parameter values constant, yielding 1,000 iterations for each habitat type. To assess the influence of each parameter value on our energy-balance estimates, we fit multiple linear regression model for each habitat type, where the sampled values of h, M, B, and S were included as predictor variables and daily energy balance was the response variable.

Parasite counts

During the waterbuck captures in 2016, we recorded the numbers of ticks (Acari) and lice (Phthiraptera) on each individual's face, neck, and ears. Separately, we estimated nematode endoparasite loads (Strongylida) by counting eggs in the fecal samples collected for diet analysis in 2017–2019. We used the modified McMaster method (Whitlock 1948): 2 g of feces were suspended in 28 mL of saturated salt solution and applied to a gridded microscope slide using a suction pipette. Nematode eggs floated to the top of the solution and were counted under 10× magnification. We estimated the density of eggs g^{-1} of feces by extrapolating the number of eggs counted on the slide grid (0.3-mL) to the total solution volume. We made two replicate egg counts per fecal sample, averaged them to reduce sampling error, and rounded to the nearest integer for statistical analysis. Due to the characteristically overdispersed nature of egg-count data, we tested for differences in endoparasite burdens between habitats and across years with a negative-binomial generalized linear model (*glm.nb* function in R package *MASS*; (Venables and Ripley 2002) with habitat type and year as fixed effects.

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Table S1. Summary of principal component analysis of body-condition data from 29 female waterbuck, 2015–2016. Each column (PC1–PC11) represents a principal component (*n* = 11 in total because 11 body-condition metrics were used in the analysis). Over 50% of the variance in these metrics is explained by the first two principal components (44% and 15%, respectively).

	PC1	PC2	PC3	PC4	PC5	PC6	PC7	PC8	PC9	PC10	PC11
Standard deviation	2.20	1.28	1.05	0.97	0.82	0.76	0.64	0.57	0.44	0.42	0.34
Proportion of Variance explained	0.44	0.15	0.10	0.09	0.06	0.05	0.04	0.03	0.02	0.02	0.01
Cumulative Proportion of Variance	0.44	0.59	0.69	0.77	0.84	0.89	0.93	0.96	0.97	0.99	1.00

Table S2. Principal component loadings for each body-condition variable from 29 female waterbuck, 2015–2016. Chest girth and the palpation scores from the sacrosciatic ligament, lumbar vertebrae, sacrum, base of the tail, and caudal vertebrae loaded most highly onto PC1 (a proxy for body fat). The thickness of the longissimus dorsi muscle and measurements of body length and hind-foot length loaded most highly onto PC2 (a proxy for body size). Maximum rump-fat depth loaded approximately equally onto PC1 and PC2, and thickness of the biceps femoris muscle loaded most highly onto Principal Component 3.

	PC1	PC2	PC3	PC4	PC5	PC6	PC7	PC8	PC9	PC10	PC11
Max_fat	0.32	0.34	-0.14	0.26	-0.21	0.20	-0.50	0.40	-0.17	0.27	-0.32
B_femoris	0.05	-0.07	0.92	-0.11	-0.01	-0.07	-0.08	0.04	0.07	0.15	-0.29
L_dorsi	0.19	-0.54	-0.17	-0.38	-0.05	-0.29	-0.03	0.62	0.14	-0.07	-0.06
SS_ligament	0.37	0.20	-0.03	-0.17	-0.03	0.23	0.64	0.05	-0.19	-0.30	-0.45
Lumbar_vert	0.32	0.06	-0.01	0.28	-0.16	-0.78	-0.08	-0.26	-0.15	-0.26	-0.10
Sacrum	0.30	-0.12	0.18	0.45	0.61	0.08	0.09	0.29	-0.23	-0.13	0.35
Base_tail	0.40	0.10	0.02	-0.06	0.07	0.22	-0.30	-0.16	0.68	-0.43	0.07
Caudal_vert	0.40	0.13	-0.11	-0.06	0.17	-0.19	0.30	-0.12	0.33	0.72	0.10
Chest_girth	0.35	0.14	0.15	-0.46	-0.30	0.08	-0.10	-0.07	-0.40	-0.01	0.59
Body_length	0.25	-0.53	-0.15	-0.13	0.25	0.21	-0.28	-0.50	-0.29	0.13	-0.30
Hind_foot	0.16	-0.46	0.07	0.48	-0.61	0.25	0.24	-0.06	0.12	0.08	0.15

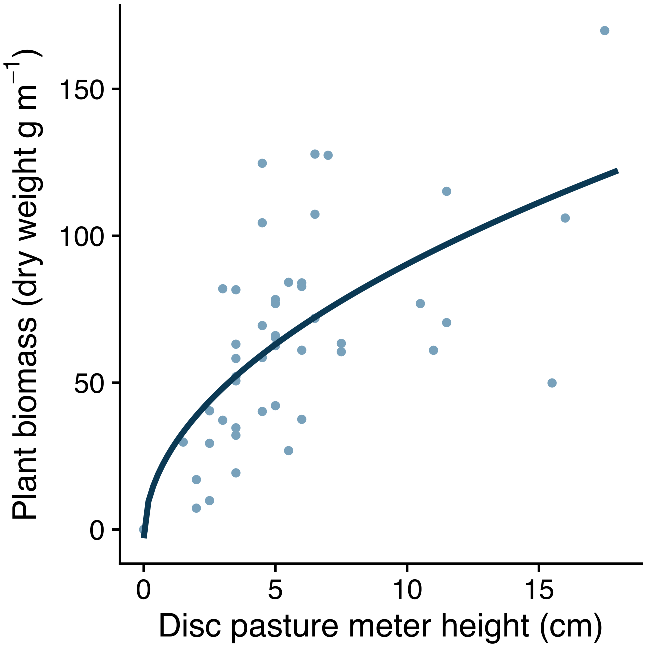

Figure S1. Calibration of the disc pasture meter for Gorongosa. In each of 48 1-m^2 quadrats, we measured the height of the herbaceous plant community using a standard disc pasture meter (cf. Trollope and Potgieter 1986; Zambatis et al. 2006). We then harvested, dried, and weighed all aboveground plant biomass within each quadrat. One extremely anomalous data point (height of 30 cm and dry biomass of 48.2 g) was excluded prior to analysis and is not shown. Plant biomass m^{-2} was estimated as $-2.97 + 29.51 \times h^{0.5}$, where h is the height of the disc pasture meter in cm. We use this equation to estimate standing forage biomass (in kg ha^{-1}) in experimental exclosure and control plots between 2015 and 2018 (Figure 1).

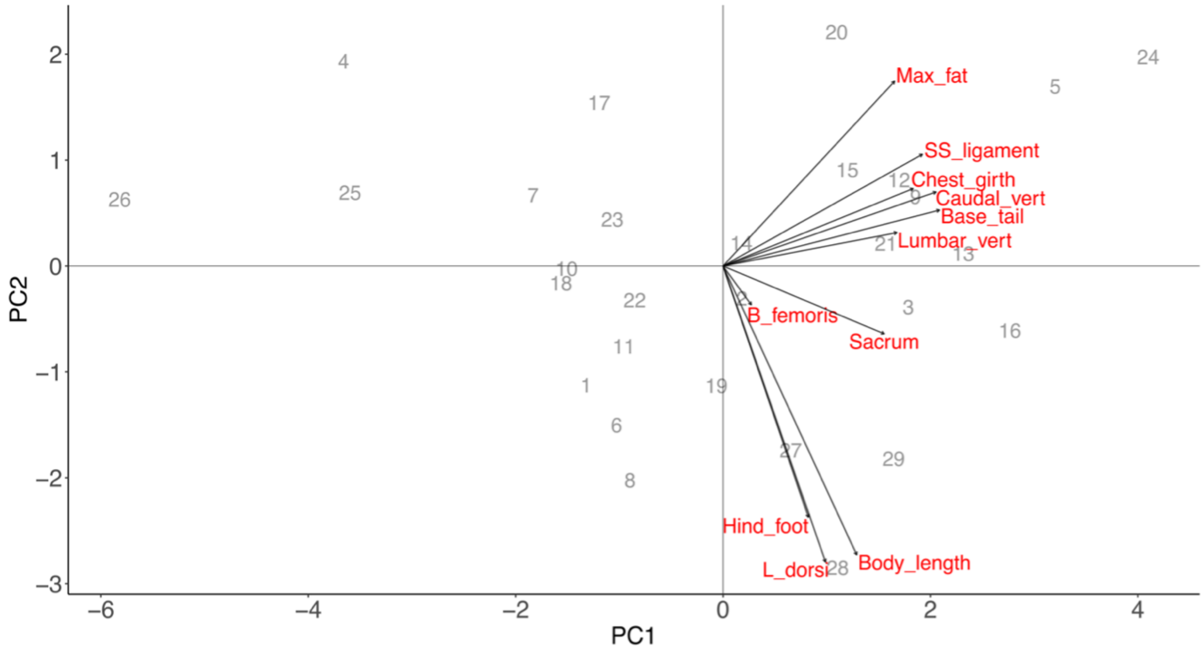

Figure S2. Principal component analysis of 11 body-condition metrics from 29 female waterbuck. The body-condition metrics included (as shown counterclockwise from lower left to upper right): hind-foot length, thickness of the longissimus dorsi, body length, thickness of the biceps femoris, chest girth, palpation scores taken at the sacrum, lumbar vertebrae, base of the tail, caudal vertebrae, and sacrosciatic ligament, and maximum rump-fat depth. Each grey number represents an individual antelope, the position of which reflects its scores on the first two principal components. Principal Component 1 (PC1, horizontal axis) and Principal Component 2 (PC2, vertical axis) together explained 59% of the variance in these data. Black arrows show the projections of the original variables. Body-condition metrics that loaded most highly onto PC1 (a proxy for body fat) were chest girth and the palpation scores from the sacrosciatic ligament, lumbar vertebrae, sacrum, base of the tail, and caudal vertebrae. Metrics that loaded most highly onto PC2 (a proxy for body size) were thickness of the longissimus dorsi, body length, and hind-foot length. Maximum rump-fat depth loaded approximately equally onto PC1 and PC2, and thickness of the biceps femoris loaded most highly onto Principal Component 3 (not plotted). All measurements were made at time of capture.

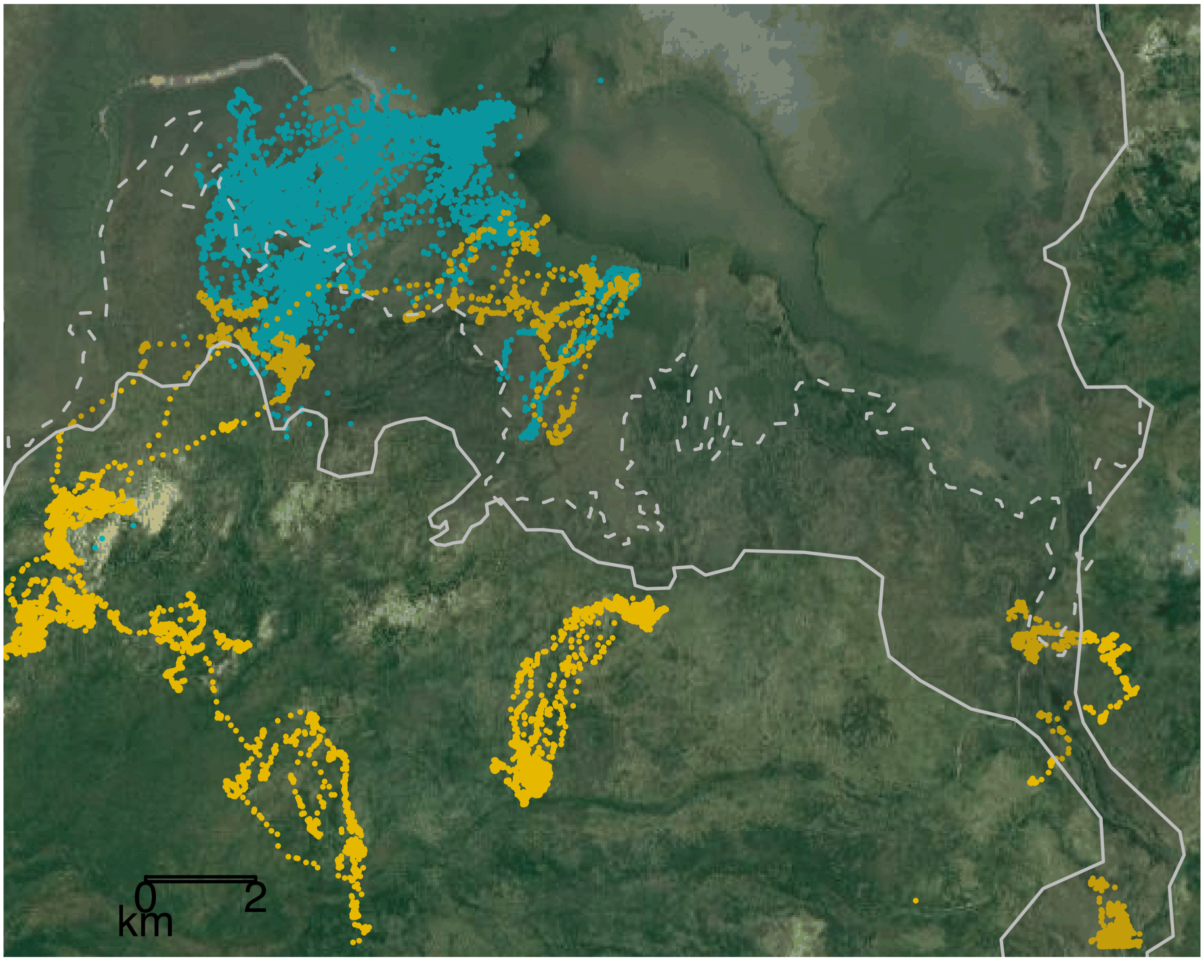

Figure S3. Habitat use by Gorongosa waterbuck in the dry seasons of 2015 and 2016. Map shows GPS locations of collared floodplain and savanna waterbuck, colored by capture location (blue, floodplain; gold, savanna and transitional palm forest between the floodplain and savanna). Solid grey line distinguishes the floodplain from the savanna; dashed grey line distinguishes the treeless floodplain grassland around Lake Urema (top center); see also Figure S6. In general, individuals showed high habitat fidelity during the study period; however individuals can and did move between habitats. To account for these movements, differences in waterbuck movement behavior (e.g., area of the 95% home-range isopleth, movement rate, activity budgets) during the collaring period were analyzed as a function of the proportion of time that individuals spent in the floodplain grassland habitat rather than on the basis of initial capture location.

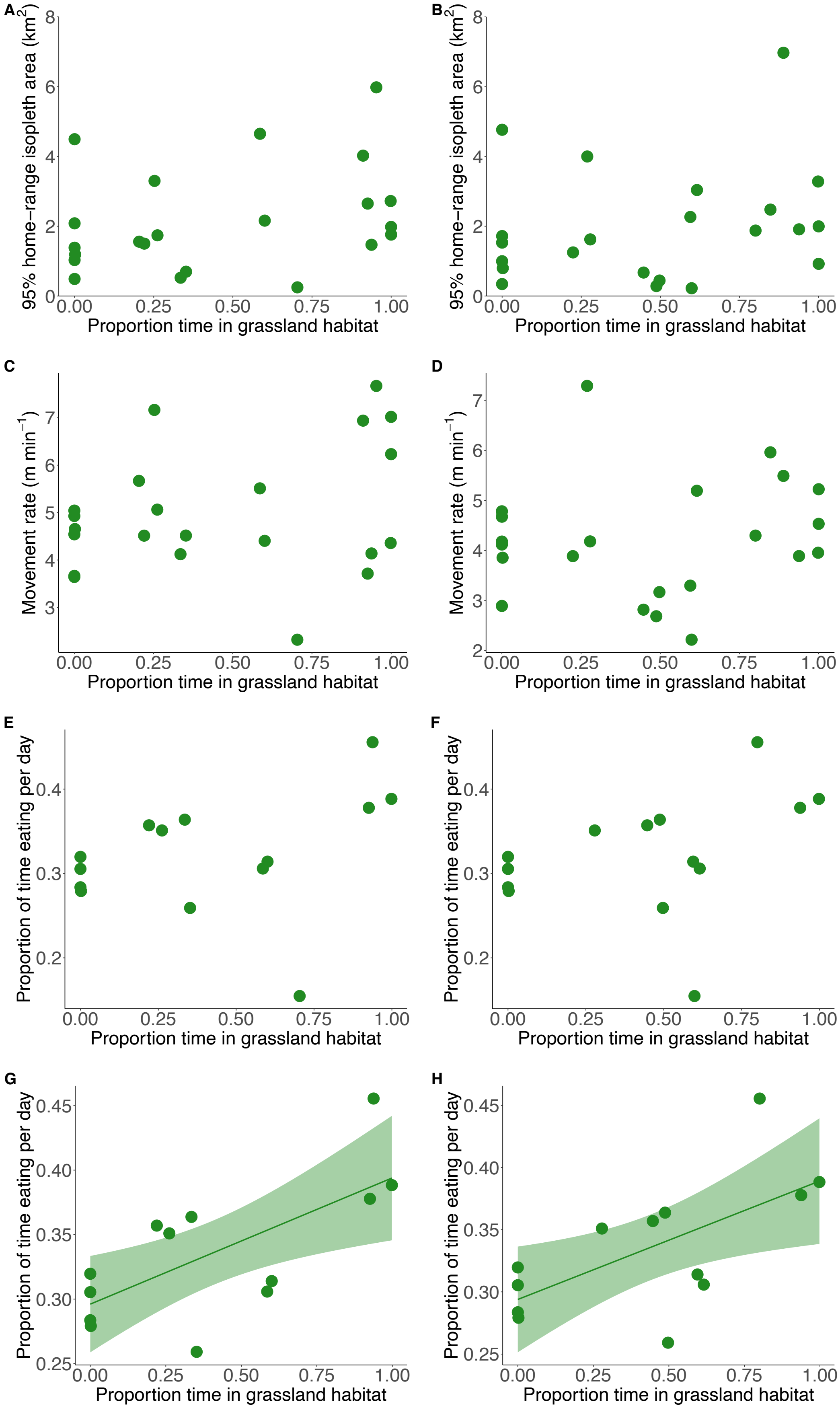
A
B
95% home−range isopleth area (km^2)
0
2
4
6
8
C
D
Movement rate (m min^{-1})
2
3
4
5
6
7
E
F
Proportion of time eating per day
0.2
0.3
0.4
G
H
0.25
0.30
0.35
0.40
0.45
0.00
0.25
0.50
0.75
1.00
Proportion time in grassland habitat

Figure S4. Waterbuck movement and activity budgets as functions of habitat affiliation. Behavioral attributes were assessed using linear regression as a function of the proportion of time each individual spent in grassland (i.e., interior floodplain, see Figure S3) during the day (left panels) and night (right panels). **(A, B)** Area of each individual's 95% home-range isopleth (i.e., relative intensity of space use, derived from the 95% utilization distribution; **A**, $R^2 = 0.03$, $F_{1,20} = 1.72$, $P = 0.21$; **B**, $R^2 = 0.0003$, $F_{1,20} = 1.01$, $P = 0.33$; area was log-transformed owing to evidence of non-normality in the data). **(C, D)** Individual movement rate (**C**, $R^2 = 0.03$, $F_{1,20} = 1.76$, $P = 0.20$; **D**, $R^2 = 0.02$, $F_{1,20} = 0.35$, $P = 0.56$). **(E, F)** Percentage of time that individuals spent eating, with the full dataset of 14 individuals plotted (**E**, $R^2 = 0.04$, $F_{1,12} = 1.56$, $P = 0.24$; **F**, $R^2 = 0.14$, $F_{1,12} = 1.98$, $P = 0.19$). **(G, H)** Percentage of time that individuals spent eating, with the outlier removed (**G**, $R^2 = 0.42$, $F_{1,11} = 9.70$, $P = 0.0098$; **H**, $R^2 = 0.35$, $F_{1,15} = 7.52$, $P = 0.019$). Behavioral states in **E–H** were determined using classification algorithms trained on the accelerometry data and verified using high-definition animal-borne video data (Park et al. 2019).

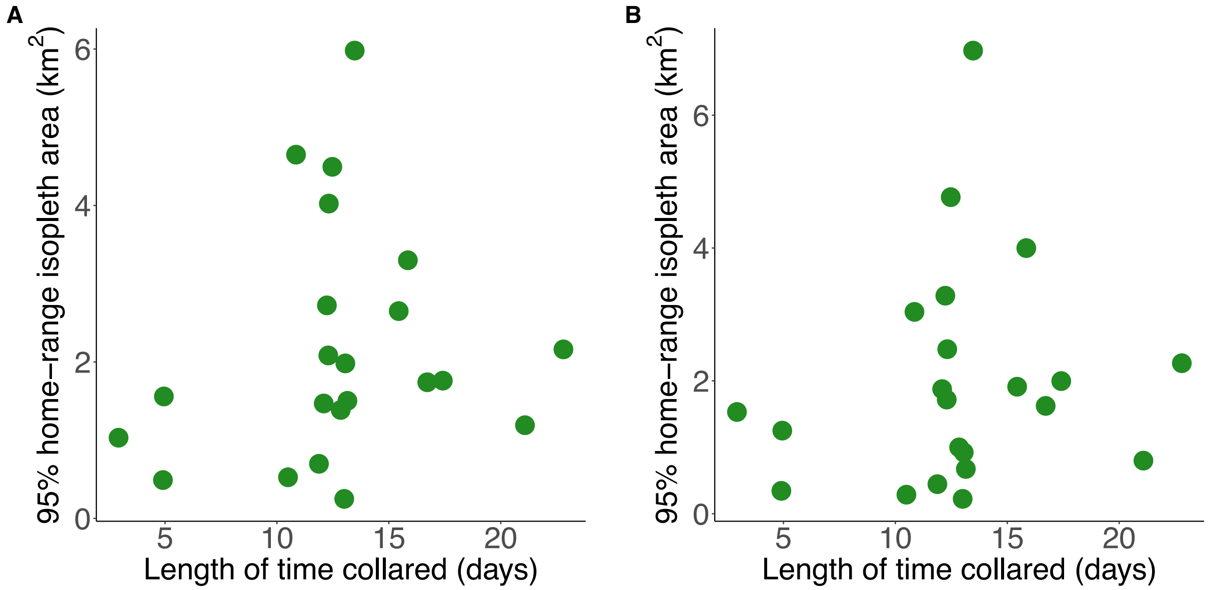

Figure S5. Waterbuck home-range area did not differ based on the duration of collar data. The relationship between each individual's 95% home-range isopleth area (i.e., the relative intensity of space use, derived from the 95% utilization distribution) during the day **(A)** and at night **(B)** and length of time each individual was collared was assessed using linear regression (**A**, $R^2 = 0.02$, $F_{1,20} = 1.34$, $P = 0.26$; **B**, $R^2 = -0.0003$, $F_{1,20} = 0.99$, $P = 0.33$).

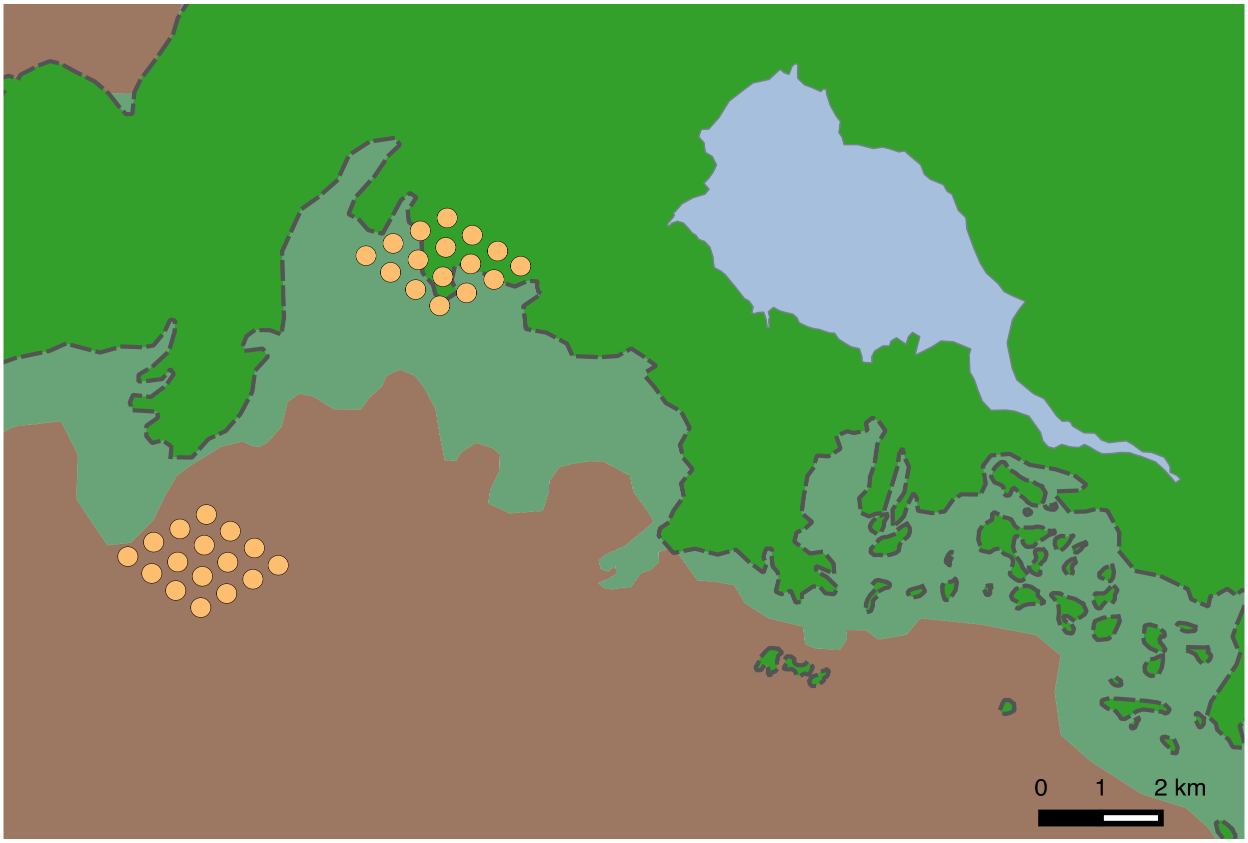

Figure S6. Locations of the camera trap grids in the floodplain and savanna. In 2017, 32 camera traps (yellow circles) were deployed in two grids of 16 cameras each in representative floodplain and savanna habitat. Cameras were placed ~500-m apart and recorded videos over a period of three weeks when triggered by heat and motion. The map shows the distinction between the floodplain and savanna habitat types; the treeless grassland surrounding Lake Urema is shown in bright green; the dashed grey line delineates the shift to the transitional floodplain habitat (in drab green); and savanna is shown in brown.

Supporting Information. Becker, J.A., M.C. Hutchinson, A.B. Potter, S. Park, J.A. Guyton, K. Abernathy, V.F. Americo, A.G. da Conceição, T.R. Kartzinel, L. Kuziel, N.E. Leonard, E. Lorenzi, N.C. Martins, J. Pansu, W.L. Scott, M.K. Stahl, K.R. Torrens, M.E. Stalmans, R.A. Long, and R.M. Pringle. 2021. Ecological and behavioral mechanisms of density-dependent habitat expansion in a recovering African ungulate population. Ecological Monographs.

Appendix S2. Additional Supplementary Figures

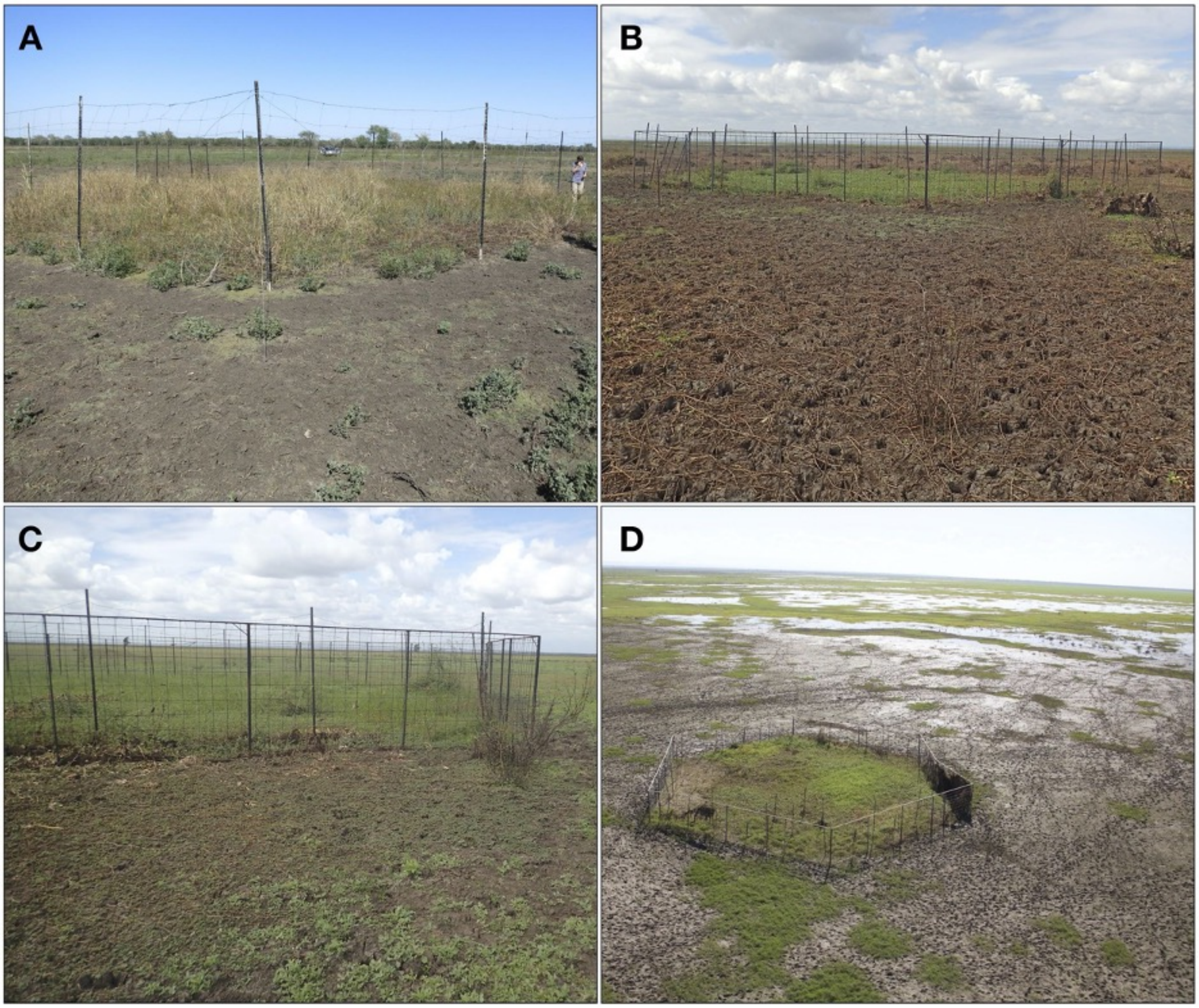

Figure S1. Depletion of floodplain food availability by ungulates in the mid-dry season. Illustrative photographs of vegetation inside and outside of fenced herbivore exclosures in June 2016 (**A**), July 2017 (**B-C**), and June 2018 (**D**). The green plants visible outside the exclosures in (**A**) and (**C**) include *Heliotropium ovalifolium* and other forbs that are strongly avoided by waterbuck in relation to their availability (see Main Text Figure 1).

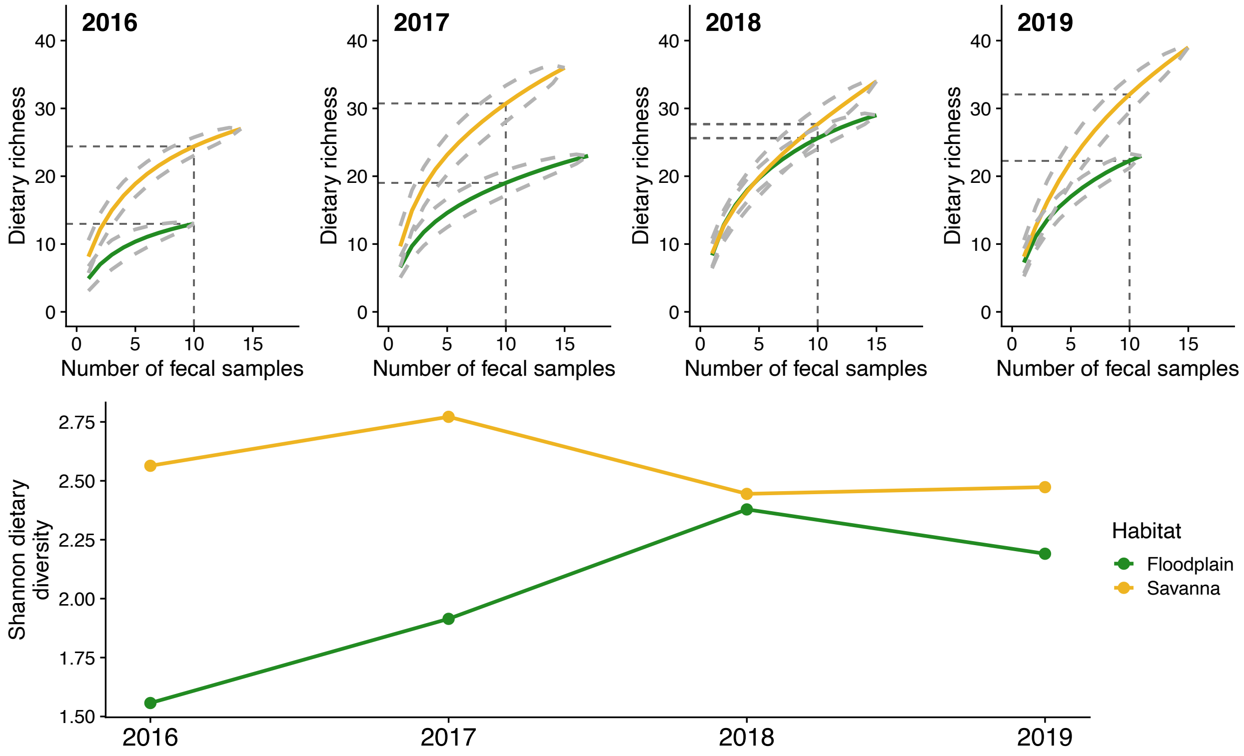

Figure S2. Waterbuck in the floodplain had lower dietary richness and diversity. *Top row:* Dietary mOTU richness in each habitat and year (2016–2019) as accumulation curves based on exact sample-based rarefaction. Dietary mOTU richness is most directly comparable at $n = 10$ fecal samples (i.e., the minimum across habitats and years); this sampling level is shown by the vertical dashed line in each panel, and the corresponding dietary richness in each habitat is shown by the horizontal dashed lines. Savanna waterbuck had consistently higher rarefied dietary richness than floodplain waterbuck (mean ± SEM: 2016, floodplain 13.0 ± 0 vs. savanna = 24.4 ± 1.3; 2017, floodplain 19.0 ± 1.8 vs. savanna 30.7 ± 2.7; 2018, floodplain 25.6 ± 1.6 vs. savanna 27.7 ± 2.4; 2019, floodplain 22.3 ± 1.1 vs. savanna 32.1 ± 2.6). *Bottom:* Savanna waterbuck likewise had higher Shannon dietary diversity (i.e., total niche width) in all years, and floodplain dietary diversity increased through time, consistent with the reduced availability of preferred food plants (Figure 1). The dominance of waterbuck diets (i.e., relative abundance of the single most common food, data not shown) also declined through time in the floodplain (43.8% in 2016 to 27.2% in 2019) but increased in savanna (19.7% in 2016 to 27.8% 2019).

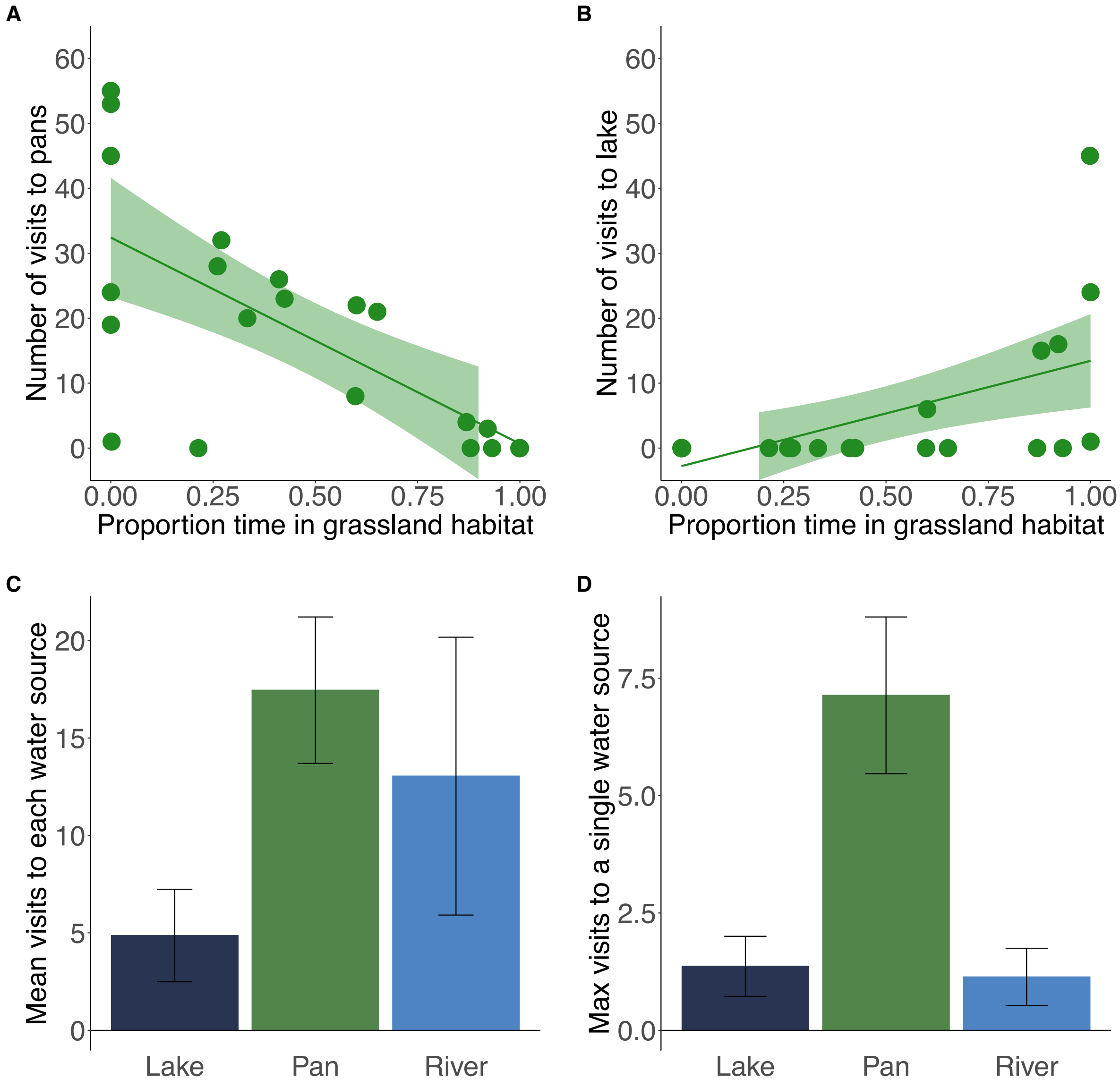

Figure S3. Use of surface-water sources by waterbuck. (**A**) Frequency of visits to pans as a function of time spent in grassland habitat ($R^2 = 0.43$, $F_{1,20} = 16.63$, $P = 0.0006$). (**B**) Frequency of visits to Lake Urema as a function of time spent in grassland habitat ($R^2 = 0.39$, $F_{1,20} = 14.51$, $P = 0.001$). (**C**) Mean number of visits by waterbuck to Lake Urema, all pans, and the Urema and Sungue rivers (difference between pan and lake, $P = 0.071$; all other pairwise comparisons non-significant). (**D**) Maximum number of visits to any given surface water location, averaged across all individuals (difference between pan and lake, $P = 0.001$; difference between pan and river, $P = 0.0007$; no significant difference between lake and river).

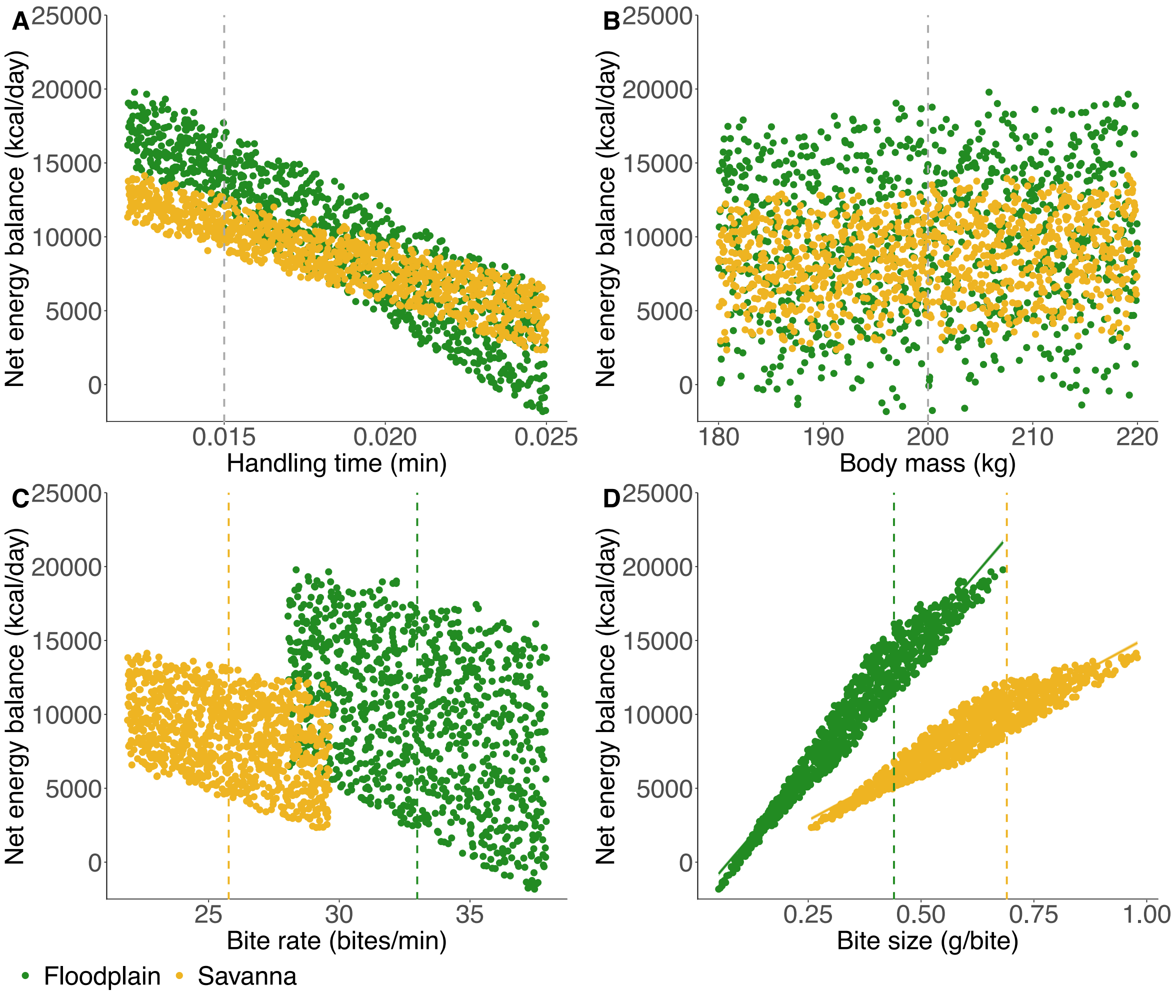

Figure S4. Sensitivity of energy-balance estimates to variation in energetic parameters. Relationships between variation in a subset of key energetic parameters and resulting estimates of net energy balance (kcal day^{-1}) in floodplain and savanna. The parameter space was sampled using Latin hypercube sampling; *h* was varied between a minimum of 0.012 and a maximum of 0.025 min/bite, *M* between 180 and 220-kg, and *B* within ±15% of the mean estimated value estimated from the camera trap video data. All other parameter values were held constant. 1,000 random samples of each of these three parameters were selected for both the floodplain and savanna waterbuck, assuming a uniform distribution for each parameter, resulting in 1,000 estimates of net energy balance for each habitat type. Dashed lines indicate the parameter values used in the calculations in the main text; two colored lines are used when different values were used for floodplain and savanna waterbuck. There were significant correlations ($P < 0.0001$) between net energy balance and all parameters for both floodplain and savanna waterbuck, albeit with substantial variation in effect size (using a linear regression model, floodplain: $R^2 = 0.99$, $F_{4,995} = 3.42\times10^4$; savanna: $R^2 = 0.99$, $F_{4,995} = 3.54\times10^4$). **(A)** Net energy balance was negatively correlated with handling time, and sensitivity was greater in floodplain than savanna, as indicated by the relative coefficient from the linear regression model (β) (floodplain: $\beta = -8.47\times10^5 \pm 4.65\times10^4$; savanna: $\beta = 4.98\times10^5 \pm 2.07\times10^4$). At handling times below and close to that used in our calculations (0.015, corresponding to the average across all large herbivores (Shipley et al.

1994), net energy balance was higher in floodplain waterbuck; but when both savanna and floodplain handling times were higher than this average value (>0.02), floodplain and savanna individuals achieved similar energy balance. **(B, C)** There was a loose positive correlation between body mass and energy balance (**B,** floodplain: $\beta = 18.21 \pm 2.24$; savanna: $\beta = 20.23 \pm 1.59$) and a negative correlation between net energy balance and bite rate (**C,** floodplain: $\beta = -3.44\times10^2 \pm 43.37$; savanna: $\beta = -2.46\times10^2 \pm 31.49$); in both cases these relationships were similar between the two habitats. **(D)** Across habitats, there was a strong positive correlation between the chosen value for bite size (g bite^{-1}) and estimated net energy balance (floodplain: $\beta = 1.20\times10^4 \pm 1.60\times10^3$; savanna: $\beta = 4.66\times10^3 \pm 7.11\times10^2$); floodplain waterbuck maintained higher net energy balance except at very small bite sizes.