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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.

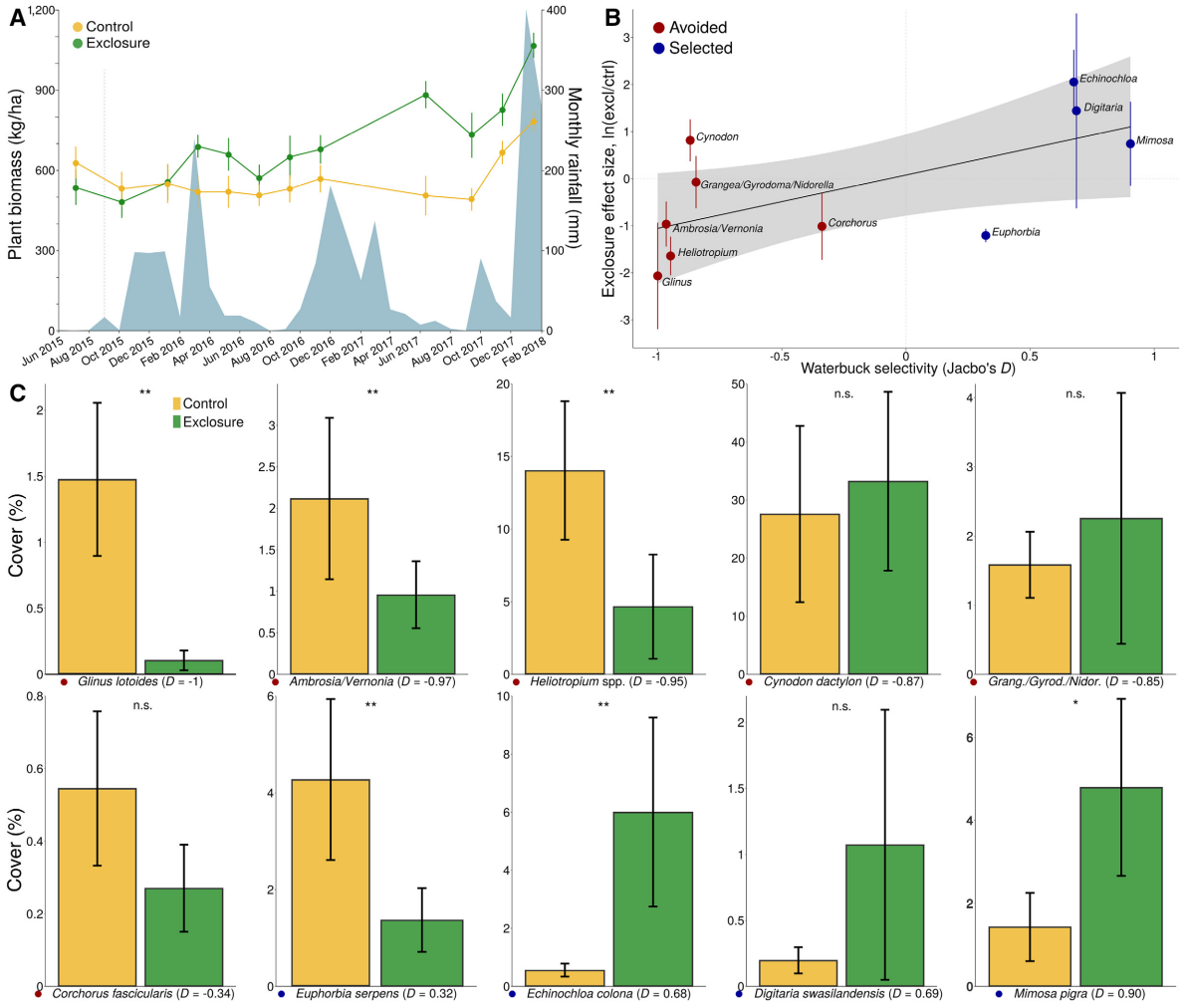


FIG. 1. Ungulates suppressed food availability in the floodplain. (A) Plant biomass (mean ± SE; left *y*-axis) in exclosure and control plots from 2015–2018, with monthly rainfall (right *y*-axis) in blue. Dashed vertical line denotes exclosure establishment in September 2015. Ungulate exclusion increased 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

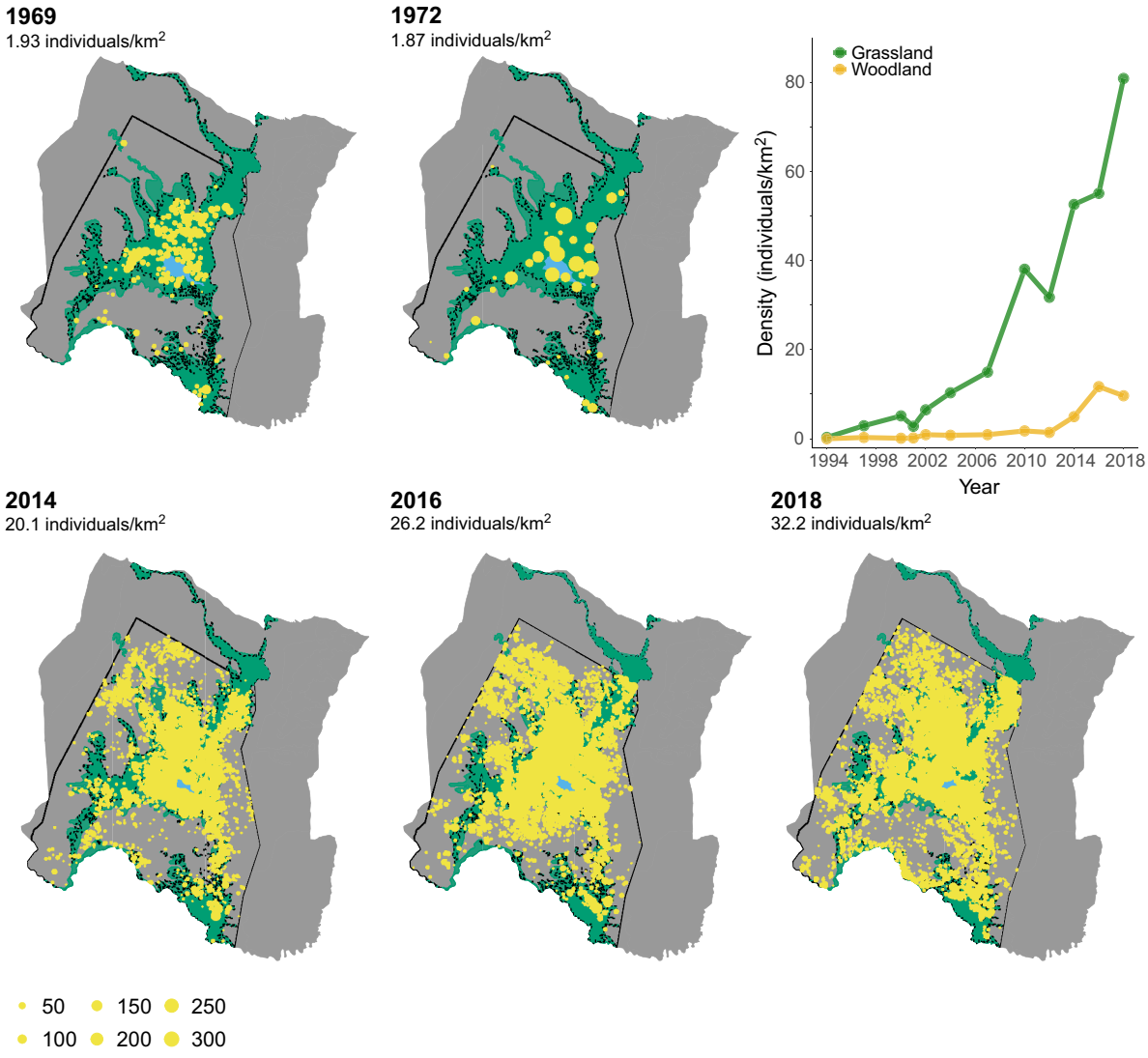


FIG. 2. Distribution and density of waterbuck in Gorongosa through time. Maps show pre-war (1969, 1972) and post-war (2014, 2016, 2018) distributions of waterbuck (yellow circles, scaled by the group size counted at each location) from aerial surveys during the late dry season (October) when visibility 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/km^2 in 2016 (a below-average rainfall year, 755 mm). In 2018, waterbuck density in the floodplain was 80.9 individuals/km^2 (~16,000 kg/km^2), which

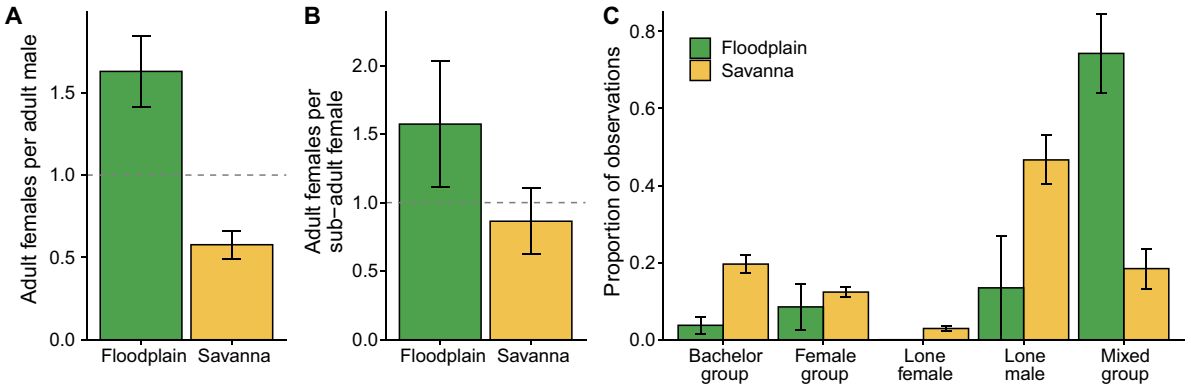


FIG. 3. Prime-age breeding waterbuck were concentrated in the floodplain. (A, B) Mean (±SE) across surveys of waterbuck sex and age ratios in 2019, with dashed horizontal lines at unity (i.e., equivalent numbers of each category). (A) In the floodplain, there were more adult females than adult males, 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

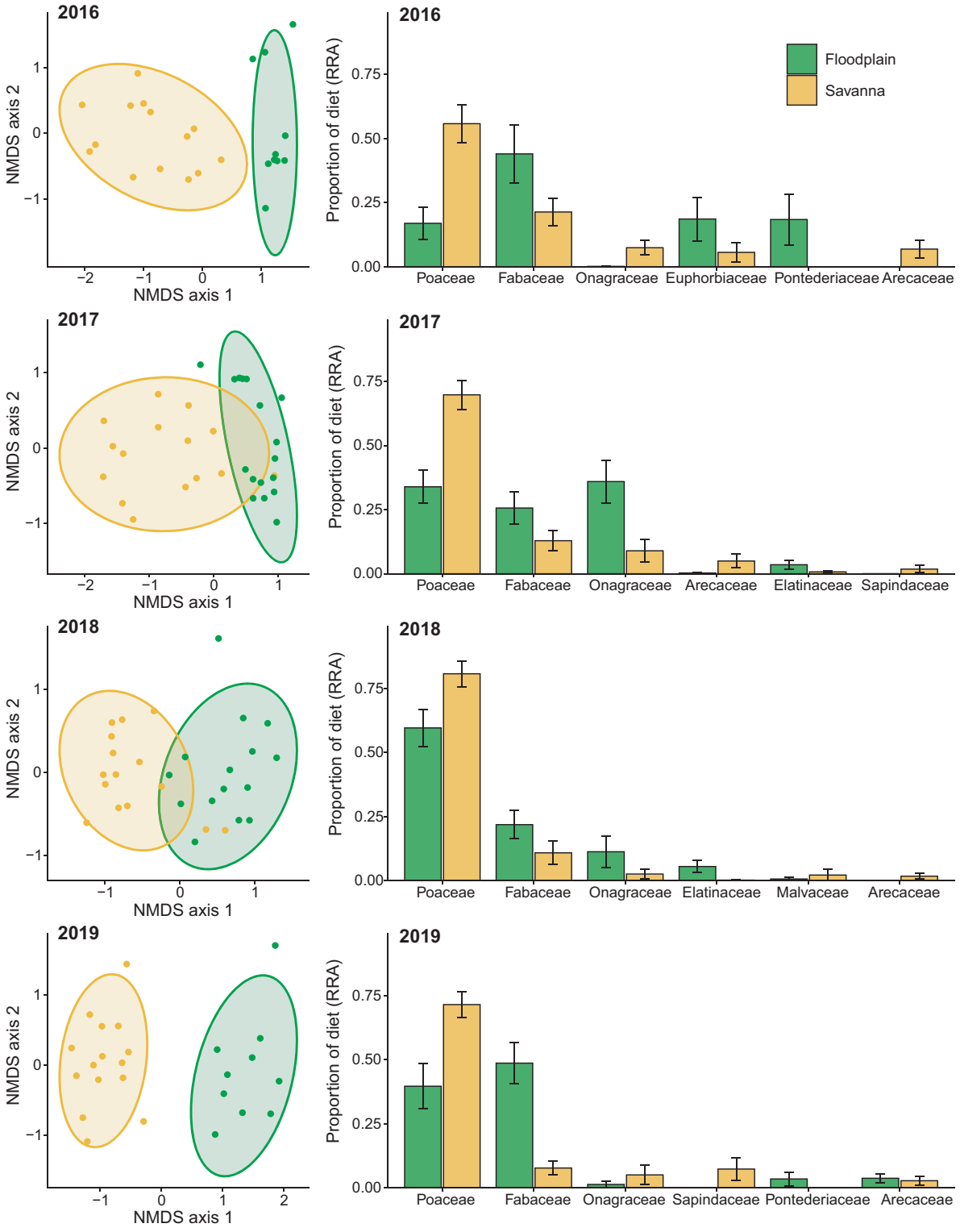


FIG. 4. Waterbuck diets differed in floodplain and savanna habitats. At left, nonmetric multidimensional scaling (NMDS) ordinations illustrate the dietary dissimilarity (at the level of plant molecular operational taxonomic units [mOTUs]) among waterbuck fecal samples collected in floodplain and savanna 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*).

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

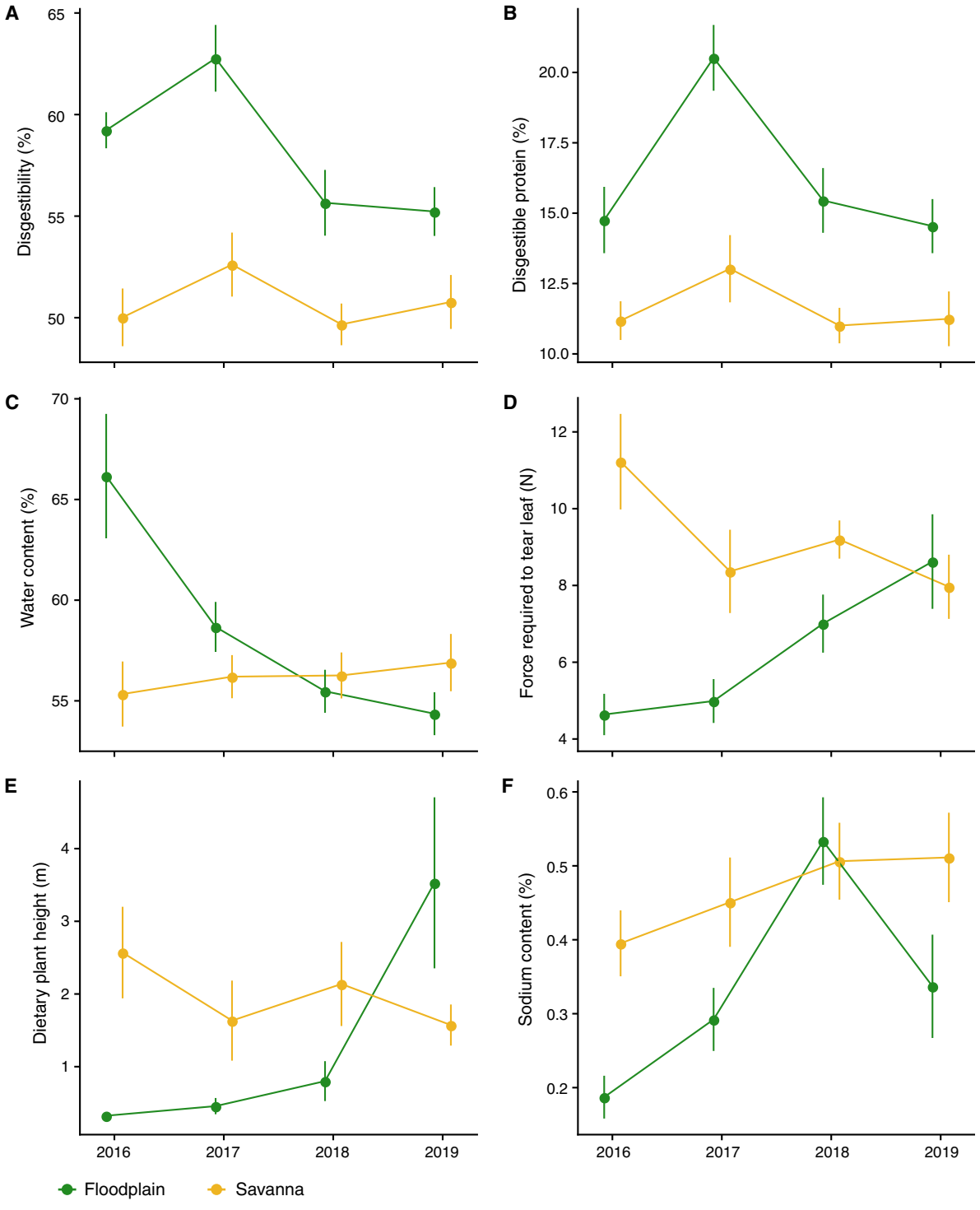


FIG. 5. Waterbuck diet quality was generally higher, but declining, in the floodplain. (A) Digestibility was higher on average but declined over time in the floodplain (linear model: habitat $F_{1,105} = 55.56$, $P < 0.001$; year $F_{1,105} = 3.91$, $P = 0.05$; habitat × year $F_{1,105} = 4.71$, $P = 0.03$). (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

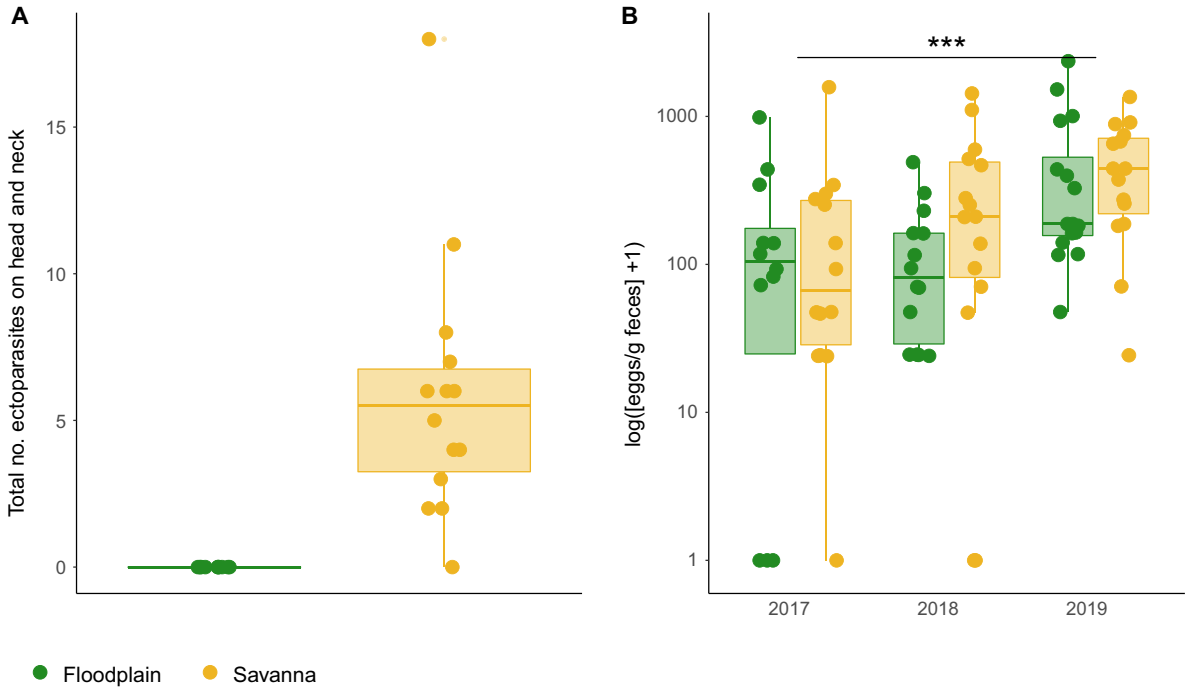


FIG. 6. Ectoparasite burdens were higher in savanna waterbuck, whereas endoparasite loads were similar across habitats. (A) No ticks or lice were counted on the ears, faces, or necks of waterbuck collared in the floodplain in 2016 ($n = 10$) whereas those collared in savanna ($n = 15$) had more. (B) 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.

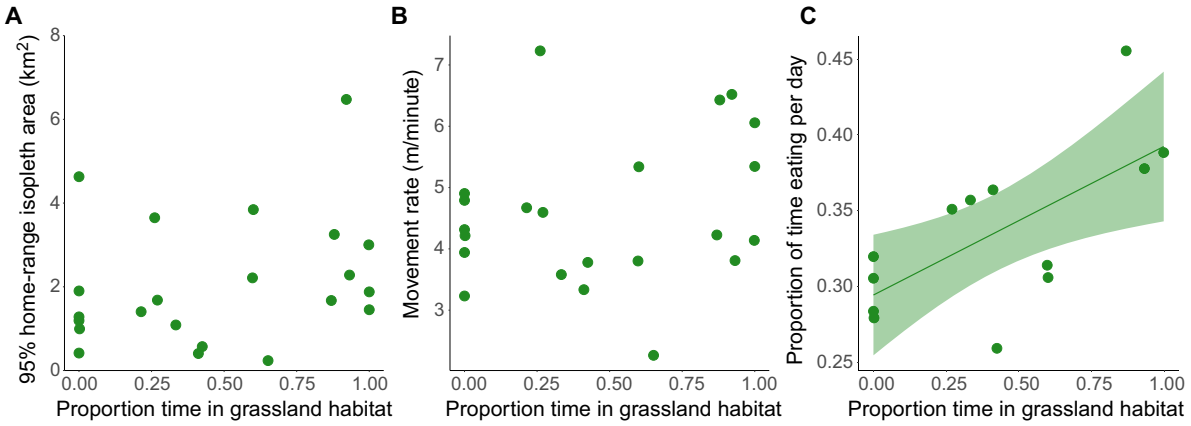
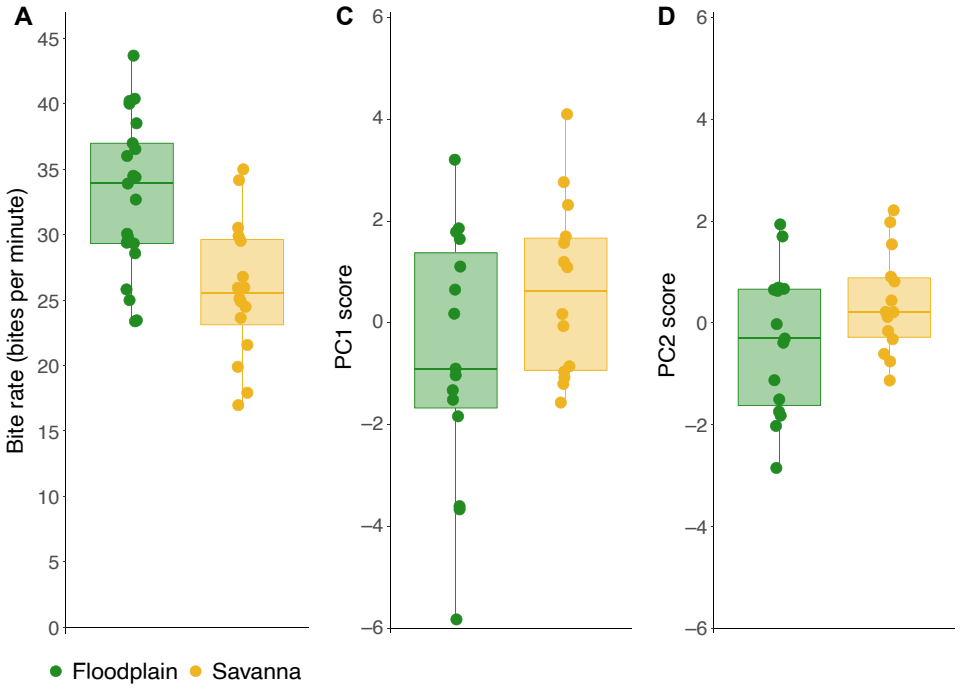


FIG. 7. Savanna waterbuck spent less time eating than floodplain waterbuck. (A) Area of each individual's 95% home-range isopleth (derived from the utilization distribution, i.e., the relative intensity of space use; $R^2 = 0.03$, $F_{1,20} = 1.56$, $P = 0.23$). (B) Individual movement rate in m/min ($R^2 < 0.01$, $F_{1,20} = 1.19$, $P = 0.29$). (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.