

ECOLOGY

Interplay of competition and facilitation in grazing succession by migrant Serengeti herbivores

T. Michael Anderson^{1*}, Staci A. Hepler², Ricardo M. Holdo³, Jason E. Donaldson³, Robert J. Erhardt², J. Grant C. Hopcraft⁴, Matthew C. Hutchinson⁵, Sarah E. Huebner⁶, Thomas A. Morrison⁴, Jeffery Muday¹, Issack N. Munuo⁷, Meredith S. Palmer⁸, Johan Pansu^{8†}, Robert M. Pringle⁸, Robert Sketch^{2‡}, Craig Packer⁶

Competition, facilitation, and predation offer alternative explanations for successional patterns of migratory herbivores. However, these interactions are difficult to measure, leaving uncertainty about the mechanisms underlying body-size-dependent grazing—and even whether succession occurs at all. We used data from an 8-year camera-trap survey, GPS-collared herbivores, and fecal DNA metabarcoding to analyze the timing, arrival order, and interactions among migratory grazers in Serengeti National Park. Temporal grazing succession is characterized by a “push-pull” dynamic: Competitive grazing nudges zebra ahead of co-migrating wildebeest, whereas grass consumption by these large-bodied migrants attracts trailing, small-bodied gazelle that benefit from facilitation. “Natural experiments” involving intense wildfires and rainfall respectively disrupted and strengthened these effects. Our results highlight a balance between facilitative and competitive forces in co-regulating large-scale ungulate migrations.

Seasonal migrations, defining features of many terrestrial and marine ecosystems worldwide (1, 2), are threatened by habitat destruction, overhunting, and climate change (3). Although migration is common in large mammalian herbivore species (4), the mechanisms underlying multispecies migration dynamics remain poorly understood (2). The annual ungulate migration in Serengeti National Park is the archetypal example of body-size-dependent “grazing succession” (5), in which zebra (*Equus quagga*; ~230 kg), wildebeest (*Connochaetes taurinus*; ~180 kg), and Thomson’s gazelle (*Eudorcas thomsonii*; ~20 kg; “gazelle” hereafter) sequentially follow the same migratory routes.

Early descriptions of grazing succession invoked facilitation to explain this pattern (6). In this scenario, bulk consumption by larger grazers keeps grasses short and regrowing, creating nutritious forage for smaller grazers that require less food (7). Removal of grass biomass may also increase the accessibility and abundance of low-growing, high-quality herbaceous eudicots favored by smaller species (8, 9). In

Serengeti, evidence for facilitation is based largely on (i) staggered arrival times of zebra, wildebeest, and gazelle, as measured at a single location over 3 years (5); (ii) partitioning of grass stem, leaf, and sheath observed in a small sample of stomach contents (9); and (iii) gazelle preference for habitat patches previously grazed by wildebeest (10).

Other lines of evidence suggest that grazing succession is instead driven by competition (11). An indirect competitive process, exploitation (table S1), may operate if multiple species use the same resource patches, but smaller grazers delay their arrival because of resource depletion by larger grazers. A direct competitive process, interference (table S1), may operate if species co-mingle and smaller herbivores propel larger herbivores onward into taller vegetation by grazing swards down to heights unprofitable for the larger species (12, 13). Citing “invasion” of wildebeest during their northernmost path, Sinclair (14) proposed that interspecific competition forced zebra to stay ahead of migrating wildebeest. A third possibility is that predators regulate migration dynamics. Mixed-species migration could reduce individuals’ risk through increased vigilance and predator satiation (14, 15), especially in areas of high vulnerability to ambush predators (16).

Disentangling the potential mechanisms that drive the movement patterns, arrival times, and foraging behaviors of the three migrating species has been hampered by a lack of long-term, detailed data at the appropriate scale (2). We conducted a landscape-scale analysis of animal movements in Serengeti by integrating three spatially and temporally overlapping datasets: (i) the citizen-science-supported Snapshot Serengeti camera-trap survey ($N_{\text{cameras}} = 48$ to

130; coverage = 1000 km²; fig. S1) that operated continuously between 2011 and 2018 [(17); Fig. 1]; (ii) GPS collar data collected in 2017 and 2018 for migratory zebra and wildebeest [(18); Fig. 1]; and (iii) dietary analysis of fecal DNA for each migrant species collected in 2017 and 2018 (19). Our study area, in the fire-prone grassland-to-woodland transition north of the Serengeti plains, lies in the center of the Serengeti migration (Fig. 1). We focused on the “transition season” (April to August), when migrants move off the plains to the northwest and plants undergo dry season senescence (20).

The biotic interactions influencing grazing succession are modulated by disturbance. Rainfall and fire may decouple associations between migratory species by controlling food availability through biomass reduction (fire) or by stimulating plant growth (rainfall and fire) (21). The extent of fire within the study area varied 33-fold across years (range: 21.3 to 694.4 km²; fig. S2); rainfall in the 4 months before the transition period varied threefold (217 to 621 mm; fig. S2); and vegetation greenness [measured as normalized difference vegetation index (NDVI)] varied >10-fold (range, 1.9- to 29.0-fold; see the supplementary materials). We exploited these extremes to probe the mechanistic underpinnings of co-migration and test three alternative hypotheses: facilitation (H1), competition (H2), and predation (H3) (table S1), which make contrasting predictions about the order, timing, and strength of species associations.

The facilitation hypothesis predicts consistent separation in migrant arrival time: zebra followed by wildebeest and then gazelle (5). Grazing by larger herbivores is expected to attract smaller herbivores, but not the reverse. Digestible energy per unit mass decreases with grass biomass (22); by creating patches of high-quality regrowth (23), fire should disrupt grazing succession and uncouple any positive associations between species because regrowth will not be restricted to previously grazed areas. By contrast, high pre-migration rainfall promotes the accumulation of stem-dominated grass biomass and should strengthen species associations by enhancing facilitation (otherwise, small herbivores would constantly encounter tall, stem-dominated swards with low digestible energy). Finally, diets should be dominated by grasses with low species partitioning between each migratory herbivore (5, 9, 10). As hind-gut fermenters (24), zebra can digest low-quality food and maximize intake from tall grass, whereas smaller ruminant species select nutritious short grasses.

The competition hypothesis predicts the same species arrival order and high dietary overlap as facilitation, but timing and species associations should depend on the form of competition. Under indirect competition (H2_i),

¹Department of Biology, Wake Forest University, Winston-Salem, NC 27109, USA. ²Department of Statistical Sciences, Wake Forest University, Winston-Salem, NC 27109, USA.

³Odum School of Ecology, University of Georgia, Athens, GA 30602, USA. ⁴School of Biodiversity, One Health and Veterinary Medicine, University of Glasgow, Glasgow G61 1QH, UK. ⁵Department of Life & Environmental Sciences, University of California Merced, Merced, CA 95343, USA.

⁶Department of Ecology, Evolution and Behavior, University of Minnesota, St. Paul, MN 55108, USA. ⁷Serengeti Wildlife Research Centre, 2113 Lemara, Arusha, TZ. ⁸Department of Ecology and Evolutionary Biology, Princeton University, Princeton, NJ 08544, USA.

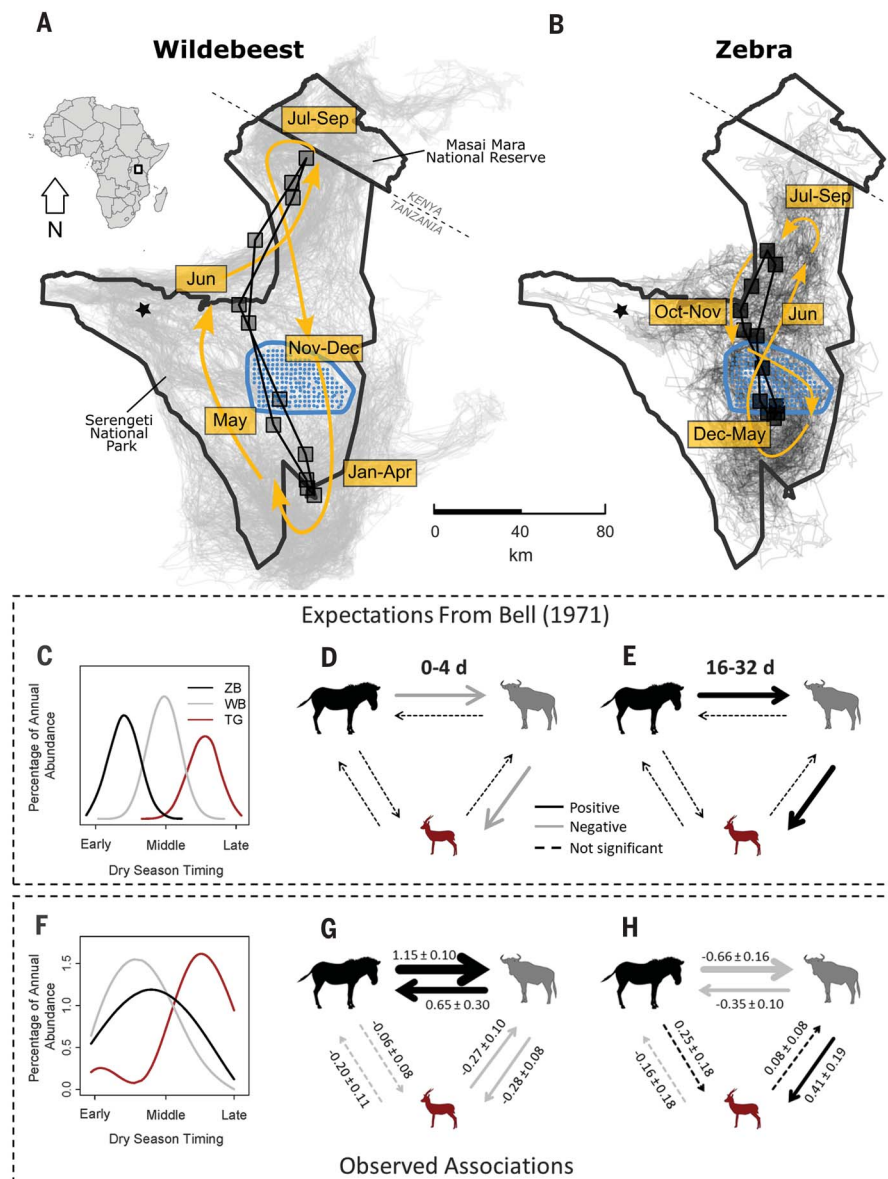
*Corresponding author. Email: anderstm@wfu.edu

†Present address: Univ Lyon, Université Claude Bernard Lyon 1, CNRS, ENTPE, UMR 5023 LEHNA, F-69622, Villeurbanne, France.

‡Present address: AquaQ Analytics US, Jersey City, NJ 07302, USA.

Fig. 1. Movements (1999 to 2020), temporal dynamics, and species interactions of migratory grazers in the Serengeti ecosystem. (A and B) Our study area (blue polygons) is a migratory transition zone linking the Serengeti plains, the western corridor, and the Masai Mara Game Reserve.

On the basis of GPS collaring data collected between 1999 and 2020 (18), 96% of collared wildebeest [$n = 54$; gray lines in (A)] and 100% of zebra [$n = 28$; black lines in (B)] passed through the study area. Boxes show monthly mean locations for wildebeest (A) and zebra (B) across the entire dataset, with orange arrows indicating the direction of movements. Camera traps (points) were separated by ~2.2 km and operated almost continuously between July 2010 and August 2018. Bell's (5) foundational study was from a single plot in the Western corridor (asterisks) at a time when the wildebeest population was ~25% of the current size (18). Thomson's gazelle have not been collared in the Serengeti National Park, so we focused our analysis of individual movements on zebra and wildebeest. (C to E) Classically hypothesized expectations from grazing succession (5, 13), including migratory species abundance over the dry season (C) and species-specific effects on the probability of other species' occurrence at 4-day intervals (D) and 16- to 32-day intervals (E). The classic model predicts unidirectional spatial associations between migrants at substantial time lags (E) driven by activities of large herbivores (e.g., foraging, trampling, and nutrient redistribution) that facilitate foraging by small herbivores. Negative interactions, not explicitly considered in early work [(5, 9); compare (13)] would appear on short time scales (D) because of lagged positive associations. (F to H) Associations observed in this study. Average abundance during the transition season (F) supported the classic model for gazelle, but not for zebra and wildebeest, which co-migrated through the study area (fig. S3). Standardized species abundances were plotted against satellite-derived vegetation greenness (an index of plant senescence during the dry season) to control for variations in migration timing across years. Within 4-day windows, zebra and wildebeest had strong reciprocal effects on each other's occupancy throughout migration, whereas lagged arrival times led to negative associations with gazelle (G). Within 16- to 32-day windows, zebra and wildebeest had positive effects on occupancy of gazelle and negative effects on each other because of their concurrent migration (H). Each arrow represents the average positive (black) or negative (gray) conditional association strength



($\gamma_{\text{species } 2|\text{species } 1}$) from Bayesian occupancy models fit at 4-day (G) or 16-day (H) time intervals across the entire study period (see the supplementary materials). Values are shown as means \pm 95% confidence intervals (95% CIs) (tables S2 and S3), with arrow widths proportional to the magnitude of the effect size. Dashed lines represent weak effects that were below or included zero in the 95% CI.

species should arrive several weeks apart to allow for grass regrowth, and the lag should be greater after longer occupancy by the first-arriving species (table S1). Under direct competition (H_{2d}), we expected little to no separation in arrival time, with larger migrants avoiding dense herds of smaller migrants that deplete food availability (table S1). In both scenarios, higher pre-migration rainfall should weaken negative associations between migrants of similar size by reducing feeding competi-

tion, whereas pre-migration fire should intensify negative associations.

The predation hypothesis predicts closer spatial proximity, especially for small-bodied species because they are vulnerable to a wider range of carnivore species (25). Positive spatial associations should be stronger in open grasslands in wet years, when taller grasses provide cover for ambush predators, and in areas with high-risk landscape features such as river courses [based on a 50-year spatial dataset of lion pre-

dation risk (26)] regardless of rainfall or fire. We rely on lion predation as an overall proxy for ambush risk because cheetahs select the same small-scale areas as lions (27) and leopards' habitat preferences are highly congruent with lions' (28). By contrast, spotted hyenas and African wild dogs make no attempt at concealment and first disturb the herds to identify vulnerable individuals (29, 30). Therefore, we consider it unlikely that risks from coursing predators would confer strong

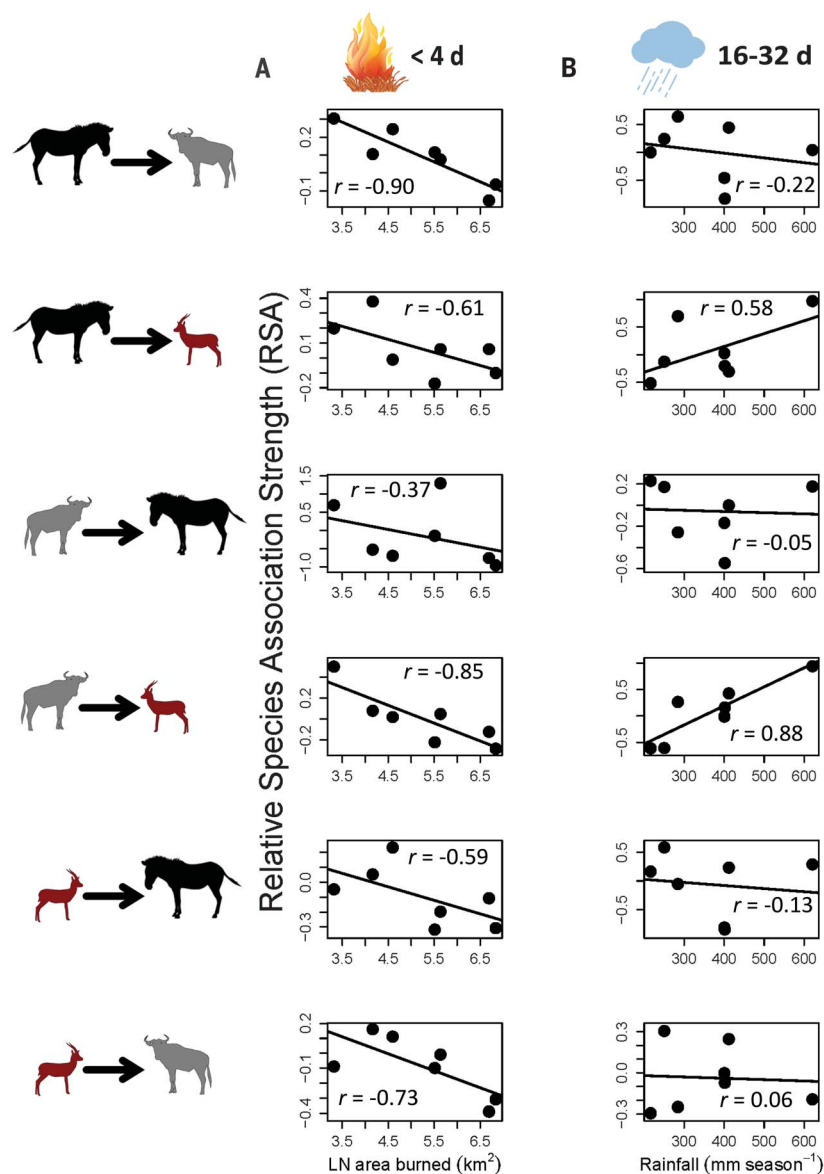


Fig. 2. Fire weakens but rainfall strengthens species associations during grazing succession. The RSA is the difference between species associations from Bayesian occupancy models fit at 4- or 16-day time interval for a given year minus the mean across all years ($RSA_i = \hat{\gamma}_i - \bar{\gamma}$; see the supplementary materials). (A and B) RSA_i values are plotted against the natural log of the burned area (A) and cumulative rainfall from January to June of year i (B). Fire was negatively related to variation in RSA_i calculated from 4-day spatial associations (A) (table S4), with the strongest correlations between smaller migrants conditioned on the presence of larger migrants [wildebeest (WB)|zebra (ZB) and Thomson's gazelle (TG)|WB]. Rainfall was positively related to variation in RSA_i calculated from 16-day spatial associations (B), but only for gazelle tracking larger migrants (TG|ZB and TG|WB). Pearson correlation coefficients (r) are shown in each graph. Active camera density during the 2015 transition season was lower than for other years (fig. S1) and was therefore excluded from these analyses.

advantages either from forming mixed-species herds or from migrating separately.

Results

Arrival order and time lags

The classic formulation of grazing succession (5) predicts consistent ~2-month separations in peak abundance of each of the species studied (Fig. 1C). However, the dates of migration

and peak abundance for zebra and wildebeest varied across years and did not exhibit separation consistent with hypotheses based on either facilitation (H1) or indirect competition (H2_i). In most years, zebra and wildebeest entered the study area simultaneously. Wildebeest numbers accumulated rapidly and reached peak abundance 7.3 ± 9.3 days (range: 22 to -6 days) before zebra, although this difference

was inconsistent (Wilcoxon signed-rank test: $v = 3.5$, $P = 0.09$, $df = 6$). By contrast, wildebeest and zebra abundance both consistently peaked 27.6 ± 15.4 days before that of gazelle (Wilcoxon signed-rank test: $v = 105$, $P < 0.001$, $df = 12$). These time lags are smaller than those reported by Bell (5), and only the separation between the larger migrants and gazelle is qualitatively consistent with classic predictions (Fig. 1). Furthermore, the observed lags are inconsistent with direct competition (H2_d) or predation (H3), which predict that smaller herbivores should maintain adjacency to larger herbivores either because their foraging drives large herbivores to sites with more food (12–14) or because they benefit the most from increased predator vigilance when foraging in mixed-species herds (14, 15).

Directionality and reciprocity of interactions

Facilitation (H1) predicts positive effects of larger herbivores on the probability of occupancy by smaller herbivores, with negligible reciprocal effects of small on large herbivores (Fig. 1). Using two-step, conditional Bayesian occupancy models (31, 32), we analyzed 4- and 16-day temporal windows to quantify concurrent and lagged associations between each pair of species for each transition season. Each model included static (i.e., landscape) and dynamic (i.e., rainfall and vegetation) environmental predictors as covariates to control for potentially confounding factors (33) and included a species-specific conditional term, $\gamma_{\text{species } 2 | \text{species } 1}$, which measured the effect of one species on the occupancy probability of another.

Over 4-day windows, we found reciprocal positive effects of zebra and wildebeest occupancy throughout the migration. Zebra increased wildebeest occupancy in 6 of 8 years (with marginally positive effects in the other 2 years), and wildebeest increased zebra occupancy in 3 of 8 years (and marginally in another year) (Fig. 1G, fig. S3, and table S2). On this 4-day scale, gazelle were not firmly associated with zebra or wildebeest occupancy in any year (table S2), exhibiting only marginal negative overall associations reflecting the temporal separation between the arrival time of gazelle and larger herbivores (Fig. 1, F and G).

At 16-day intervals, and consistent with the facilitation hypothesis, we detected positive effects of larger grazers on gazelle in 5 of 8 years, and gazelle were more strongly associated with locations previously occupied by wildebeest than by zebra (Fig. 1H, fig. S3, and table S3). Zebra-wildebeest associations on this longer time scale were consistently negative, reflecting their positive associations on shorter time scales (Fig. 1, F and H).

Influences of fire and rainfall on species associations

Exceptions to the prevailing patterns were related to environmental extremes. The 2 years

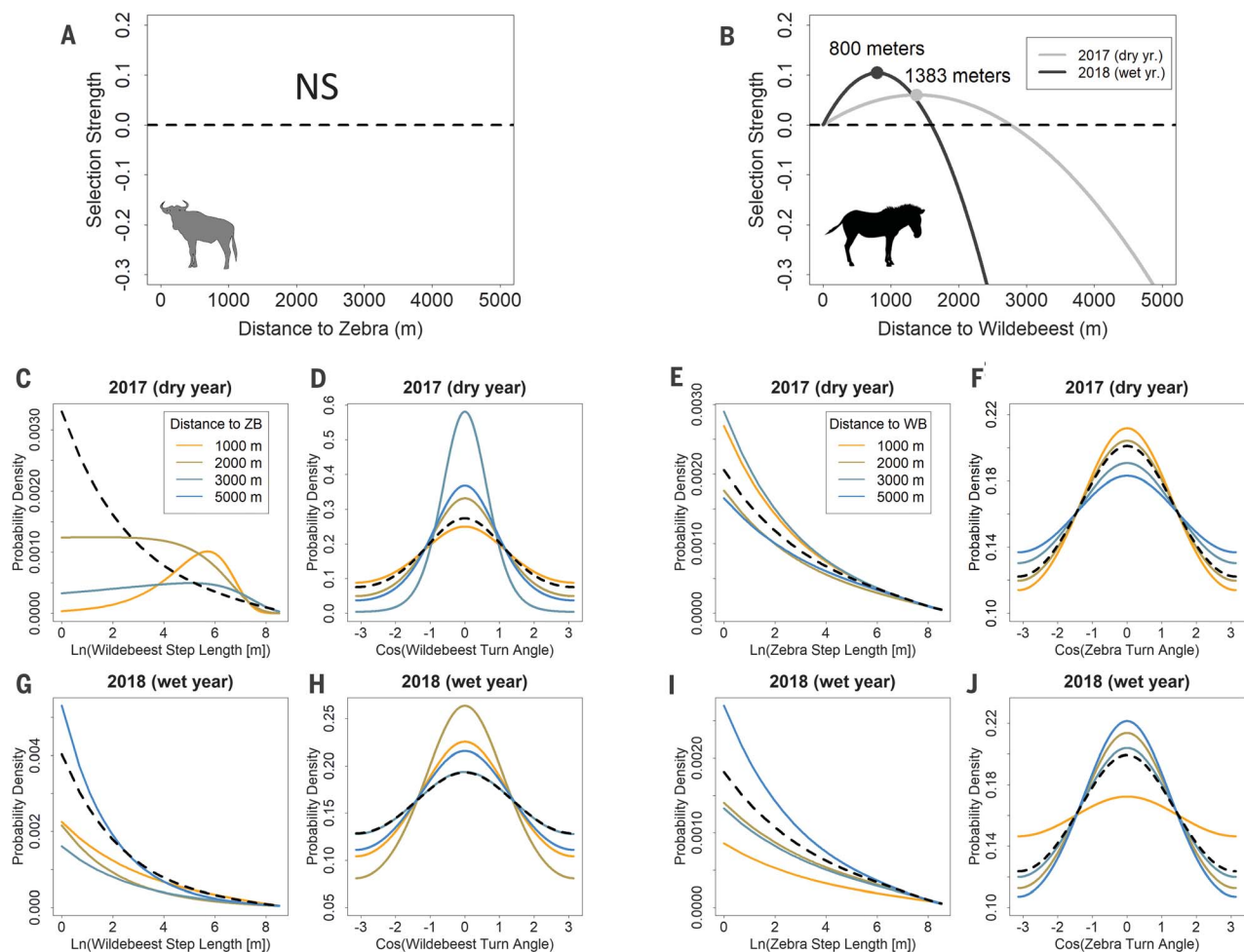


Fig. 3. Wildebeest and zebra movements during one dry (2017) and one wet (2018) year. (A and B) Movement models of collared individuals were analyzed in relation to distances from large heterospecific herds as determined by camera-trap data (see the supplementary materials). (A) In both dry (2017) and wet (2018) years, wildebeest selected habitat independently of distance to large, dense zebra herds. (B) By contrast, zebra selected sites at moderate distances from dense wildebeest herds, with greater distances in the dry year (light gray line; mode = 1383 m) compared with the wet year (dark gray line; mode = 800 m). (C to J) Foraging behaviors inferred from movement data. In the dry year, wildebeest moved with large step lengths of ~400 m between GPS fixes (4-hour fixed rate), especially individuals toward the front of the migration nearest to zebra (C), indicating directed movement (D).

(E) Zebra step lengths during the dry year were marginally larger than the expected from the tentative distribution. (G) In the wet year (2018), wildebeest used smaller step lengths than expected from the tentative distribution, consistent with greater local resource availability and foraging behavior. (I and J) Zebra movement changed substantially in the wet year, with smaller step lengths and wide, circuitous turn angles, especially for individuals within 1000 m from dense wildebeest herds, suggesting decreased competitive effects of heterospecifics. Black dashed lines show "tentative" distributions derived from the average movement of animals during a migration season. Color gradients represent binned wildebeest [(C) and (D), (G) and (H)] or zebra [(E) and (F), (I) and (J)] distances to large heterospecific herds as determined by camera-trap data (see the supplementary materials).

without 4-day conditional effects of zebra and wildebeest, 2013 and 2016, also showed the most extensive fires. Further, 2 of the 3 years without 16-day lagged effects of larger species on gazelle, 2014 and 2017, had the lowest rainfall in the entire study period (fig. S3 and table S2), suggesting that species associations were resource dependent.

To test the effect of environmental conditions, we analyzed the relative strength of association between species for each year i (RSA_i) as functions of fire and rainfall from January to June (fig. S3). We predicted that RSA_i should be negatively associated with fire

and positively associated with pre-migration rainfall. Indeed, RSA_i in 4-day intervals declined with area burned (Fig. 2 and table S4). This correlation was directionally consistent but strongest for zebra on wildebeest and for wildebeest on gazelle, size-adjacent species that precede each other in the migration, likely because fire mimics large herbivores by reducing grass height and promoting regrowth in ways that benefit small herbivores (23). RSA_i in 16-day intervals increased with rainfall for gazelle trailing wildebeest and zebra (Fig. 2). Thus, gazelle more closely tracked the larger migrants in years with higher her-

baceous production, suggesting greater reliance on the facilitative effects of biomass removal (H1).

RSA_i for zebra and wildebeest occupancies did not vary in response to rainfall at either time scale despite their reciprocal spatial associations (Fig. 2). For additional insight, we examined paths of GPS-collared individuals for one dry year, 2017, and one wet year, 2018, to test whether movements measured at 4-hour intervals revealed subtler responses to heterospecifics. Wildebeest habitat selection was independent of proximity to dense herds of zebra (Fig. 3A). By contrast, zebra selected

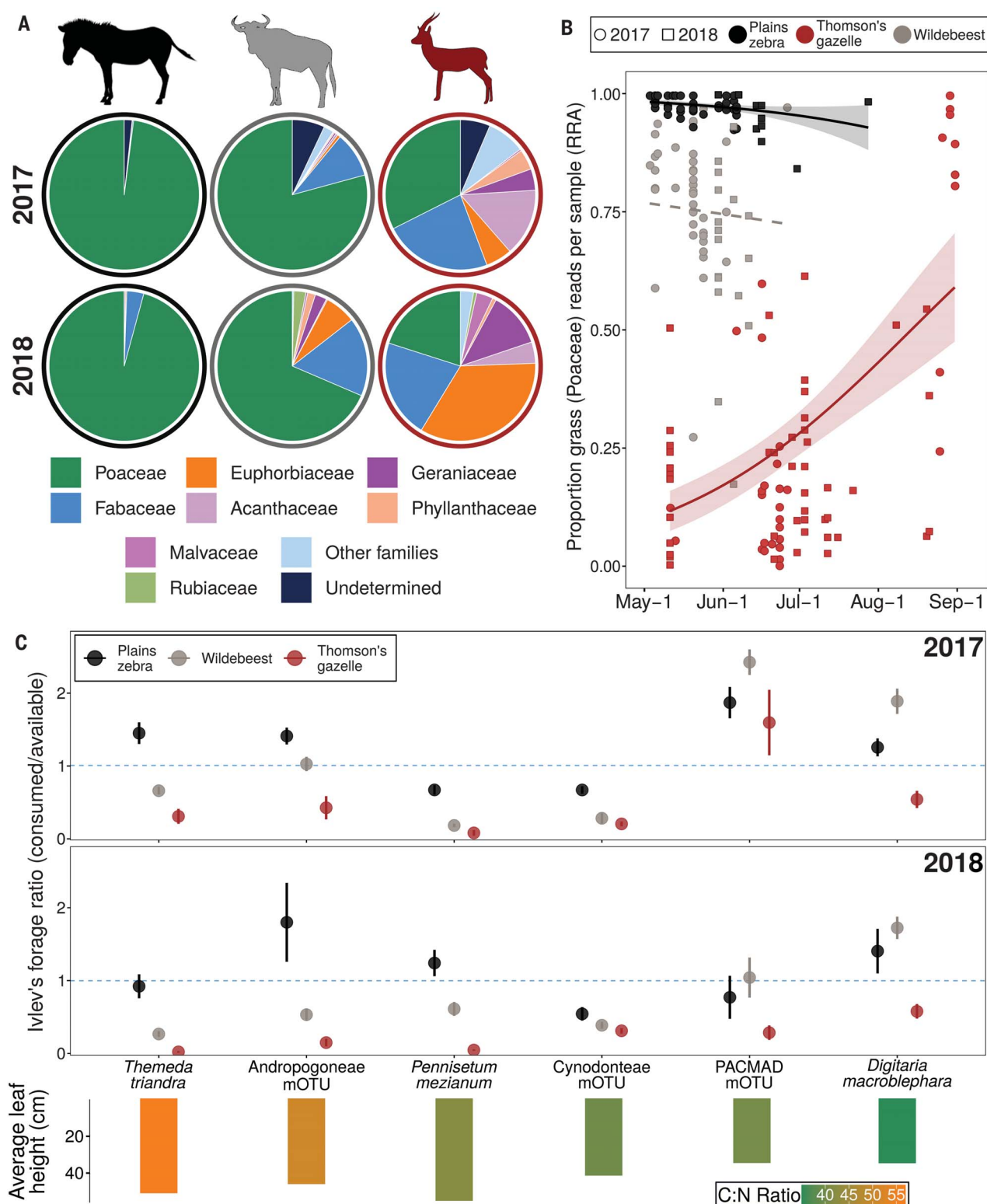


Fig. 4. Differential consumption of plant taxa of varying nutritional quality.

(A) Mean diet composition by plant family (colors) during the migration period in a dry year (2017) and a wet year (2018) showing unexpectedly high consumption of high-quality (fig. S15) forbs, notably legumes (Fabaceae), by wildebeest and gazelle. (B) Proportional grass consumption by gazelle shifted throughout the migration, increasing late in the season after zebra and wildebeest had moved on (beta regression, effect of date: $\beta = 0.02$, $Z = 6.15$, $P < 0.001$, $R^2_{adj} = 0.35$).

(C) Ivlev's selectivity (proportion consumed/proportion of available forage) for the six most abundant grass taxa in the study area. Taxa are identified to the lowest possible level based on fecal DNA sequences, including species, tribe (Andropogoneae, Cynodonteae), and clade (PACMAD). Bars below plot show C:N ratio (colors and lower values indicate higher quality) and leaf height (length) of each grass taxon. Dashed line at selectivity 1 indicates consumption in proportion to availability; positive values, selection; negative values, avoidance. Data underlying (A) are provided in table S6.

habitat distant from dense wildebeest herds in both years and farther in the dry year (1.4 km) than the wet year (0.8 km) (Fig. 3B and table S5). Wildebeest and zebra step lengths and turn angles also depended on rainfall and distance to heterospecifics. During the leaner dry year, wildebeest used larger step lengths of ~400 m as they searched for food, especially when they were near dense zebra herds; in the more plentiful wet year, wildebeest used smaller step lengths indicative of active foraging (Fig. 3 and table S5). Zebra step lengths in the dry year were larger than the null expectation. However, in the wet year, zebra migrating close to dense wildebeest herds had smaller step lengths and more circuitous turn angles, indicating greater local food availability (Fig. 3 and table S5). This last inference is also supported by evidence that both species avoided senescing vegetation more strongly in the wet than in the dry year (scaled change in NDVI from table S5). Altogether, these fine-scale movements are most consistent with asymmetric direct competition (H2_d) between the two species, meaning that wildebeest habitat selection is governed by resource availability independently of zebra, whereas zebra are subject to interference competition and locally repelled from massive wildebeest herds, especially in dry years (14).

No evidence for a role of predation risk

We tested whether spatial associations were stronger in risky areas (H3) by analyzing conditional occupancy probabilities relative to the distribution of ambush-predation risk inferred from lion densities and kills [(34); fig. S4]. Conditional species associations were indistinguishable between high- and low-risk areas at both 4- and 16-day time scales (figs. S5 to S12). The results are also incongruent with the predictions from H3 that associations in high-risk areas would be stronger in years with higher rainfall and more pronounced for associations involving gazelle.

Diet selection and overlap

We used fecal DNA metabarcoding in 2017 and 2018 to identify plant taxa and estimate their relative abundance in herbivore diets [(19, 35); see the supplementary materials]. Zebra diets consisted almost exclusively of grasses (96.9% of sequence reads on average), and wildebeest diets were also grass dominated (73.9%) but also included substantial proportions of herbaceous eudicots, mostly legumes (Fig. 4, A and B, and table S6). By contrast, grasses were a minority of gazelle diets (26.2%), especially in earlier months (May to July), before the larger species departed from the study area (Fig. 4, A and B). In both years, zebra and wildebeest ate highly overlapping sets of plant taxa (mean niche overlap, 0.82), whereas overlap was lower for wildebeest and gazelle (0.53) and lowest for

zebra and gazelle (0.34). Wildebeest and gazelle avoided common tall grasses of middling to low quality, whereas zebra showed higher selectivity for these taxa (Fig. 4C). In later months, however, gazelle increased consumption of high-quality grasses such as *Digitaria macroblephara*, which were likely regrowing after being grazed earlier in the season (figs. S14 and S15; see the supplementary materials).

Accounts that grazers partition grass stems and leaves without reference to plant identity (9) were integral to the classic grazing-succession model (5) and later elaborations (7, 11–13, 36). The generally high overlap in plant taxa eaten by zebra and wildebeest is compatible with this mechanism and with both facilitative and competitive interpretations, although the differential selectivity for grass species (Fig. 4C) aligns with the fine-scale competitive displacement inferred from movement data (Fig. 3B). However, we also found new support for a facilitative mechanism first proposed in 1968 (9) in which larger migrants benefit gazelle by opening the grass canopy and providing access to nutrient-rich prostrate eudicots (fig. S15), at least until the late dry season, when the gazelle switch to high-quality grasses grazed by earlier migrants (Fig. 4B and fig. S14). Coupled with the observed lags in occupancy, these dietary differences are incompatible with the idea that gazelle competitively displace larger migrants (13) and may also help to explain the gazelle's stable population size after the rapid increase in wildebeest numbers following rinderpest eradication in the 1960s (36).

Discussion

Our findings provide insight into the drivers of the iconic Serengeti migration. We found no evidence that grazing succession is driven by predation risk (H3). Risk from lions, leopards, and cheetahs is especially high in the north-western region of our study area [(37); fig. S4], and if risk mitigation were a key reason for co-migration, then strong species associations should have persisted near high-risk landscape features (26), even after fire. Previous analyses had suggested that high herbaceous biomass promotes mixed-species group formation to reduce predation risk (16); however, the low prevalence of multispecies associations in camera-trap photos (only 1.1% of gazelle detections, 5.7% of wildebeest detections, and 4.6% of zebra detections included any of the other species) does not support a general anti-predator response. Instead, our analyses of occupancy, animal movement, and diet provide strong evidence that foraging processes underlie grazing succession, occurring at short intervals (< 4-day) between zebra and wildebeest and longer intervals (16 to 32 days) between larger migrants and gazelle. Multiple lines of evidence point to a “push-and-pull” dynamic in which wildebeest, the dominant grazer,

push zebra ahead by reducing grass biomass (H2_d) while pulling along gazelle through facilitation (H1). Our study helps to reconcile decades of conflicting results (5, 6, 9–14) by demonstrating that competition and facilitation operate concurrently during animal migration with effect sizes that depend on resource availability (7).

A similar seasonal shift between competition and facilitation was observed in Kenyan rangeland, where interactions between cattle and wild grazers shifted from facilitation during the wet season to competition in the dry season (38). In our study, smaller migratory herbivores benefited both during both dry and wet periods (20), when they selected regrowing high-quality grasses previously consumed by the preceding larger-bodied migrants (Fig. 4C and fig. S13) and/or gained improved access to protein- and mineral-rich legumes and other forbs (figs. S14 and S15). In a typical year, habitat use by gazelle tracked co-migrating zebra and wildebeest migration, and this association intensified with increasing rainfall. In high-fire years, short-term movements among grazers were largely uncoupled, indicating that gazelle benefit from grass removal and regrowth regardless of whether it results from migratory herbivores or fire. We do not claim that the effects of zebra and wildebeest on gazelle are purely facilitative, but rather that facilitation is an important process during herbivore migration, likely helping to stabilize populations of smaller herbivores (22). Herbivore population dynamics are not strongly coupled at the ecosystem level (11), which implies that extrinsic factors are important, but facilitation may still be a key stabilizing force and driver of individual behavior during critical periods of the annual migration.

Multispecies migratory systems were once common across tropical savannas (3, 39) and probably involved a similarly nuanced interplay of positive and negative interactions (40). Large herbivores have suffered disproportionate extinction since the Quaternary (41), especially among migratory species (4), resulting in concomitant degradation of ecosystem functions (42). Our findings identify a previously unappreciated role of plant functional diversity in sustaining megafaunal migratory systems and indicate that fire management can help to maintain species persistence. Any disruption of the vegetative phenology that underlies herbivore movements would alter the strong systemwide consequences of migration (43) and portend additional challenges associated with extreme climate and weather events in coming years (44).

REFERENCES AND NOTES

1. N. Putman, *Curr. Biol.* **28**, R972–R976 (2018).
2. M. J. Kauffman et al., *Annu. Rev. Ecol. Evol. Syst.* **52**, 453–478 (2021).
3. D. S. Wilcove, M. Wikelski, *PLOS Biol.* **6**, e188 (2008).

4. J. O. Abraham, N. S. Upham, A. Damian-Serrano, B. R. Jesmer, *Nat. Ecol. Evol.* **6**, 998–1006 (2022).
5. R. H. Bell, *Sci. Am.* **225**, 86–93 (1971).
6. D. F. Vesey-FitzGerald, *J. Mammal.* **41**, 161–172 (1960).
7. R. Arsenault, N. Owen-Smith, *Oikos* **97**, 313–318 (2002).
8. A. M. Louthan, D. F. Doak, J. R. Goheen, T. M. Palmer, R. M. Pringle, *Proc. Biol. Sci.* **281**, 20132647 (2014).
9. M. D. Gwynne, R. H. V. Bell, *Nature* **220**, 390–393 (1968).
10. S. J. McNaughton, *Science* **191**, 92–94 (1976).
11. A. R. E. Sinclair, M. Norton-Griffiths, *Oecologia* **53**, 364–369 (1982).
12. A. W. Illius, I. J. Gordon, *J. Anim. Ecol.* **56**, 989–999 (1987).
13. J. T. du Toit, H. Olff, *Oecologia* **174**, 1075–1083 (2014).
14. A. R. E. Sinclair, *J. Anim. Ecol.* **54**, 899–918 (1985).
15. K. Stears, M. H. Schmitt, C. C. Wilmers, A. M. Shrader, *Proc. Biol. Sci.* **287**, 20192555 (2020).
16. L. Beaudrot, M. S. Palmer, T. M. Anderson, C. Packer, *Ecology* **101**, e03163 (2020).
17. A. Swanson *et al.*, *Sci. Data* **2**, 150026 (2015).
18. J. G. C. Hopcraft *et al.*, *Ecol. Monogr.* **84**, 355–372 (2014).
19. T. R. Kartzinel *et al.*, *Proc. Natl. Acad. Sci. U.S.A.* **112**, 8019–8024 (2015).
20. S. J. McNaughton, *Am. Nat.* **113**, 691–703 (1979).
21. W. J. Bond, J. E. Keeley, *Trends Ecol. Evol.* **20**, 387–394 (2005).
22. J. M. Fryxell *et al.*, *Ecol. Lett.* **8**, 328–335 (2005).
23. J. E. Donaldson *et al.*, *J. Appl. Ecol.* **55**, 225–235 (2018).
24. P. J. Van Soest, *Zoo Biol.* **15**, 455–479 (1996).
25. A. R. Sinclair, S. Mduma, J. S. Brashares, *Nature* **425**, 288–290 (2003).
26. J. G. C. Hopcraft, A. R. Sinclair, C. Packer, *J. Anim. Ecol.* **74**, 559–566 (2005).
27. A. Swanson *et al.*, *J. Anim. Ecol.* **83**, 1418–1427 (2014).
28. P. Strampelli, P. Henschel, C. E. Searle, D. W. Macdonald, A. J. Dickman, *PLOS ONE* **18**, e0280420 (2023).
29. H. Kruuk, *J. Zool.* **166**, 233–244 (1972).
30. C. D. FitzGibbon, J. H. Fanshawe, *Behav. Ecol. Sociobiol.* **23**, 69–74 (1988).
31. L. Sun, M. K. Clayton, *Biometrics* **64**, 74–84 (2008).
32. S. A. Hepler, R. Erhardt, T. M. Anderson, *Ecology* **99**, 2152–2158 (2018).
33. P. C. Caragea, E. Berg, *J. Agric. Biol. Environ. Stat.* **19**, 451–469 (2014).
34. M. S. Palmer, J. Fieberg, A. Swanson, M. Kosmala, C. Packer, *Ecol. Lett.* **20**, 1364–1373 (2017).
35. J. Pansu *et al.*, *Proc. Natl. Acad. Sci. U.S.A.* **119**, e2204400119 (2022).
36. J. M. Fryxell *et al.*, in *Serengeti III: Human Impacts on Ecosystem Dynamics*, A. R. E. Sinclair, C. Packer, S. A. R. Mduma, J. M. Fryxell, Eds. (Univ. of Chicago Press, 2008), pp. 277–300.
37. A. Mosser, J. M. Fryxell, L. Eberly, C. Packer, *Ecol. Lett.* **12**, 1050–1060 (2009).
38. W. O. Odadi, M. K. Karachi, S. A. Abdulrazak, T. P. Young, *Science* **333**, 1753–1755 (2011).
39. N. Owen-Smith *et al.*, *Mammal Rev.* **50**, 252–266 (2020).
40. G. Harris, S. Thirgood, J. G. C. Hopcraft, J. P. Cromsight, J. Berger, *Endanger. Species Res.* **7**, 55–76 (2009).
41. F. A. Smith, R. E. Elliott Smith, S. K. Lyons, J. L. Payne, *Science* **360**, 310–313 (2018).
42. E. J. Lundgren *et al.*, *Proc. Natl. Acad. Sci. U.S.A.* **117**, 7871–7878 (2020).
43. E. O. Aikens *et al.*, *Glob. Chang. Biol.* **26**, 4215–4225 (2020).
44. Intergovernmental Panel on Climate Change (IPCC), “Climate change 2022 – Impacts, adaptation, and vulnerability. Working Group II contribution to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change” (IPCC, 2023); <https://doi.org/10.1017/9781009325844>.
45. Camera trap occupancy data, GPS collar data, filtered dietary sequencing data, and R scripts, used to produce the results of the (i) 4- and 16-day Bayesian occupancy models, (ii) integrated step selection models, and (iii) dietary analysis for: T. M. Anderson, S. A. Hepler, R. M. Holdo, J. E. Donaldson, R. J. Erhardt, M. C. Hutchinson, S. E. Huebner, T. A. Morrison, J. Muday, I. N. Munuo, M. S. Palmer, J. Pansu, R. M. Pringle, R. Sketch, C. Packer, Interplay of competition and facilitation in grazing succession by migrant Serengeti herbivores, Dryad (2024); <https://doi.org/10.5061/dryad.7sqv9s4zk>.

ACKNOWLEDGMENTS

We thank the more than 130,000 volunteers from 77 countries who classified images on Snapshot Serengeti, as well as the team at Zooniverse for their support in hosting imagery. The Minnesota Supercomputing Institute and Wake Forest University High Performance Computing Cluster provided resources that contributed to data storage and processing. Snapshot Serengeti was publicized by the Association of Zoos and Aquariums’ “Saving Animals from Extinction” (SAFE) program and the Disney Conservation Fund’s “Protect the Pride” campaign. We thank C. Nutter for her laboratory work that facilitated the construction of the local DNA reference library for Serengeti grasses. Research clearance was provided by the Tanzania Wildlife Research Institute and Tanzania National Parks. **Funding:** This work was supported by the National Geographic Society (grants WW-025R-17 and

NGS-52921R-18 to T.M.A.); the National Science Foundation (grant BCS-1461728 to T.M.A. and R.M.H.; grants PRFB-1810586, IIS-1619177, and OAC-1835530 to C.P.; and grants IOS-1656527 and DEB-1457697 to R.M.P.); European Union’s Horizon 2020 Research and Innovation Program (grant 641918 to J.G.C.H. and T.A.M.); the Frankfurt Zoological Society (J.G.C.H. and T.A.M.); and the British Ecological Society (J.G.C.H. and T.A.M.). **Author contributions:** Conceptualization: T.M.A., S.A.H., R.M.H., J.E.D., R.J.E., J.G.C.H., M.C.H., T.A.M., J.P., R.M.P., C.P.; Data curation: T.M.A., M.C.H., S.H.E., J.M., I.N.M., J.P.; Formal analysis: T.M.A., S.A.H., R.M.H., R.J.E., M.C.H., T.A.M., J.P.; Funding acquisition: T.M.A., J.G.C.H., R.M.P., C.P.; Investigation: T.M.A., S.A.H., R.M.H., R.J.E., M.C.H., T.A.M., J.P., R.S.; Methodology and data collection: T.M.A., S.A.H., R.M.H., J.E.D., R.J.E., J.G.C.H., M.C.H., S.E.H., T.A.M., J.M., I.N.M., M.S.P., J.P., R.M.P., R.S., C.P.; Project administration: T.M.A., S.A.H., J.E.D., R.J.E., J.G.C.H., M.C.H., S.E.H., T.A.M., J.M., J.P., R.M.P., C.P.; Writing – original draft: T.M.A.; Writing – review and editing: T.M.A., S.A.H., R.M.H., J.E.D., R.J.E., J.G.C.H., M.C.H., S.E.H., T.A.M., J.M., M.S.P., J.P., R.M.P., C.P.; **Competing interests:** The authors declare no competing interests. **Data and materials availability:** Movement data collected with GPS collars for migratory Serengeti wildebeest and zebra presented in Fig. 1 are available through MoveBank (<https://www.movebank.org/>) with the unique identifiers “Wildebeest (Western White-Bearded) Hopcraft Serengeti-Mara” and “Plains zebra Hopcraft Serengeti-Mara.” Camera trap occupancy data, GPS collar data, filtered dietary sequencing data, and R scripts, used to produce the results of the (i) 4- and 16-day Bayesian occupancy models, (ii) integrated step selection models, and (iii) dietary analysis presented here (45) have been deposited to Dryad. **License information:** Copyright © 2024 the authors, some rights reserved; exclusive licensee American Association for the Advancement of Science. No claim to original US government works. <https://www.science.org/about/science-licenses-journal-article-reuse>

SUPPLEMENTARY MATERIALS

science.org/doi/10.1126/science.adg0744
Materials and Methods
Supplementary Text
Tables S1 to S6
Figs. S1 to S15
References (46–114)
MDAR Reproducibility Checklist
Data S1 to S6
Submitted 30 November 2022; accepted 10 January 2024
[10.1126/science.adg0744](https://doi.org/10.1126/science.adg0744)