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

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Abstract: 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 eight-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, while grass consumption by these large-bodied migrants attracts trailing, small-bodied gazelles 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.

One-Sentence Summary: Movement, occupancy, and diet data show how biotic interactions and abiotic factors influence multi-species mass-migration patterns.

Main Text: 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 multi-species 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), where 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 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 gazelles, as measured at a single location over three 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 due to resource depletion by larger grazers. A direct competitive process (interference; Table S1) may operate if species commingle and smaller herbivores propel larger herbivores onwards 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 ($N_{\text{cameras}} = 48 - 130$; coverage = 1000 km²; Fig. S1) that operated continuously between 2011 – 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 – August), when migrants move off the plains to the north-west 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 stimulating plant growth (both) (21). The extent of fire within the study area varied 33-fold across years (range: 21.3 – 694.4 km²; Fig. S2), rainfall in the four months prior to the transition period varied three-fold (217 – 621 mm; Fig. S2), and

5 vegetation greenness (normalized difference vegetation index; *NDVI*) varied over ten-fold (1.9 – 29.0; 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) that make contrasting predictions about the order, timing, and strength of species associations.

10 The facilitation hypothesis predicts consistent separation in migrant arrival time: zebra followed by wildebeest then gazelles (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. In contrast, high pre-migration rainfall promotes 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, while smaller ruminant species select nutritious short grasses.

20 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 ($H2_i$), 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 ($H2_d$) 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 competition, whereas pre-migration fire should intensify negative associations.

30 The predation hypothesis predicts closer spatial proximity especially for small-bodied species, as 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 predation risk; 26) regardless of rainfall or fire. We rely on lion predation as an overall proxy for ambush risk as cheetahs select the same small-scale areas as lions (27) and leopards' habitat preferences are highly congruent with lions' (28). In contrast, spotted hyenas and African wild dogs make no attempt at concealment and first disturb the herds to identify vulnerable individuals (29, 30). Hence, we consider it unlikely that risks from coursing predators would confer strong advantages either from forming mixed-species herds or from migrating separately.

RESULTS

Arrival order and time lags

45 The classic formulation of grazing succession (5) predicts consistent ~2-month separations in peak abundance of each species (Fig. 1C). However, 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 d (range: 22 to -6 d) before zebra, although this difference was inconsistent (Wilcoxon signed-rank test: $v = 3.5$, $P = 0.09$, $df = 6$). In contrast, wildebeest and zebra abundance both consistently peaked 27.6 ± 15.4 d before gazelle (Wilcoxon sign 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 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 four-day and sixteen-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 unique species-specific conditional term ($Y_{species\ 2|species\ 1}$) that measured the effect of one species on the occupancy probability of another.

Over four-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), and wildebeest increased zebra occupancy in 3 of 8 years (and marginally in another) (Fig. 1G; Fig. S3; Table S2). On this four-day scale, gazelles 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 gazelles and larger herbivores (Fig. 1F, 1G).

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

Influences of fire and rainfall on species' associations

Exceptions to the prevailing patterns were related to environmental extremes. The two years without four-day conditional effects of zebra and wildebeest also showed the most extensive fires (2013 and 2016). Further, 2 of the 3 years without sixteen-day lagged effects of larger species on gazelles had the lowest rainfall in the entire study period (2014 and 2017; Fig. S3; 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 (RSA_i) as functions of fire and rainfall from January–June each year (Fig. S3). We predicted that RSA_i should be negatively associated with fire and positively associated with pre-migration rainfall. Indeed, RSA_i in four-day intervals declined with area burned (Fig. 2;

Table S4). This correlation was directionally consistent but strongest for zebra on wildebeest and for wildebeest on gazelles—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 sixteen-day intervals increased with rainfall for gazelles trailing wildebeest and zebra (Fig. 2). Thus, gazelles more closely tracked the larger migrants in years with higher herbaceous 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 timescale, despite their reciprocal spatial associations (Fig. 2). For additional insight, we examined paths of GPS-collared individuals for one dry (2017) and one wet (2018) year to test whether movements measured at four-hour intervals revealed subtler responses to heterospecifics. Wildebeest habitat selection was independent of proximity to dense herds of zebra (Fig. 3A). In contrast, zebra selected habitat distant from dense wildebeest herds in both years, and farther in the dry (1.4 km) than the wet (0.8 km) year (Fig. 3B, 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 near dense zebra herds; in the more plentiful wet year, wildebeest used smaller step lengths indicative of active foraging (Fig. 3; 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; Table S5). This last inference is also supported by evidence that both species avoided senescing vegetation more strongly in the wet than 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: wildebeest habitat selection is governed by resource availability independent of zebra, while 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 (Fig. S4; 34). Conditional species associations were indistinguishable between high- and low-risk areas at both four-day and sixteen-day timescales (figs. S5–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; Supplemental Materials). Zebra diets consisted almost exclusively of grasses (96.9% of sequence reads on average); wildebeest diets were grass-dominated (73.9%) but included substantial proportions of herbaceous eudicots, mostly legumes (Fig. 4A, B; Table S6). In contrast, grasses were a minority of gazelle diets (26.2%), especially in earlier months (May–July) before the larger species departed from the study area (Fig. 4A, B). In both years, zebra and wildebeest ate highly overlapping sets of plant taxa (mean niche overlap 0.82), while overlap was lower for wildebeest and gazelles (0.53) and lowest for zebra and gazelles (0.34). Wildebeest and gazelles avoided common tall grasses of middling to low quality, whereas zebra showed higher selectivity for these taxa (Fig. 4C). In later months, however, gazelles increased consumption of high-quality grasses such as *Digitaria macroblephara* that

were likely regrowing after being grazed earlier in the season (figs. S14, S15; Supplemental 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 find new support for a facilitative mechanism first proposed in 1968 (9) whereby larger migrants benefit gazelles by opening the grass canopy and providing access to nutrient-rich prostrate eudicots (Fig. S15), at least until the late dry season when gazelles switch to high-quality grasses grazed by earlier migrants (Fig. 4B; Fig. S14). Coupled with the observed lags in occupancy, these dietary differences are incompatible with the idea that gazelles competitively displace larger migrants (13) and may also help explain the gazelles' stable population size following 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 the grazing succession is driven by predation risk (H3). Risk from lions, leopards, and cheetahs is especially high in the northwestern region of our study area (Fig. S4; 38), and if risk mitigation were a key reason for co-migration, 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 multi-species 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 (< four-day) between zebra and wildebeest and longer intervals (sixteen- to thirty-two-day) between larger migrants and gazelles. 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 gazelles via 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 (37). In our study, smaller migratory herbivores benefitted 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; Fig. S13) and/or gained improved access to protein- and mineral-rich legumes and other forbs (Fig. S14, Fig. S15). In a typical year, habitat use by gazelles tracks co-migrating zebra and wildebeest migration, and this association intensifies with increasing rainfall. In high-fire years, short-term movements among grazers are largely uncoupled, indicating that gazelles benefit from grass removal and regrowth, regardless of whether it results from migratory herbivores or fire. We do not claim that effects of zebra on wildebeest or of both species on gazelles 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.

Multi-species migratory systems were once common across tropical savannas (3, 39) and probably involved 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 portends additional challenges associated with extreme climate and weather events in coming years (44).

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Data and materials availability:

- 30 Movement data collected with GPS collars for migratory Serengeti wildebeest and zebra presented in Figure 1 are made available through MoveBank with unique identifiers: “Wildebeest (Western White-Bearded) Hopcraft Serengeti-Mara” and “Plains zebra Hopcraft Serengeti-Mara”. Raw and filtered dietary sequencing data are deposited in DRYAD with the unique doi: 10.5061/dryad.br15dvcj. Data, code, and materials used for the Bayesian occupancy
35 models, integrated step selection models of migratory herbivores, and R scripts to produce the dietary results presented here are made available through DRYAD with the unique doi: 10.5061/dryad.7sqv9s4zk.

Supplementary Materials:

- Materials and Methods
40 Supplementary Text
Tables S1 – S6
Figs. S1 – S15
References (45–115)
Data S1 – S5

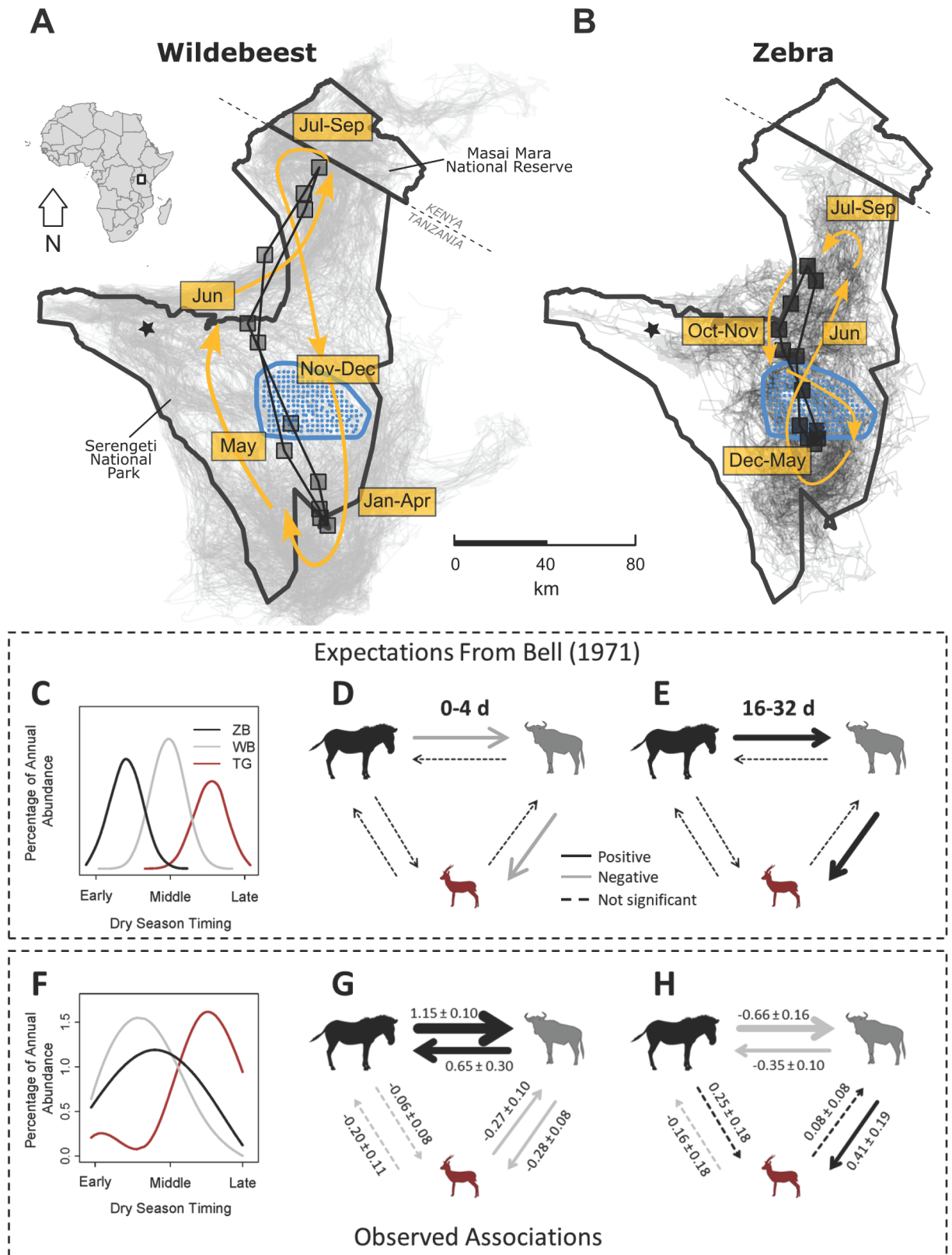


Fig. 1. Movements (1999-2020), temporal dynamics, and species interactions of migratory grazers in the Serengeti ecosystem. Our study area (blue polygons in A, B) is a migratory transition zone linking the Serengeti plains, Western corridor, and Masai Mara Game Reserve.

Based on GPS collaring data collected between 1999-2020 (18), 96% of collared wildebeest ($n = 54$, grey lines in **A**) and 100% of zebra ($n = 28$, black lines in **B**) passed through the study area. Grey 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 in **A**, **B**) are 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 (asterisk in **A**, **B**) at a time when the wildebeest population was approximately 25% of their current size (18). Thomson's gazelles have not been collared in the Serengeti National Park; consequently, we focused our analysis of individual movements on zebra and wildebeest. (C–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 four-day (D) and sixteen- to thirty-two-day intervals (E). The classic model predicts unidirectional spatial associations between migrants at substantial time lags (E) driven by activities of large herbivores (foraging, trampling, nutrient redistribution) that facilitate foraging by small herbivores. Negative interactions, not explicitly considered in early work (5, 9; cf. 13), would appear on short timescales (D) because of lagged positive associations. (F–H) Associations observed in this study. Average abundance during the transition season (F) supported the classic model for gazelles, 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 variation in migration timing across years. Within four-day windows, zebra and wildebeest had strong reciprocal effects on each other's occupancy throughout migration, while lagged arrival times led to negative associations with gazelles (G). Within sixteen-thirty-two-day windows, zebra and wildebeest had positive effects on occupancy of gazelles, and negative effects on each other due to their concurrent migration (H). Each arrow represents the average positive (black) or negative (grey) conditional association strength ($\gamma_{species\ 2|species\ 1}$) from Bayesian occupancy models fit at four-day (G) or sixteen-day (H) time intervals across the entire study period (Supplemental Materials). Values are mean \pm 95% confidence intervals (CI; tables S2 and S3) with arrow widths proportional to the magnitude of the effect size. Dashed lines represent weak effects that were below included zero in the 95% CI.

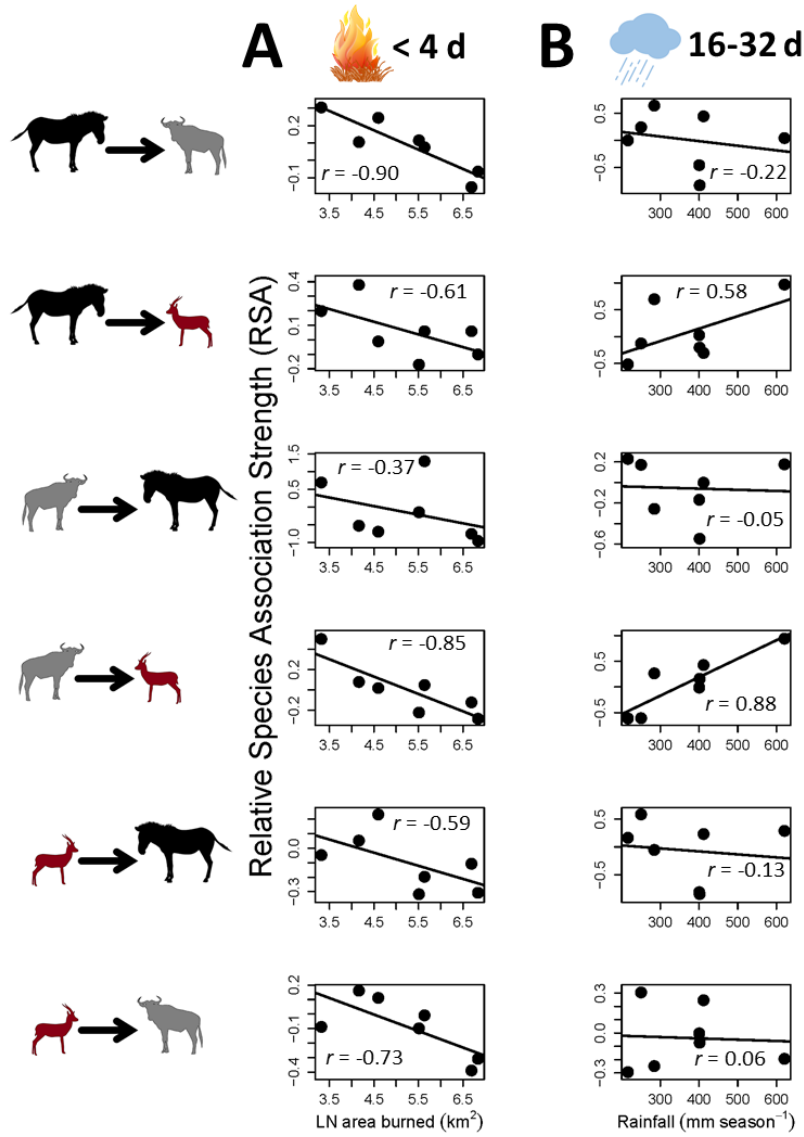


Fig. 2. Fire weakens but rainfall strengthens species associations during grazing succession.

The relative strength of species association (RSA) is the difference between species associations from Bayesian occupancy models fit at four-day or sixteen-day time interval for a given year minus the mean across all years ($RSA_i = \hat{\gamma}_i - \bar{\gamma}$; Supplementary Materials). RSA_i values are plotted against (A) the natural log of the burned area and (B) cumulative rainfall from January–June of year i . Fire was negatively related to variation in RSA_i calculated from four-day spatial associations (A; Table S4), with the strongest correlations between smaller migrants conditioned on the presence of larger migrants (WB|ZB and TG|WB); rainfall was positively related to variation in RSA_i calculated from sixteen-day spatial associations (B), but only for Thomson’s gazelles 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.

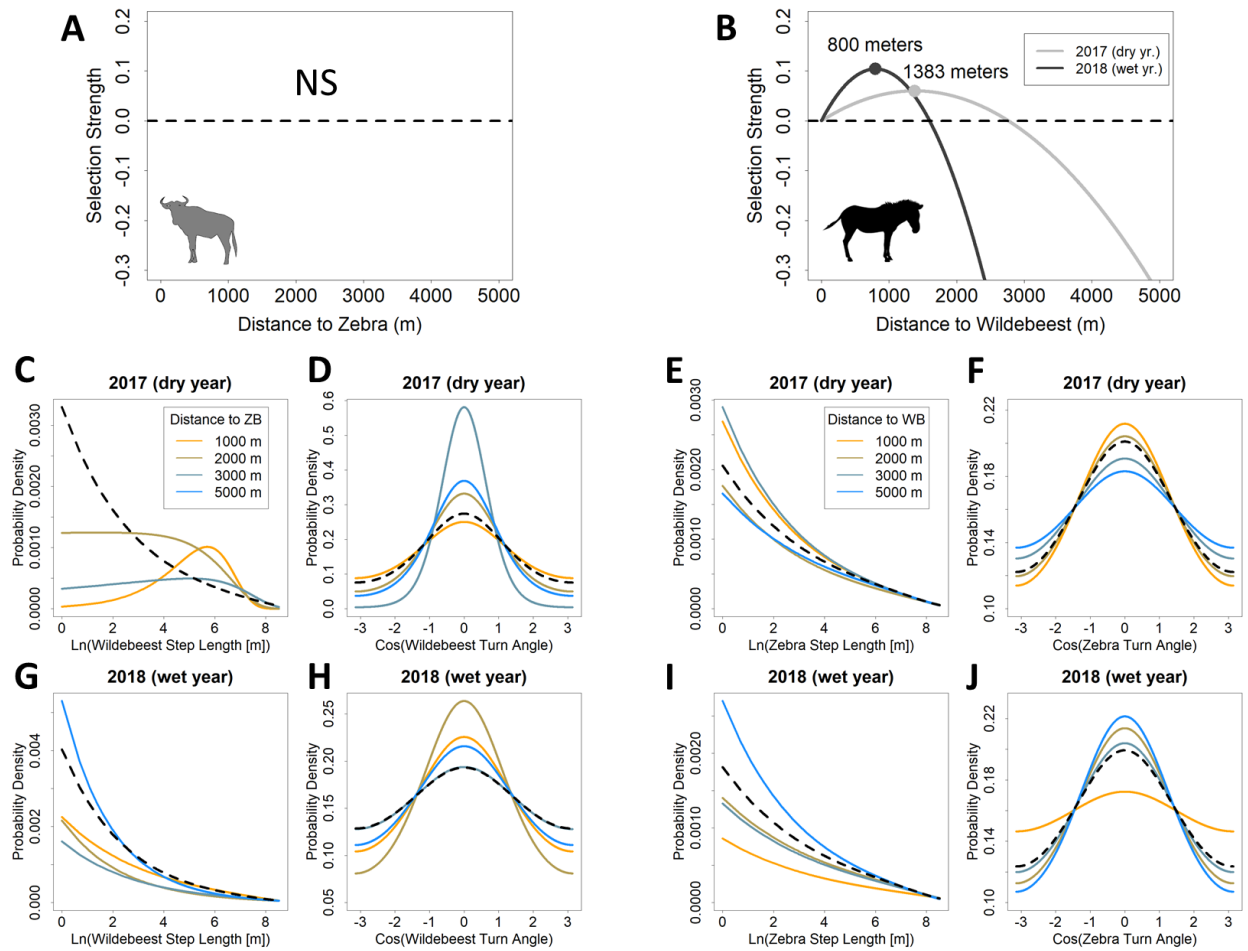


Fig. 3. Wildebeest and zebra movements during one dry and one wet year.

(A–B) Movement models of collared individuals were analyzed in relation to distances from large heterospecific herds as determined by camera trap data (see Supplementary Materials). In both dry (2017) and wet (2018) years, wildebeest selected habitat independent of distance to large, dense zebra herds (A). In contrast, zebra selected sites at moderate distances from dense wildebeest herds (B), with greater distances in the dry (light grey line, mode = 1383 m) compared to wet year (dark grey line; mode = 800 m). (C–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 towards the front of the migration nearest to zebra (C), indicating directed movement (D). Zebra step lengths during the dry year were marginally larger than the expected from the tentative distribution (E). In the wet year (2018) wildebeest used smaller step lengths than expected from the tentative distribution (G), consistent with greater local resource availability and foraging behavior. Zebra movement changed dramatically in the wet year, with smaller step lengths and wide, circuitous turn angles, especially for individuals within 1000 m from dense wildebeest herds (I, J), 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 zebra (C, D) or wildebeest (E, F) distances to large heterospecific herds as determined by camera trap data (see Supplementary Materials).

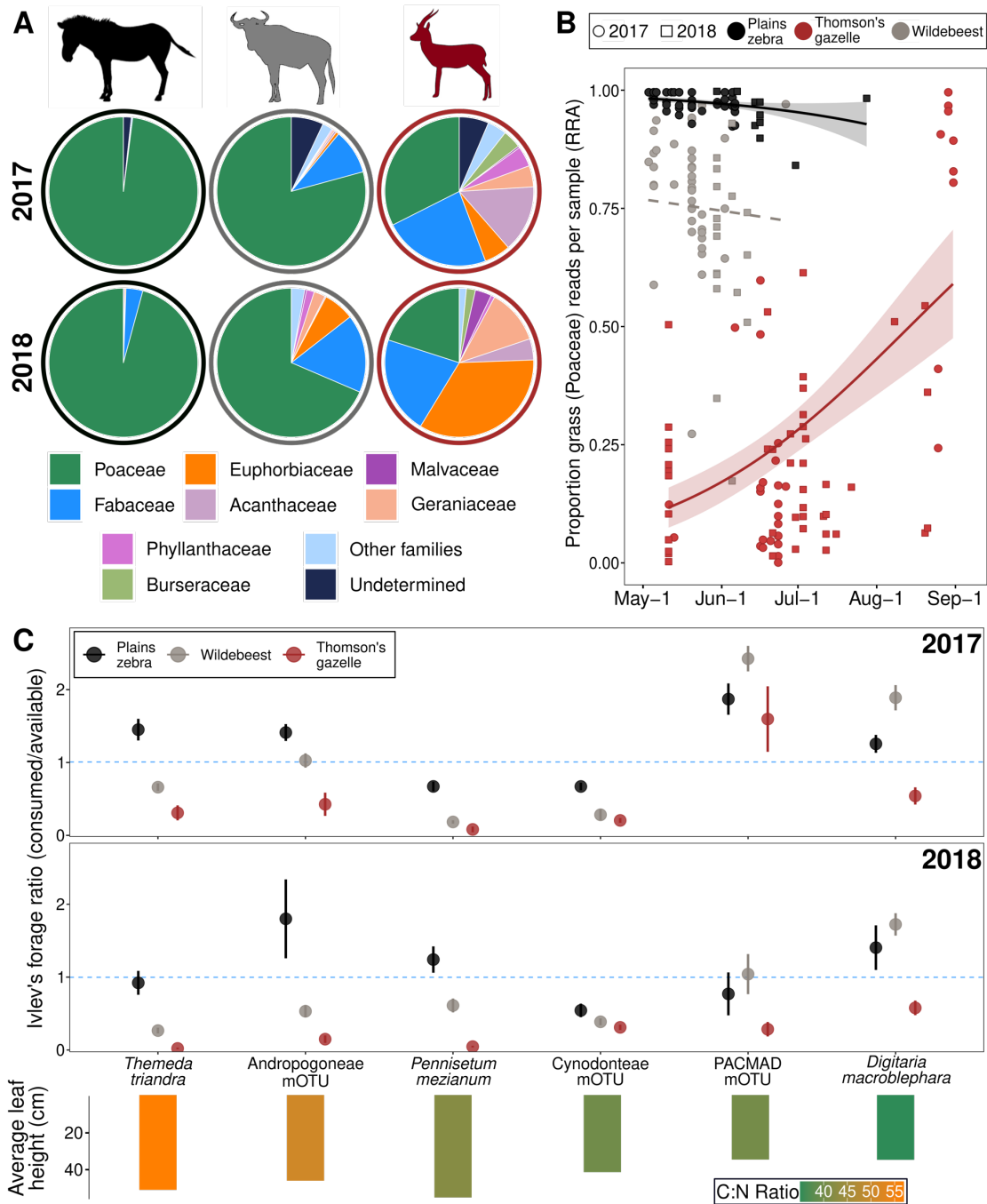


Fig. 4. Differential consumption of plant taxa of varying nutritional quality.

(A) Mean diet composition by plant family (colors) during the migration period in dry (2017) and wet years (2018), showing unexpectedly high consumption of high-quality (Fig. S15) forbs by wildebeest and gazelles, notably legumes (Fabaceae). (B) Proportional grass consumption by gazelles 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 heavily eaten grass taxa; 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, 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 in Table S6.