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The Amboseli migrations: Causes, changes and the conservation of a viable ecosystem

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Introduction

Seasonal migrations of large herbivores are typical of the world's arid and semi-arid rangelands. Examples include the wildebeest of Serengeti, the white-eared kob in Sudan, the zebra migrations of the Kalahari in Botswana, the chiru on the Tibetan Plateau, Saiga antelope in Central Asia, and caribou in northern Europe and Alaska. Indigenous pastoral herders in the Asia and Africa often migrated in lockstep with wildlife but have largely vanished with growing human activity and a breakdown of traditional husbandry practices.

Amboseli is the only area where the wildlife and traditional livestock migrations were studied in detail before extensive changes in traditional livestock economies and migrations (Western, 1973, 1975). The Amboseli Conservation Program (ACP) began studying the wildlife and Maasai migrations in 1967 and has continued monitoring the changes since then. In this bulletin we describe the seasonal distribution of wildlife and livestock before the creation of Amboseli National Park and subdivision of group ranches in the early 1970s. The maps track the visual changes over the following half century in response to growing human activity.

We have not included non-migratory species in our analysis. The browsers including giraffe, Grant's gazelle, impala, gerenuk and lesser kudu, show little seasonal movements. We focus on the main migratory species, Maasai livestock, wildebeest and zebras which together account for over ninety percent of the liveweight of all species. We reported separately on the changing numbers, distribution and elephant migrations in a separate article (Western and Mose, 2023).

The aerial and ground count methods for tracking the Amboseli migrations are given in the publications listed in the reference. We use production, the yield of each species, rather than biomass to adjust for metabolic weight differences (Western and Mose, 2021). We use heat maps to show the intensity of production for each counting grid.

The Amboseli ecosystem map used in the Amboseli Ecosystem Management Plan 2020-2030 (AEMP) is defined by the Minimum Viable Conservation Area (MVCA) needed to sustain the migratory species. In this report we focus on the changes in the migratory species, the causes of the migrations, and the MVCA needed to sustain the migratory populations.

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Aerial counts

The sample aerial counts based on a 5 km by 5 km grids cover 8,500 km² of eastern Kajiado, including the Ilkisongo, Kaputei and Matapatu sections shown in the map below. The counts were first flown in 1973 when the Ilkisongo Maasai still migrated freely between wet season dispersal and dry season concentration areas centered on the swamps stretching from Amboseli to the Chyulu Hills. The Kaputei Section to the north begun subdividing the traditional communal lands into group ranches and private allotments in the late 1960s. Ilkisongo was divided into group ranches in the early 1970s but remained open to seasonal migrations.

A rapid shift from seasonal migrations to permanent settlements in Ilkisongo was well underway by the late 1980s and early 1990s, over 20 years before subdivision into private allotments. We use the pre-1989 counts to capture the traditional free-ranging migration before and the post-1989 counts to illustrate the settlement phase which followed.

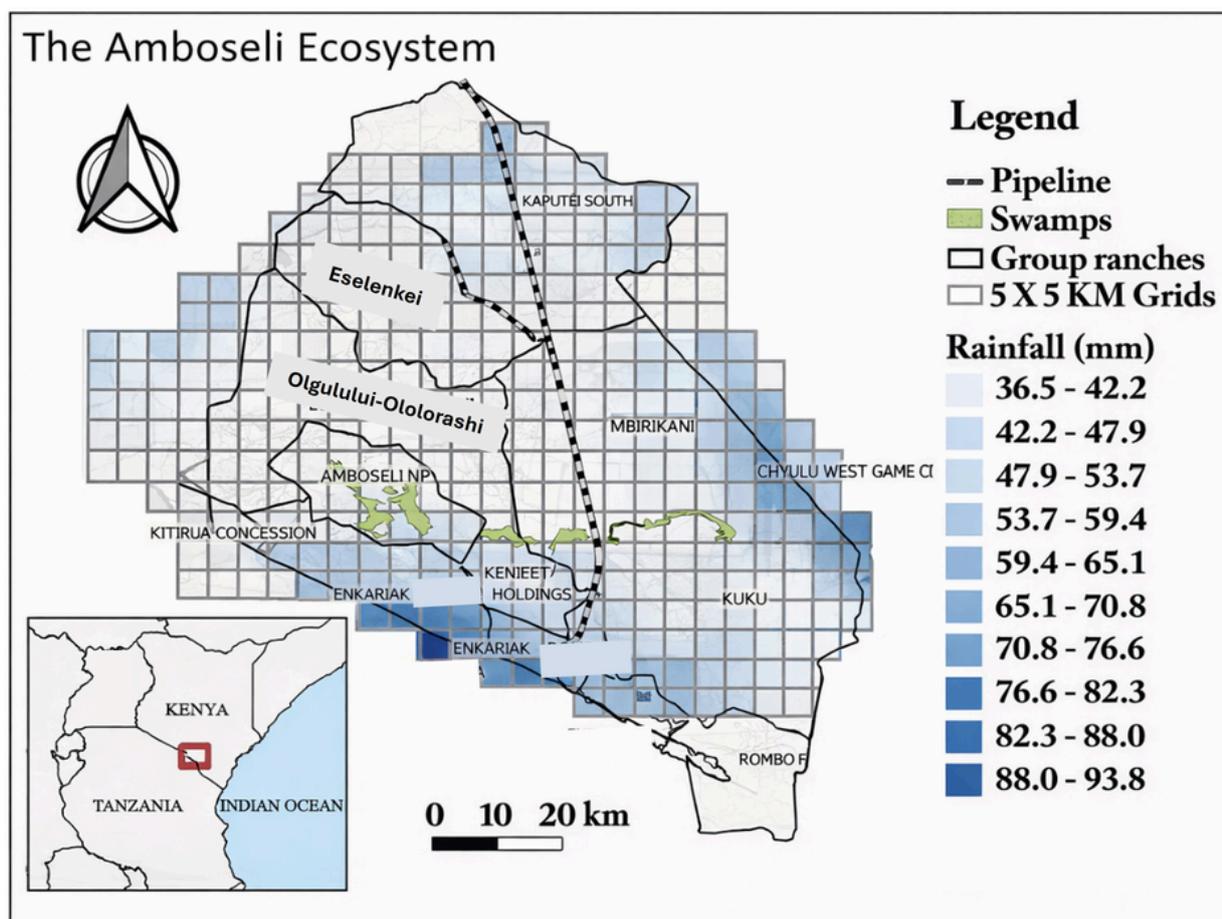


Figure 1: A map of eastern Kajiado showing the area covered on aerial counts overlaid on the 5 km by 5 km grid used on transect counts. The Amboseli wet season migrations fall largely within the ecosystem and concentrate around the permanent swamps given in green in the dry season. The counts cover adjacent wildlife and livestock populations which overlap the Amboseli migrations.

The changing distribution of wildlife and livestock

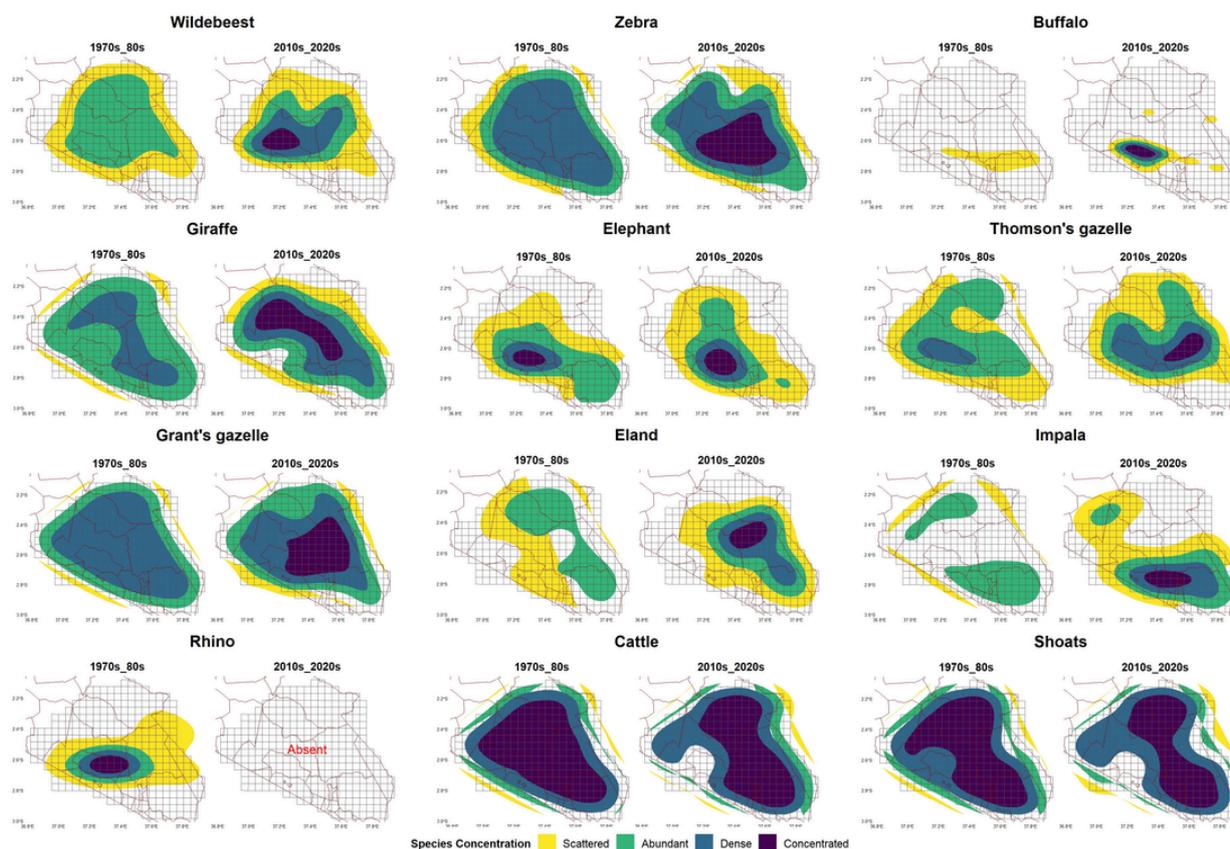


Figure 2: The maps show the changing distribution of wildlife and livestock from the free-ranging period in the 1970 to late 1980s to the 2010 to 2020s following land demarcation. Note the sharp drop in the Kaputei ranches to the north following land subdivision and a shift to permanent settlements. Cattle, sheep and goat (shoats) distributions remain widespread but have increased in the central region due to water provision along the Loitokitok pipeline, and decreased marginally south of Amboseli National Park.

Livestock and wildlife still moved freely with the seasons before the creation of Amboseli National Park and subdivision of the communal lands into group ranches in the 1970s. Zebras, buffaloes and elephants, concentrated around the swamps stretching from Amboseli to the Chyulus Hills in the dry season and dispersed widely in the rains. Maasai livestock followed a similar seasonal migration between dry and wet season ranges. Buffalo and eland populations in the Chyulus and eland on Kilimanjaro migrated to the lowlands during the rains. The free-ranging movements of livestock and wildlife before the creation of Amboseli National Park and group ranches was documented at the time (Western, 1973, 1975).

The expansion of farms and shift from seasonal migrations to permanent settlements has caused large changes in the distribution and movement of all species in eastern Kajiado (Western and Mose, 2021). The subdivision of Kaputei Group Ranch in the 1970s is a case in point, The subdivision and permanent settlement of Kaputei Section led to a collapse of the wildebeest and zebra migrations (Western et al, 2009). Few wildebeest are now found on Kaputei. Zebras manage subdivision and settlement better but in far smaller numbers.

In the following maps, we compare the average wet and dry season distributions of livestock and wildlife before and after 1989. We then narrow down to the pre- and post-settlement phases for the two most abundant migrants, wildebeest and zebras. We next give “sky-scraper” maps for wet and dry and season distributions of both species across the group ranches. The high-level definition spotlights the areas on the group ranches needed to secure the migrations.

Finally, we give a visual image of satellite-tracked collared wildebeest showing the movement between wet and dry season ranges in yet greater detail. The distribution of the collared animals matches the MVCA given in the AEMP 2020-2030. The maps also identify the main areas used on Olgulului-Ololorashi, Mbrikani and Eselenkei Group Ranches, and the areas needed to keep the connections between them and migratory routes into Ngaserai in Tanzania. The Mbikirani connections link the Amboseli populations of wildebeest and zebras to separate wildebeest populations in Tsavo West and Tanzania, both of which are vital in ensuring the viability of the Amboseli migrants. The collapse of the wildebeest population from over 7,000 to 200 during the 2009 drought was only restored by wildebeest immigrating from Tsavo West and Ngaserai in the aftermath of the drought.

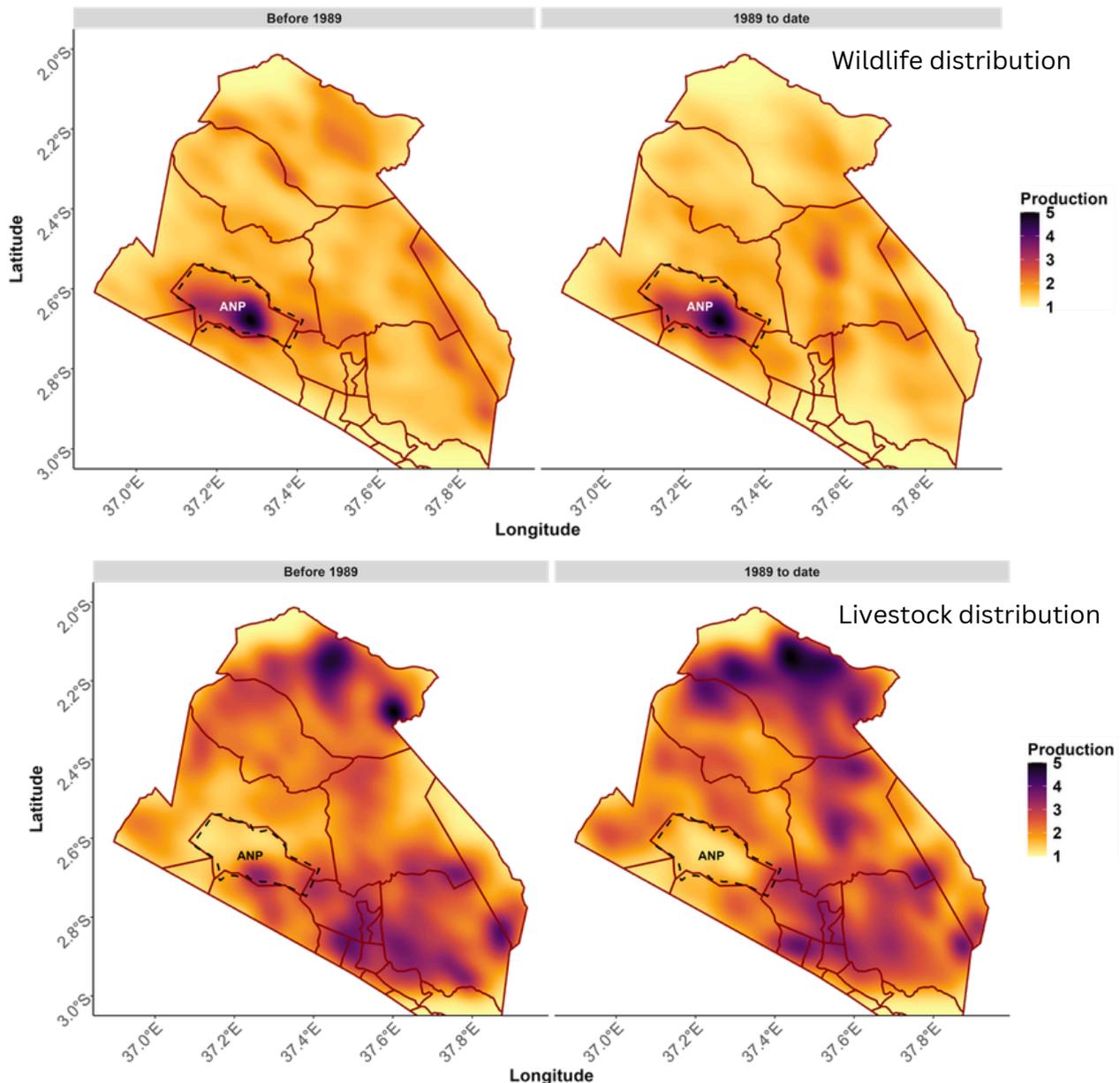


Figure 3: Production heat maps showing changes in the distribution of wildlife (top) and livestock (below) before and after the shift from mobile to permanent settlements. Livestock use of the slopes of Kilimanjaro fell with the spread of farms downslope. Livestock numbers increased on the subdivided Kaputei Ranch and along the Loitokitok Pipeline with the spread of water outlets. Wildlife numbers fell steeply on the subdivided Kaputei Ranch, increased on Mbrikani which remained open to migrations, and dropped to remnant populations along the base of the Chyulu Hills as upstream irrigation dried the feeder rivers.

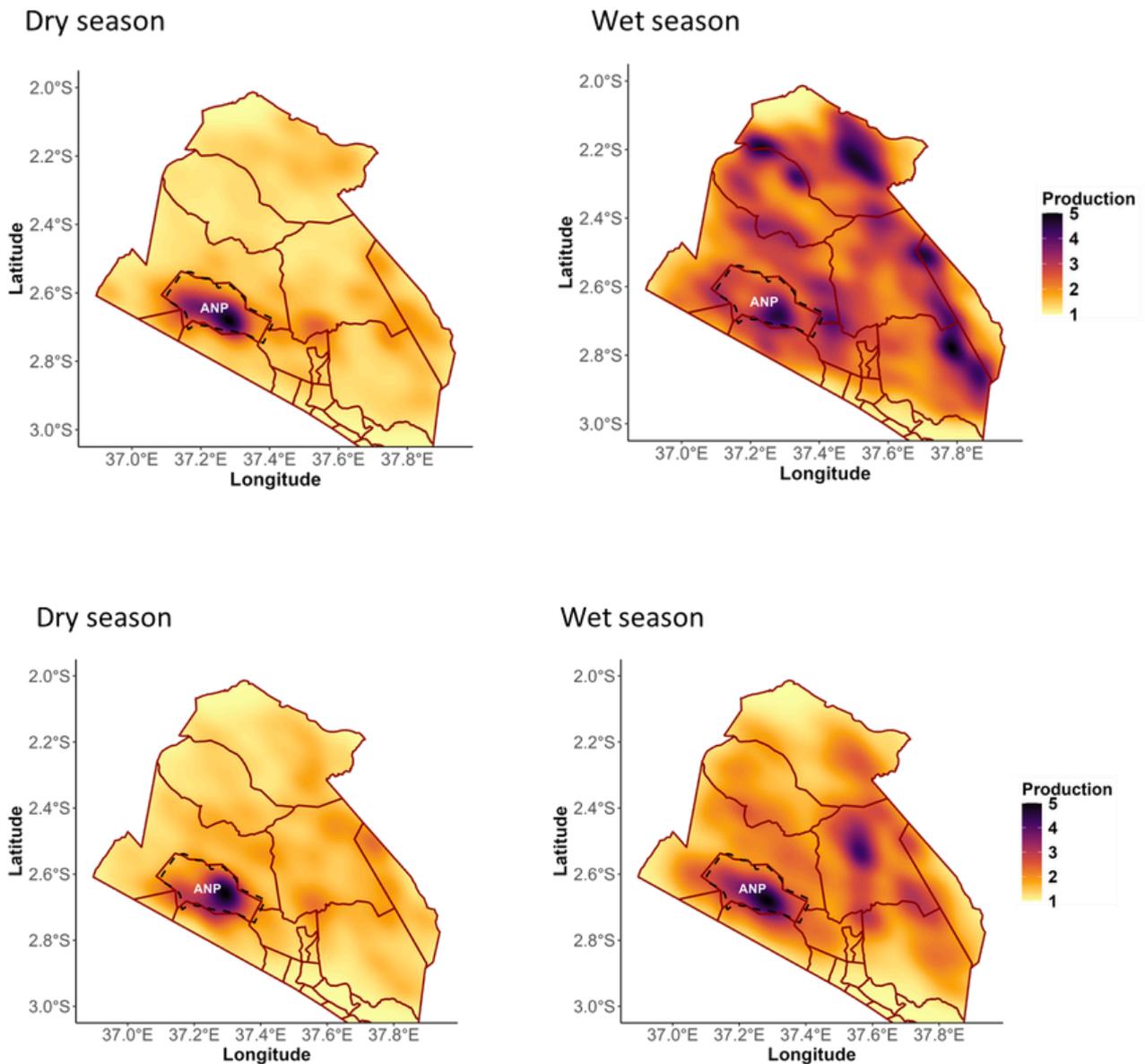


Figure 4: Heat maps for all wildlife for wet and dry seasons before (top) and after the settlement phase (bottom). Wildlife fell sharply in the subdivided Kaputei ranches with subdivision and permanent settlements. Wildlife numbers also fell sharply along the base of the Chyulu Hills with the loss of permanent swamps due to upstream irrigation.

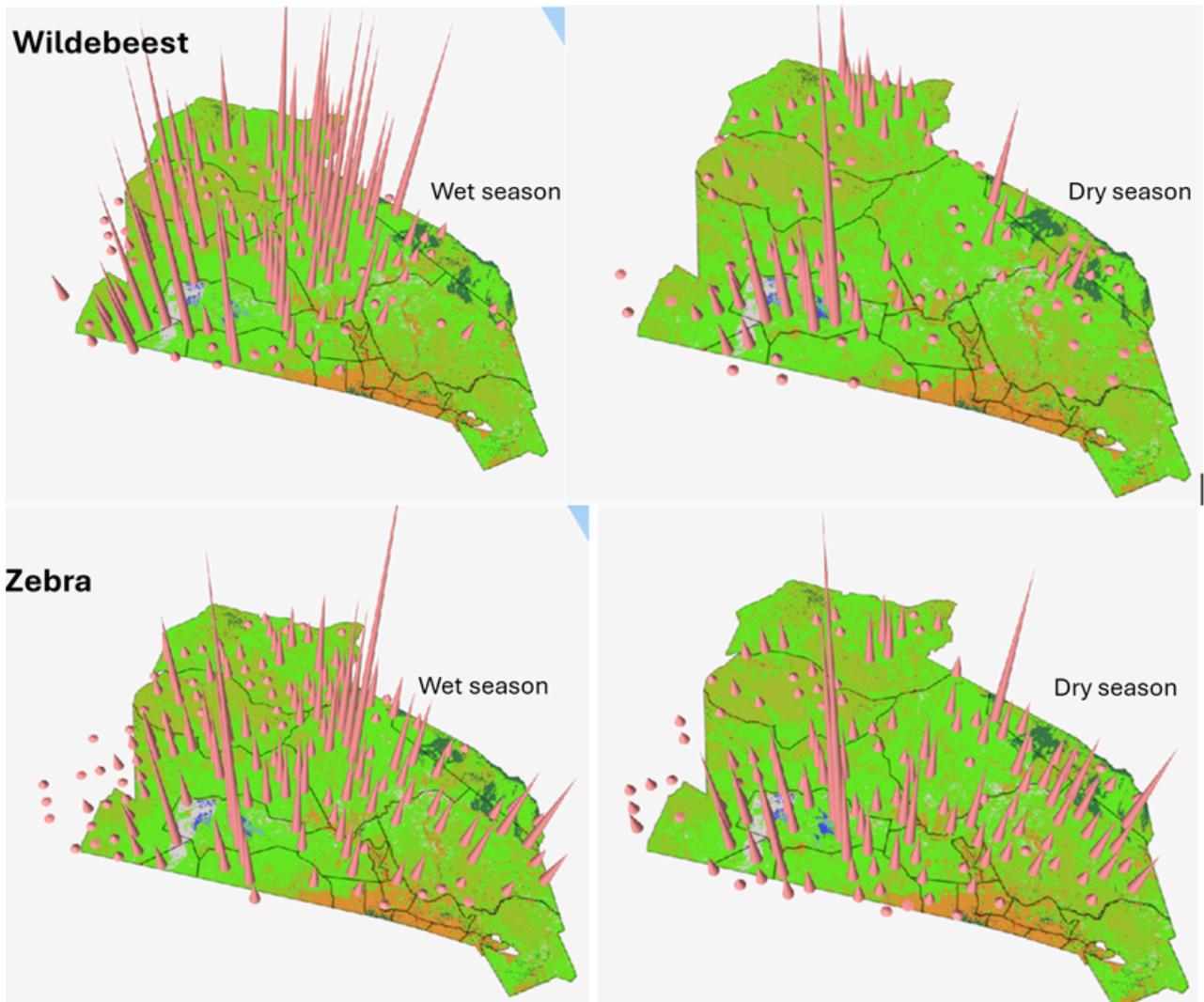


Figure 5: “Sky scraper” seasonal maps of the density of wildebeest (top) and zebras (bottom). The maps show the far greater seasonality and dry season concentration of wildebeest than zebras, and their greater vulnerability to land fragmentation.

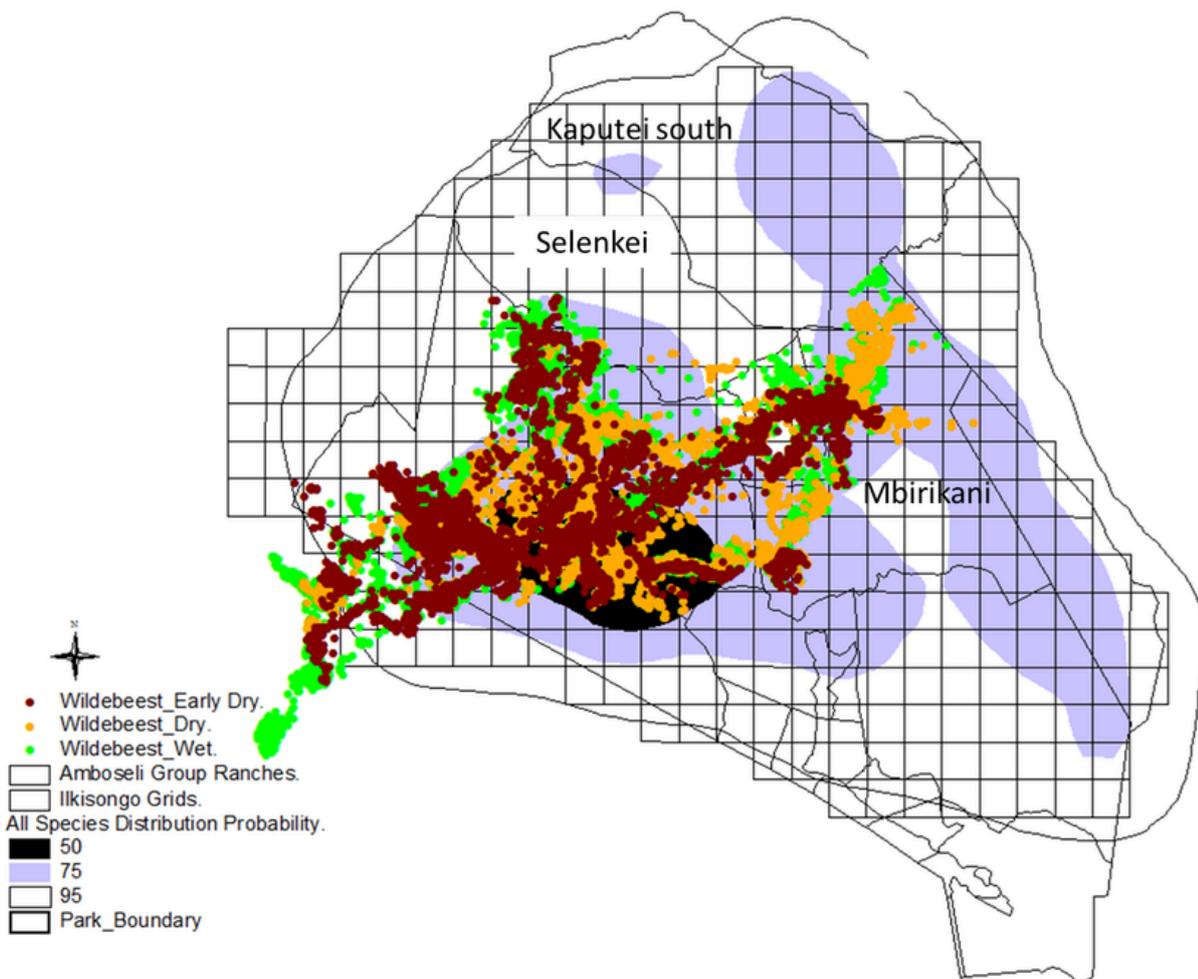


Figure 6: Satellite-tagged wildebeest (coloured points) show seasonal migration patterns, concentrating around the Amboseli swamps during the dry season and dispersing during the rains. The main migratory pathways extend north to Olgulului-Olorashi, northwest to Mbirikani, and southwest into Tanzania. The satellite-tracking data are overlaid on kernel probability distribution maps for all wildlife generated from aerial survey data and categorized into 50%, 75%, and 95% concentration levels. The satellite-collar and aerial survey data overlap strongly, clearly demonstrating areas of wildlife concentration in relation to seasonality.



Wildebeest grazing the short grass plains in Amboseli.

The causes of change

The main causes of change in wildlife distributions and the migratory herds have been covered in detail in Western and Mose (2021). Subdivision and settlement have severed the migrations on Kaputei. Drylands farming has displaced wildlife from the Kilimanjaro foot slopes. Crop irrigation in swamps has severely reduced populations in the Namelog, Kimana, Olengarua and Lenker Swamps. Small-holdings springing up along the Loitokitok pipeline running north-south through the ecosystem have pinched and threaten to cut off the seasonal migrations between Amboseli and Mbirikani.

The shift from seasonal migrations to settled lives has caused heavy grazing and a drop in pasture production across the Amboseli migratory range (Western et al, 2015). The intensified grazing has in turn caused a loss of large herbivores production, both for livestock and wildlife (Western and Mose, 2021). The Amboseli swamps have, on the other hand expanded due to heavy runoff from surrounding settlements flooding into the national park since 1990.

The late season pastures in and around the swamps have more than doubled in area and resulted in far higher concentrations of wildlife. Zebra, wildebeest, Thomson's gazelle numbers have grown sharply in the park as a result, and the migrants have returned earlier each season due to heavy grazing on the group ranches.

Elephant numbers have more than doubled after the heavy poaching of the 1970s. The poaching concentrated elephants in the park in the following decades when the migrations resumed, but in reverse. Elephants now feed on the swamps as soon as the sedges recover in the rains and leave when they are grazed down in the late dry season (Western and Mose, 2023).

The seasonal rhythms

The unimpeded seasonal rhythm of the migrations in the 1960s before the creation of the national park and group ranches has been described in detail (Western, 1975). The migrations, triggered by the first heavy rains, dispersed into the northern bushlands with smaller movements south of Amboseli. At the height of the rains only the browsers, giraffe, impalas, Grant's gazelle, lesser kudu and bushbuck, remained in the Amboseli Basin. Thomson's gazelle moved the short distance onto the short grassy plains of the northern bushlands.

The migrants returned 30 to 50 days after the rains ended. Zebras, wildebeest, elephants and Maasai livestock concentrated in the Amboseli Basin and swamps as the waterholes dried and pastures in the dispersal area were grazed down. The extent of the dry season movements was defined by the distance the water-dependent migrants forage from water, up to 15 kilometers for wildlife, 22 kilometers or more for non-milking cattle herds (Western, 1975).

The returning migrants shifted from the northern bushlands, onto the plains, into the woodlands and around the swamp margins in the course of the dry season. The annual grazing cycle during the free-ranging migrations of the 1960s is shown in the diagram below.

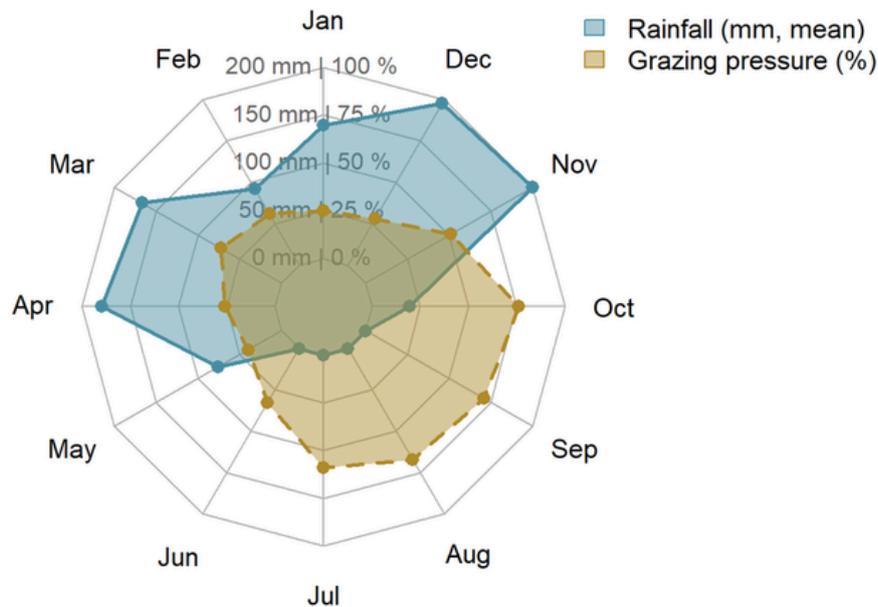


Figure 7: During the rainy months, migratory herbivores disperse out of the Amboseli basin in response to widespread forage availability, resulting in reduced grazing pressure within the basin. In contrast, during the dry months animals concentrate back into the basin as surrounding areas dry out, leading to increased grazing pressure around permanent water and key forage areas.

Causes and benefits of migration: ecological monitoring

ACP has monitored twenty permanent vegetation plots across the Amboseli Basin since 1975. The plots, measured monthly by David Maitumo, track grass height, cover, biomass, greenness, grazing pressure and animal occupancy through the seasons. The protein and fiber content of each plot has been recorded to give a measure of pasture quality across the Amboseli habitats through the seasons. The variations in animal movements are considerable due to the small sampling fraction, patchy rainfall and varied grazing movements. The variations from season to season are dampened and become far clearer when lumped for each habitat and by wet, dry and drought seasons. The following diagrams summarize the Amboseli migrations through seasons and across the habitats.

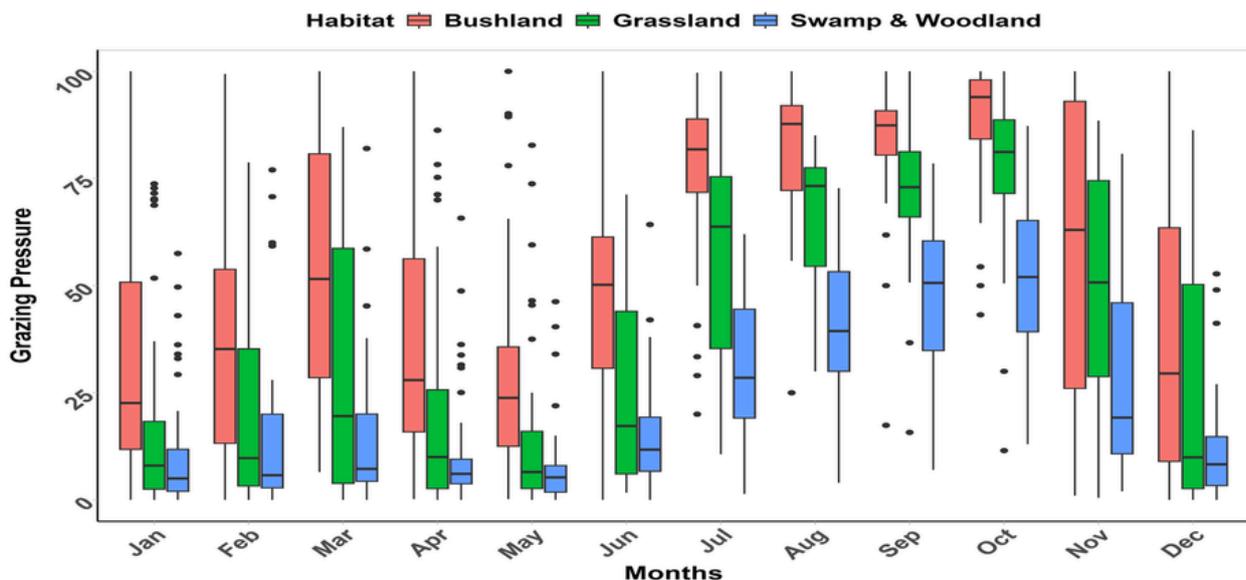


Figure 8: The grazing pressure gives a clear picture of the seasonal migrations through the habitats. The grazing pressure builds up in the bushlands during the migrations, then shifts to the plains and swamps as the short dry season progresses. The grazing pressure is relieved when the long rains revive the pastures. The ensuing long dry season is harsher than the short dry period, building first in the bushlands, then plains, and finally swamps as the pastures of last resort.

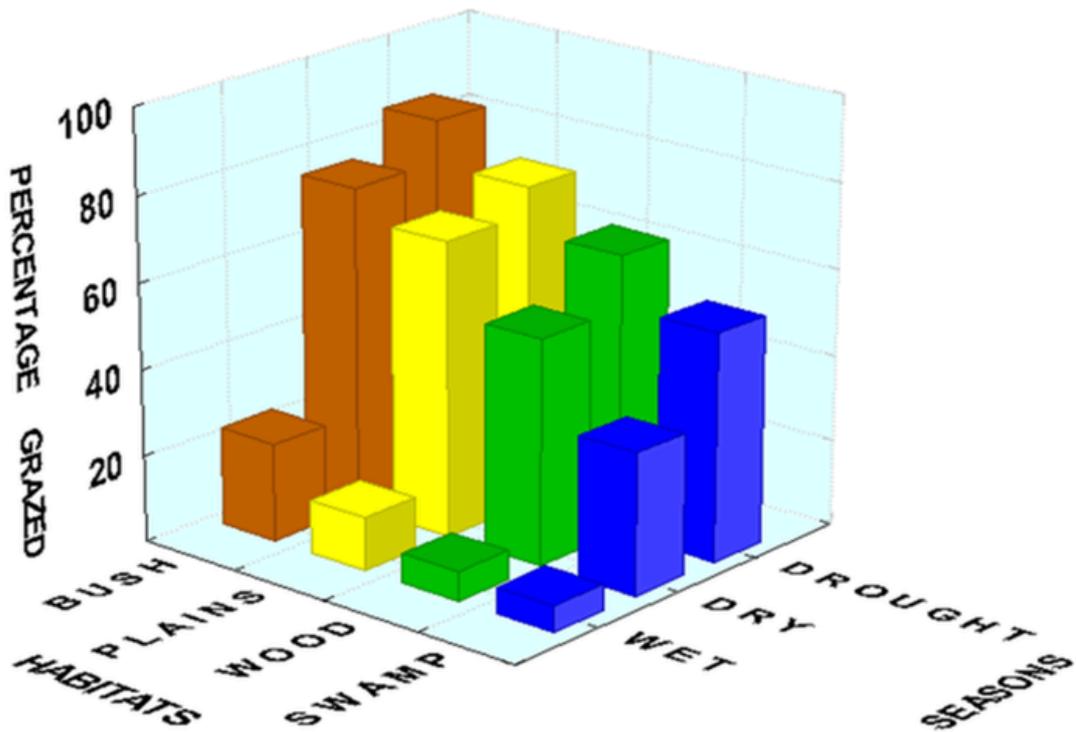


Figure 9: An aggregated 3-D diagram of grazing pressure in each habitat gives a clear picture of the migrations. The grazing pressure shifts through the habitats from the bushlands during the rains, to the plains early dry season, woodlands and finally, the swamps in the late dry season. In severe droughts most of the migrants concentrate in the grazing arenas around the swamp edges and grazed down sedges in the swamps.

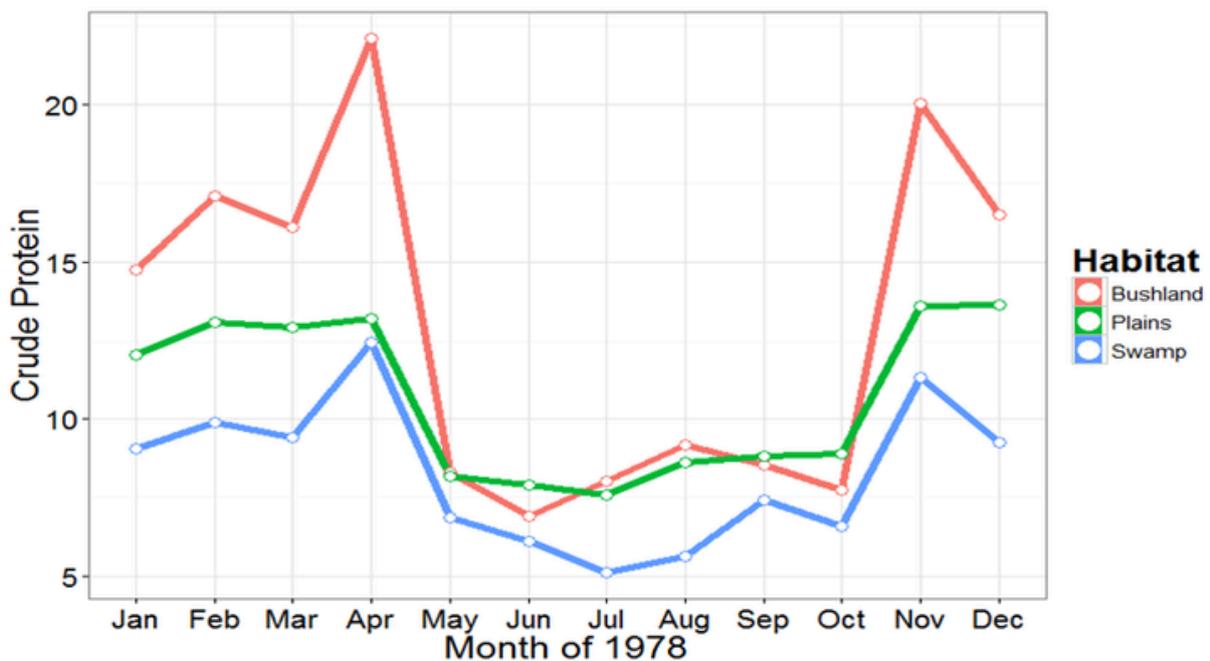


Figure 10: Grass quality drives the migrations. Crude protein is a good measure of pasture quality. Herbivores select pastures high in protein to achieve maximum digestibility. The progression of the migrants through the habitats tracks the changing pasture quality through the seasons. During the rains the migrants select the high-quality pastures in the bushlands first, then shift down the quality gradient to plains and swamps as the richer pastures are grazed down.

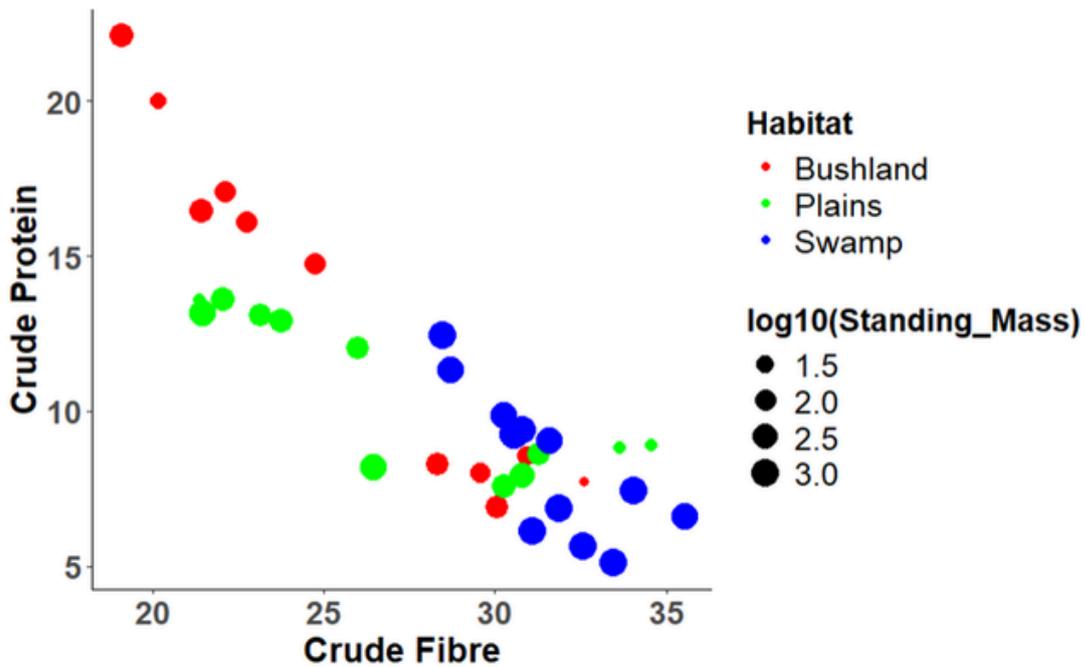


Figure 11: Herbivore digestion increases with crude protein and decreases with crude fiber. The progression of the migrants through the Amboseli habitats tracks the short richer grasses in the rains, moves to the poorer plains grasses next, ends in the bulkier poorer quality swamp grasses and sedges in the late dry season.

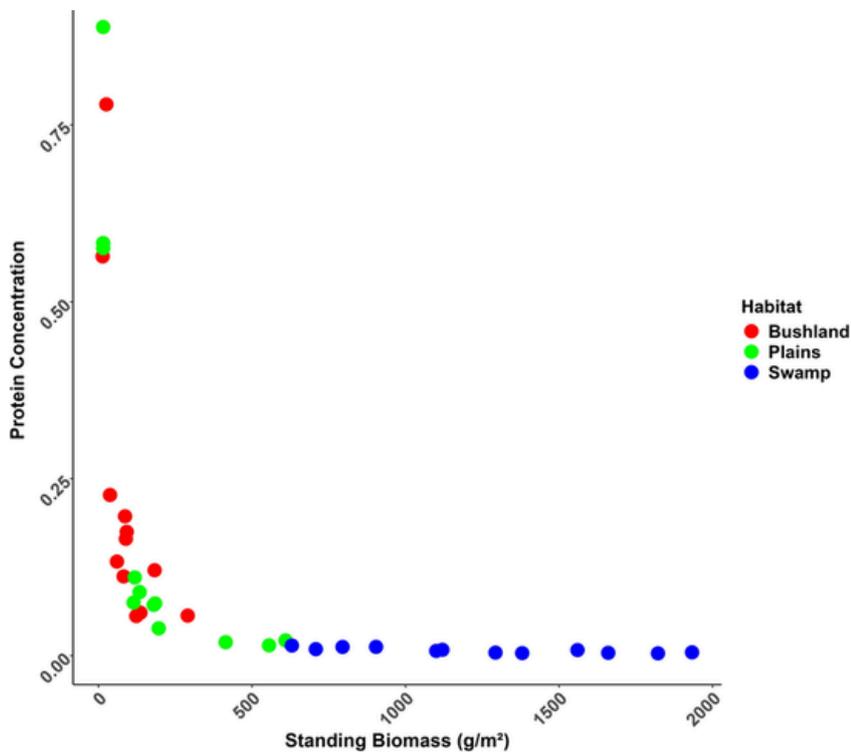


Figure 12: The protein concentration of pastures is related to their biomass. The bulkier the pastures, the higher the fibrous tissue needed to support them and the lower the protein content. The relationship explains why all herbivores select the shorter richer pastures during the rains then move on to the bulkier poorer pastures as the dry season hardens. The relationship of protein content to pasture biomass also explains why the larger herbivores move sooner through the quality sequence than smaller species to sustain their greater energy demands.

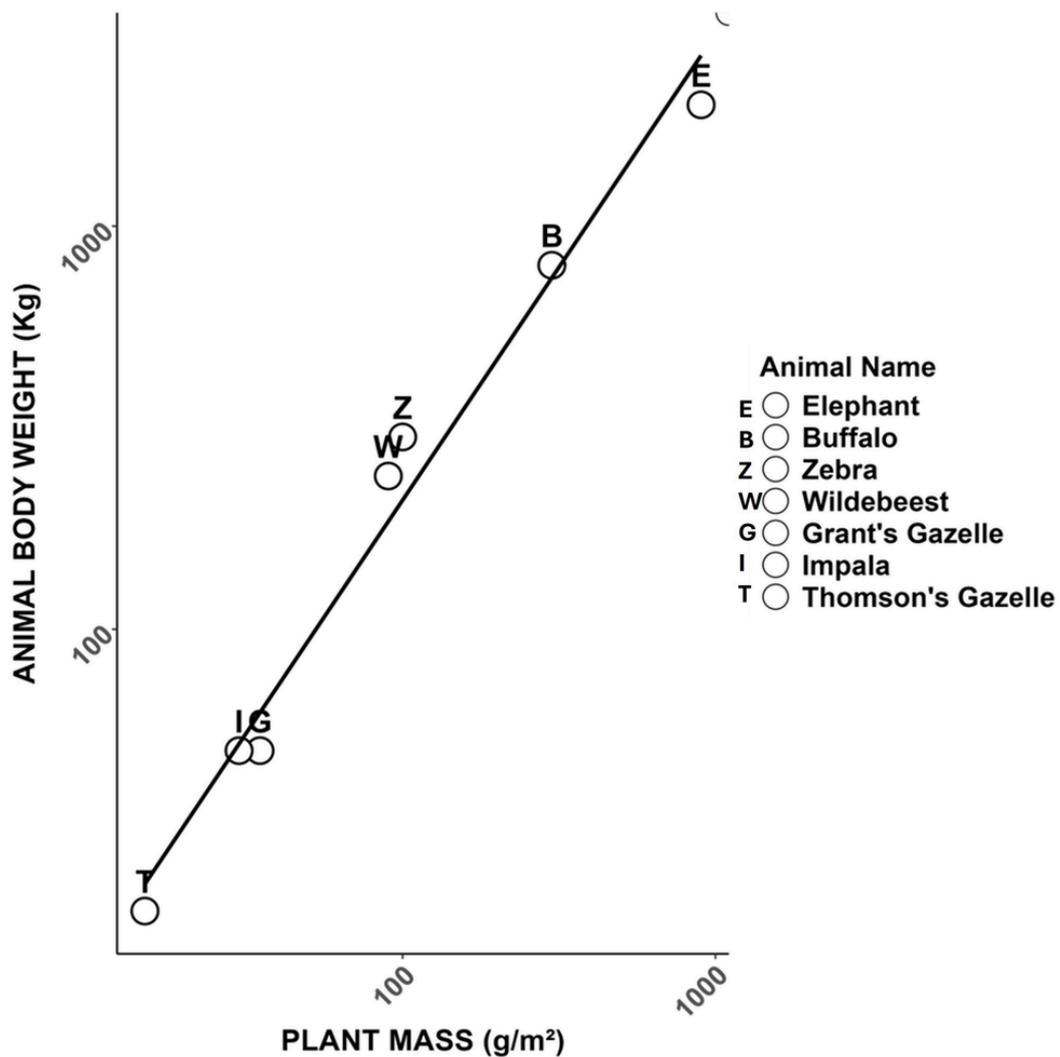


Figure 13: The relationship of body weight to pasture biomass measured across the Amboseli pastures. Larger herbivores select bulkier pastures to support their body weight. The pasture selection by body size results in a grazing succession in which larger species move earlier through the habitats in the course of seasonal migrations.

The long-term monitoring of pasture conditions and animal movements gives a fairly clear picture of the causes of migration and the common axis of movements from rich to poor pastures. Calculations of the early free-ranging migrations prior to the creation of Amboseli National Park and the group ranches showed the benefits of migrating herds to be 30 percent greater than sedentary herds. As a result, the concentrations of herbivores on the late season pastures of Amboseli was 88 percent higher than if the herds were resident year-round (Western, 1975). Later experiments comparing grazed and matching ungrazed fenced plots along the migratory pathway showed a similar energy bonus. In tracking the most nutritive grasses, herbivores boost forage digestibility by 40 percent compared with sedentary herds.

The clearest evidence of the benefits of migration comes from the Maasai herders themselves. As they put it, we track the richest pastures sufficient to fill a cow's stomach. The richer pastures restoke our famished herds, replenish the cows' udder and fill our gourds so our calves survive better and grow faster. The rains give us time to socialize, celebrate and visit friends. We leave behind the ticks, fleas and predators, and allow the depleted pastures to recover.

Modelling the migrations

Forage and water availability, climatic variability, predation risks and competition have long been recognized as core drivers of animal movements (Fryxell Sinclair, 1988; Fryxell et al., 2004). The forage maturation hypothesis (FMH) posits that ungulates migrate to exploit asynchronous waves of young, nutrient-rich vegetation (Fryxell et al., 2004). Gut morphology determines the efficiency of extracting nutrients from pastures (Van Soest, 1985), and body size governs metabolic requirements and the balance between forage quality and quantity (Illius & Gordon, 1992; Demment & Van Soest, 1985).

We developed a spatial model using the FMH model to test the causes of the Amboseli herbivore migrations (Mose et al., 2012, 2013). The model combines Ideal Free Distribution (IFD) theory (Kshatriya, 1998) with allometric diet rules to describe how herbivores respond to changes in vegetation quantity and quality and are attracted to other patches. We used long-term aerial monitoring to determine changes through the seasons using a total least squares approach (Van Huffel & Vandewalle, 1991).

Our model shows dry-season movements are tightly governed by shifts in both pasture greenness and biomass. Smaller-bodied herbivores were very sensitive to forage quality in line with the FMH model and metabolic demands (Sensenig et al., 2010). Larger herbivores balanced forage quantity and quality as expected based on their digestive capacity to process more fibrous forage (Owen-Smith, 2002). All species concentrated around the swamps in the late dry season in line with monitoring data (Western, 1975).

Wet season movements proved far less predictable due to the wide-spread availability of high-quality forage calling for less selectivity. Habitat preferences of species played a stronger role in the wet season when forage and water were not limiting (Williamson et al., 1988). Despite this broader distribution, the model continued to explain distinct species-level differences due to gut physiology and energetic constraints.

The IFD–allometric model accurately reproduced seasonal movements and body-size-dependent grazing succession detected in our long-term ecological monitoring. The findings are consistent with the “green wave” hypothesis (Rivrud et al., 2016) in which herbivores track advancing fronts of nutritious plant growth (Fryxell et al., 2004; Wilshurst et al., 1999).

Our model (Mose et al., 2012, 2013, Mose, 2013) shows the migrations increase the digestive efficiency of migrants tracking high-quality forage. The gains are far greater during droughts when animals can move to better areas to avoid depleted pastures (Williamson et al., 1988), underscoring the role of mobility in increasing herbivores resilience to harsh years.

The assumptions of the model closely match the ecological studies in Amboseli showing the migrations are shaped largely by shifting patterns of forage quality and diet selection according to body size.

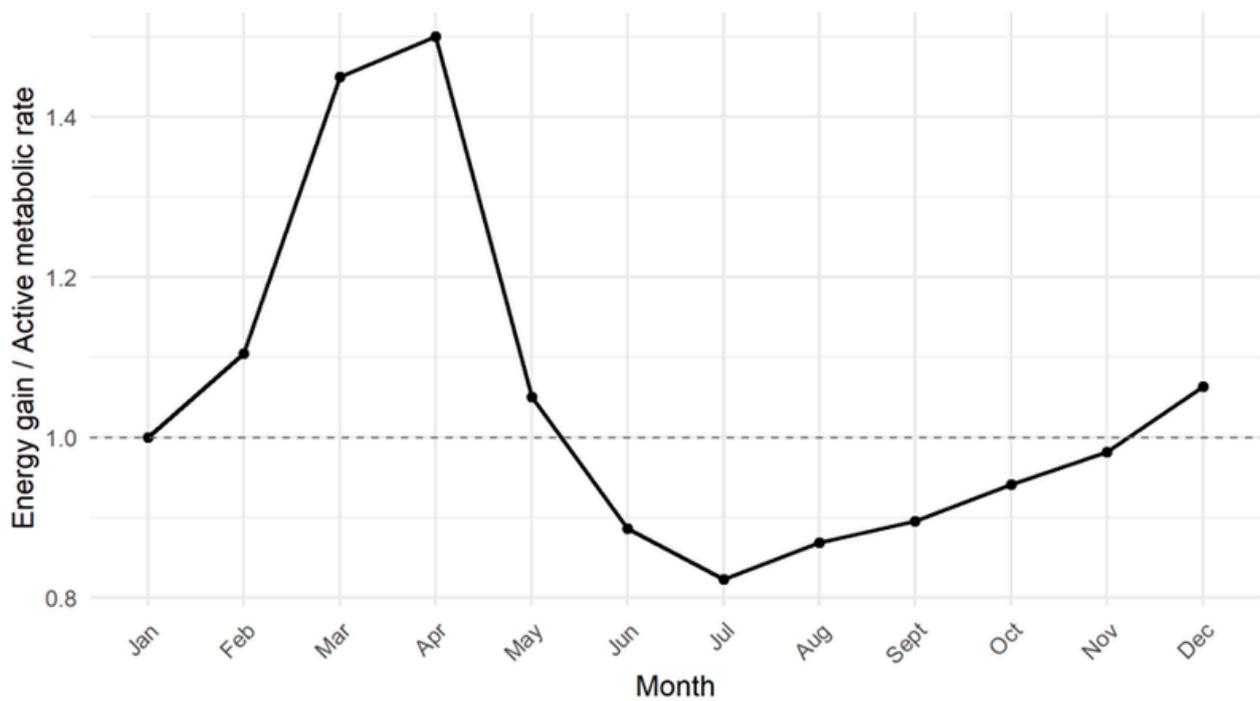


Figure 14: Model results of the aggregated energy gain of herbivores peaks during the wet months of March and April, when migrants move to high-quality pastures outside Amboseli National Park. Energy gain declines during the dry months due to poor pasture quality and the necessity to concentrate in late-season habitats where forage outside the park is limited. In other words, herbivores lost condition due to the poor pasture quality in the dry season and recover condition during the rains. The energy gains losses twice a year reflect the two rain seasons in Amboseli.



The grazing succession set up by elephants opening up the thickets around the Amboseli swamps to create grasslands grazed by smaller herbivores.

Discussion

Maasai and wildlife moved freely with the seasons before the creation of Amboseli National Park and the subdivision of group ranches. The ACP studies at the time showed livestock and wildlife migrations shadowing each other through the seasons. Both tracked the highest quality pastures across the bush country during rains and concentrated in the Amboseli Basin in the dry season to access permanent water and late season forage.

The migrations increased the populations of wildlife and livestock in the dry season range by 40 percent, and the late season concentrations around the swamps by almost 90 percent. The peak concentrations around the Amboseli swamps at the end of the dry season covers only 10 percent of the ecosystem, making the park one of the greatest wildlife spectacles in Africa.

Subdivision and settlement of Kaputei Section severed the wildlife migrations and displaced herds relative to Mbirikani where wildlife has increased due to water provision. Farming, irrigation and the pipeline further decreased wildlife ranges. The loss of Namelok, Kimana, Lenker and Soit Pus has reduced once vibrant herds to a fragment, along with dry season forage for pastoralists.

The switch from seasonal migrations to permanent settlements in Ilkisongo starting in the late 1980s caused heavy persistent grazing and a loss of pasture production. The loss of pasture and range loss to settlement has reduced livestock production, shortened the seasonal wildlife migrations, and lengthened the dry season. The upshot is an increased frequency and intensity of droughts for both livestock and wildlife, and consequently, increased competition for forage.

The doubling of the Amboseli swamps due the erosion on the heavily grazed areas around the park has increased late season grazing in the park. The expanded swamps have buffered wildlife from the rangeland degradation on the group ranches. Zebra, wildebeest, Thompson's gazelle and elephant numbers in the park are now far higher than in the 1960s when the herds moved freely on migrations. The flooding has also expanded the Conch Swamp on Lake Amboseli and the late season forage available to livestock.



The large lake in the centre of Amboseli caused by flooding in the post-settlement period, leading to colonization by flamingoes.

The Amboseli Ecosystem Management Plan 2020-2030 and the Olgulului-Olororashi subdivision plan both make provisions for keeping the wildlife migrations open by zoning the dispersal areas as pastoral-cum-wildlife areas. Land sales underway threaten the future of seasonal movements of pastoral and wildlife herds alike. The wildlife herds will fall steeply if the migrations are severed and the tourist spectacle of the herds clustered around the swamps will be lost.

A Strategy and Vision for a Third Generation Park 2024-2026 drawn up by the Technical Committee overseeing the transfer of Amboseli National Park to the Kajiado County aims to fully integrate the park into the ecosystem and Maasai community. The success of the plan depends on defining the Minimum Viable Conservation Area (MVCA) needed to sustain the migrations.

The descriptions we have given lays out the extent, causes and ecological benefits of the Amboseli migrations. The map below gives the MVCA adopted by the Strategy and Vision for the third-generation Amboseli Park.

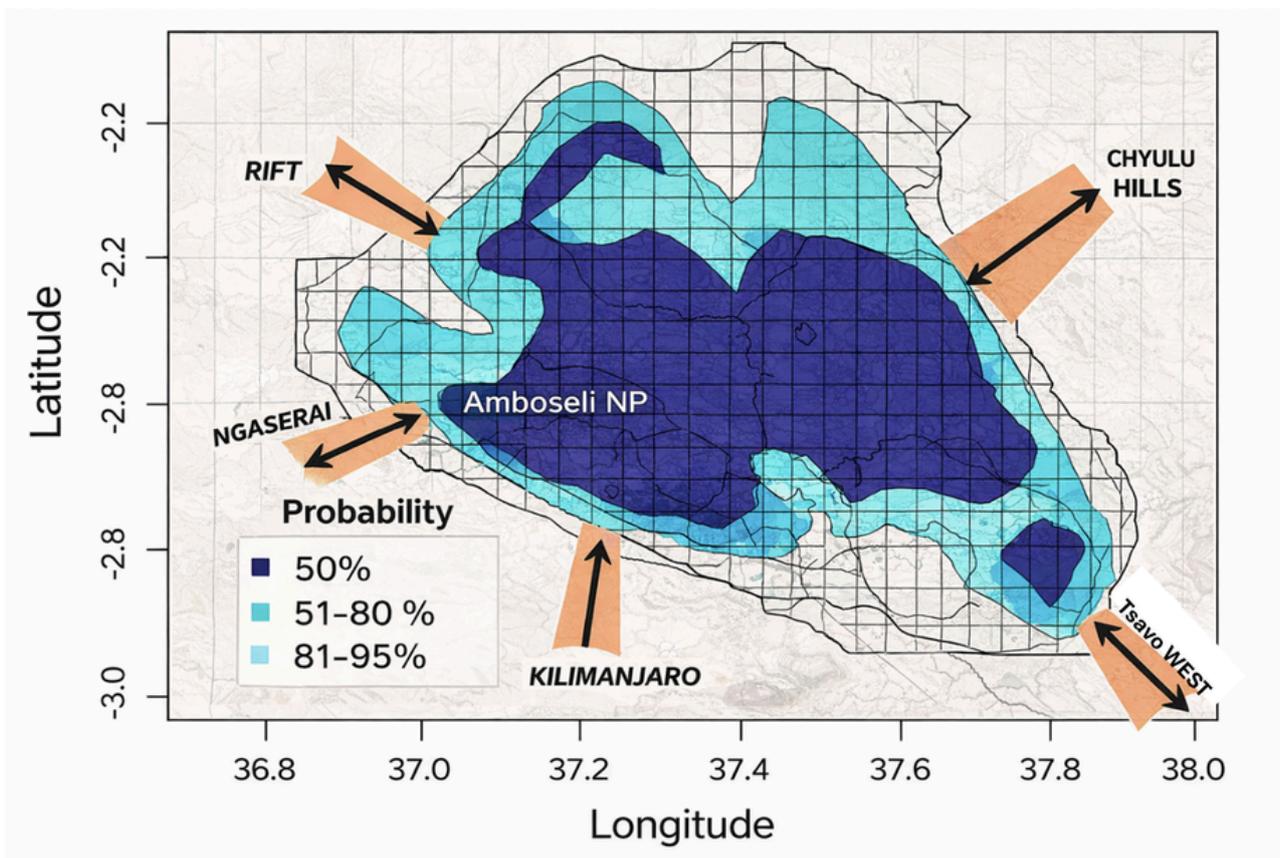


Figure 15: The MVCA, as adopted in the Amboseli Strategy and Vision, defines the spatial extent required to sustain seasonal wildlife movements and ecological processes. While migratory pathways north of the ecosystem, particularly in Kaputei, have been largely lost, recent data indicate that wildlife populations continue to thrive within the remaining migratory areas, highlighted by the dark blue zone. Securing the long-term viability of the Amboseli ecosystem through protection and management of the MVCA is therefore critical to maintaining these populations and the seasonal migrations that underpin ecosystem resilience.

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