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From single steps to mass migration: The problem of scale in the movement ecology of the Serengeti wildebeest

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Abstract

A central question in ecology is how to link processes that occur over different scales. The daily interactions of individual organisms ultimately determine community dynamics, population fluctuations and the functioning of entire ecosystems. Observations of these multiscale ecological processes are constrained by various technological, biological, or logistical issues, and there are often vast discrepancies between the scale at which observation is possible and the scale of the question of interest. Animal movement is characterized by processes that act over multiple spatial and temporal scales. Second-by-second decisions accumulate to produce annual movement patterns. Individuals influence, and are influenced by, collective movement decisions, which then govern the spatial distribution of populations and the connectivity of meta-populations. While the field of movement ecology is experiencing unprecedented growth in the availability of movement data, there remain challenges in integrating observations with questions of ecological interest. In this article we present the major challenges of addressing these issues within the context of the Serengeti wildebeest migration, a keystone ecological phenomena that crosses multiple scales of space, time, and biological complexity.

1. Introduction

The challenge of understanding processes that operate at multiple scales is common to all scientific disciplines. Dynamics such as decadal economic cycles, or the progression of scientific discoveries are the accumulation of fine-scale events; daily struggles lead to results and findings, these results aggregate to form a body of knowledge, this knowledge defines a discipline, and so on. Often, when studying natural or social systems a scale of observation is selected, and the challenge then arises when attempting to relate what is observed at one scale with the phenomena that emerge at another, and the feedback processes that occur among scales.

The issue of scale is universal, and the field of ecology is no exception. At the broadest level, ecosystems provide the services that are essential for our survival [1] but these services are the result of the myriad direct and indirect interactions among individual organisms. Understanding how ecosystem services emerge from, and feedback to influence, micro-scale processes is a central problem in ecology [2] and it is the key to

understanding how best these services can be protected. Schneider [3] identified the three components that define the problem of scale in ecology; firstly, core ecological questions often concern population-level, macro-scale processes; secondly, observations are constrained to relatively fine-scale measurements and sampling; and third, when dealing with complex biological systems, processes do not scale simply from one level of description to another.

In the context of movement ecology, examples of large-scale ecological questions concern the potential impacts of the cessation of a migration, the amount of connectivity required to maintain a viable metapopulation, or the ecosystem impacts of reductions in animal movement [4–6]. These questions are addressed through monitoring and data collection on the movement of individual animals and groups [7, 8]. Connecting these observations with population- or community-level processes is an unresolved task [9–11] and one that in essence involves extrapolating from second-by-second movements to annual migration patterns, from resource selection and risk avoidance to survival and fe-

cundity rates [12], and from individual behaviours to population dynamics and persistence.

2. The Serengeti wildebeest migration

Wildebeest are an iconic example of a migratory species that plays a dominant role in the ecology of the area it inhabits. The annual migration of the blue wildebeest (*Connochaetes taurinus*) covers the entire range of the Greater Serengeti ecosystem, a round-trip that far exceeds the straight-line distance of 650km, with data from GPS collars suggesting that the true distance covered is over 1500km [13]. Herds head south from their dry season refuge in the Masai Mara (Kenya) as the short rains begin in early November, and spend the wet season (December to May) in the fertile southern short grass plains of Tanzania, defined by the extent of the volcanic ash soils and the mean annual precipitation. Calving season in February coincides with this period of peak primary production. Calves are highly precocial and will follow their mothers within hours [14]. The wildebeest migration is constantly moving, with females having an average daily displacement of 4.5km [15], opting for high rainfall areas in the Western Corridor before continuing northwest to the Masai Mara by July. The dry season (August to November) is spent in the northern woodlands of the Serengeti National Park and the Masai Mara National Reserve, before the cycle begins again (see Figure 1).

This mass migration of animals is not only an awe-inspiring visual spectacle but also plays a keystone role in the region's ecosystem. The migrants transport nutrients, consuming around 4,500 tons of grass per day, which is constantly getting digested and relocated as they move around the ecosystem [16], and are a source of food for multiple species of predator and scavenger [14, 17, 18]. Movement enables the wildebeest population to be much more abundant than expected based on the environment [19]. In total, Serengeti wildebeest are about twice the biomass of the next twelve most abundant large mammals in the ecosystem combined [20]. By moving among seasonal areas, migratory wildebeest increase their access to food and therefore avoid being regulated by its availability at the local scale [21]. Furthermore, the natural rotational grazing system inherent in the annual migration facilitates compensatory growth in the grasses. The grasses grow more rapidly after being grazed, thereby increasing the total annual biomass of available forage [22]. Thirdly, by migrating en masse the population avoids becoming regulated by predators either by swamping the local resident predator popula-

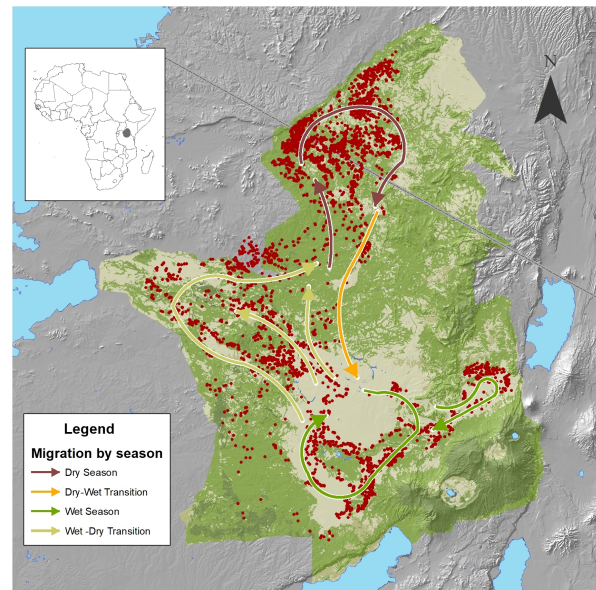


Figure 1: The Serengeti wildebeest migration. The figure shows the annual movements of 8 female wildebeest that were collared and monitored between 1999 and 2001.

tion and thereby decreasing the per capita mortality rate, or by improving their detection of predators [23].

Without the annual migratory cycle much of the region's biodiversity would decline [24], as the passage of the 1.3 million migrants affects virtually every other ecological interaction from below ground nutrient cycles, to insects and avifauna abundance, to predator-prey interactions of resident herbivores and carnivores as well as the services this ecosystem provisions for the communities around it [25]. Hence movement is the force that drives the ecosystem dynamics in the area and there would be fundamental changes in the ecology and its services if it were to stop [26].

The migration is inherently a multiscale phenomenon. Wildebeest aggregate in herds ranging from tens of individuals to up to 400,000 [27]. The highly synchronous calving of Serengeti wildebeest could be an emergent property of the seasonal environment where the cost of reproduction is high but only energetically possible in certain areas and during short periods of time [28], rather than be an adaptive response to predation. Breeding synchrony ultimately leads to all reproductively active females (about 450,000 animals) requiring the same resources at the same time. This leads to competition between individuals for limited resources in the local environment, forcing them to search further afield for adequate forage and water [20]. From

a food-intake perspective, it would be more advantageous for individuals to remain solitary as they would be able to maximize their intake rate (i.e. the biomass per bite). However, from a safety point of view solitary animals are more exposed to predation; it is the balance between food and security operating at different scales and at different times that interact to form volatile fission-fusion dynamics of the herd. Therefore, movement decisions of individuals are influenced by multiple factors including physiology, social interactions, environmental cues, resource availability, memory and predation risk [15, 28–30]. Disentangling these competing, hierarchical drivers of movement is a substantial task, however it is a challenge that must be met in order to develop the evidence-based policy required to protect vital ecosystem services in the region.

3. From individual to collective movement

3.1. Connecting tracks with cues

We are now obtaining unprecedented levels of data on the movement trajectories of animals, and moving toward collecting lifetime tracks of individuals of certain species [7]. A current major challenge is relating these data to the underlying environmental and/or social drivers of movement. Without connecting movement decisions with the instantaneous conditions the animal was experiencing we are only able to make crude inference on remotely collected data such as response to season or large landscape-scale effects.

When trying to integrate animal movement data with cues and drivers there are two issues of scale. The first is the ability to collect data at a resolution that is relevant to the animal’s decisions. Metrics relating to vegetation quality may be collected from satellite imagery [31–33] however these data are often at a far coarser scale than the movement trajectories [7, 11] and taken at different times. Normally there is a trade-off between increased spatial resolution and the amount of time-delay between the movement and the environmental observation [31]. This lack of temporal synchrony is not an issue when considering long-lasting features of the environment such as trails [34] but when dealing with vegetation that is growing rapidly and being consumed by large numbers of herbivores it may be a significant factor. The second issue of scale is that the individuals respond to their environment at different and often unknown scales [35], therefore even if it were possible to collect environmental data instantaneously, at any resolution, it is a priori unknown what the correct resolution to select should be; indeed, there probably is not a single correct resolution. Wildebeest may be responding to

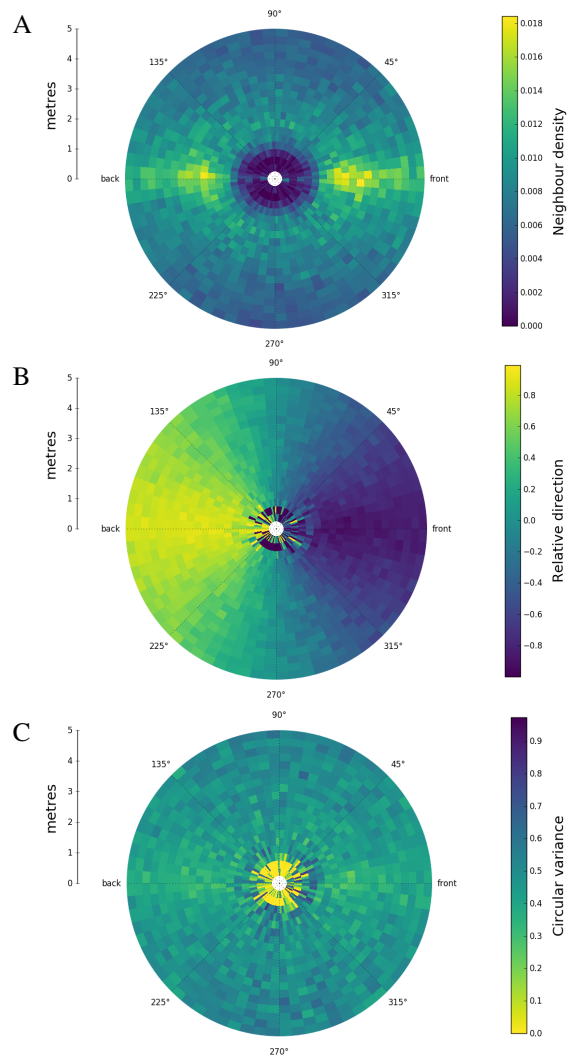


Figure 2: Fine-scale dynamics of wildebeest herds. Data is taken from UAV-borne video. (A) Spatial distribution of near-neighbours relative to a focal individual. Wildebeest display a well-defined inter-individual spacing with greater density to the front and rear of the focal individual. (B) Relative direction of neighbours. This is calculated as the dot product of neighbour heading vector with the vector toward the focal individual. Higher values indicate the neighbour is heading toward the focal individual, lower values mean the neighbour is moving away. (C) Circular variance in heading of near-neighbours. Variation in heading is greater either side of the focal individual. (Plots B and C effectively show the first and second moments respectively of the local distribution of neighbour headings.) Combined, these data suggest that wildebeest tend to align and follow each other in linear formations.

vegetation gradients [36], (i.e. the so-called green-wave hypothesis [37, 38]), intermediate-range cues such as rain storms (discussed in [29]), risk factors relating to predation [15], memory [30], or a combination of these

factors.

In the future, greater satellite resolution and on-demand coverage may help to resolve some of these issues, with disruptive technologies such as wide-area motion imagery (WAMI) offering a potential step-change in our ability to collect environmental data. Advances in on-board sensors that accompany GPS collars also facilitate the collection of social and environmental data [39–41].

The importance of traditional behavioural ecology in this context should not be underestimated, and the use of GPS collars has been criticised for their inability to provide behavioural and social context [11]. While GPS collars and satellite images are unrivalled in terms of sheer volume of data, detailed-on-the ground observations still remain an irreplaceable tool for understanding behaviour.

3.2. *Social context and interaction rules*

While GPS collars on individual animals are providing tremendous insight into individual behaviour they rarely reveal any information about social interactions due to the difficulty associated with tracking a large proportion of a group (aside from some notable exceptions e.g. [34, 42, 43]). For ungulates the role of social interactions has been examined in the situation where collared animals have been released together [44], while signatures of collective behaviour have been detected by analysing the temporal autocorrelation of trajectories at the same spatial location [45, 46]. For species such as wildebeest where herds number in the thousands and group membership is usually weakly cohesive and dynamic, GPS collars are not a viable method to investigate social interactions and alternate methods need to be found. This is imperative as for social species such as wildebeest, the behaviour of conspecifics is likely as important as environmental cues. When herds potentially span kilometers, social interactions represent a mechanism of collective sensing that far exceeds the sensory range of an individual [29, 47, 48].

If movement decisions of wildebeest are collective decisions then studying individual behaviour will inevitably omit an important aspect of the migration. The first stage in addressing this deficit is creating a picture of interactions such as has been achieved in the study of other species [49–52]. Increasingly aerial filming using platforms such as drones, blimps or balloons offer a partial solution. Figure 2 shows the relative spatial distribution and orientation of near neighbours of migrating wildebeest based on data collected from a UAV-borne camera. These type of data provide an entirely different

insight into movement dynamics as compared to long-term individual track data. Track lengths are of the order of seconds or minutes, instead of years, while hundreds of individuals may be simultaneously tracked for short amounts of time.

To fully leverage these novel data streams an approach is required that integrates different multiscale data collection techniques. To link long-term studies of individuals with fine timescale observations from other platforms it is necessary to identify collared animals within video images, something that is now possible due to the data logging capacity of modern aerial filming platforms [53].

3.3. *Conflict, mutual benefits and emergence*

The interplay between the individual and the collective create a feedback mechanism that amplifies or inhibits behaviour. In effect the social context is both driven by, and drives, the behaviour of individuals. These feedbacks operate over multiple time scales from the pressure to conform to directional choices in order to avoid predation, to the evolutionary dynamics of exploitation and information production in contexts such as vigilance [23] or navigation [54, 55]. The net effect of the individual on the collective behaviour of the herd is likely a function of the behaviour of the initiator and the internal state of the recipient, such that persistent behaviour is required to motivate a large lethargic group, but a small inadvertent action can have large effects for an anxious highly-vigilant group.

The unpredictable relationship between the actions of individuals and the behaviour of the collective is the focus of complex systems science. At the heart of this discipline is the notion that interactions at lower levels give rise to properties at the higher level e.g. a collective phenomenon that might not have been predicted from observations of individuals in isolation [56]. For example, the lengthscale of the spatial structure of grazing wave fronts of wildebeest far exceed the perception range of an individual. The structure is therefore an emergent phenomenon and the product of both the individual-level behaviour and the inter-individual interactions [57]. These concepts mean that observations of individual movement only provide a partial picture of the migration.

Without considering collective dynamics, observations may appear counterintuitive. For example, for wildebeest the correlation between movement speed and environment quality switches from negative to positive as the density of grazers increases. Hopcraft et al. [15] showed that for herds of wildebeest there was a positive relationship between speed and forage quality,

i.e. animals moved faster through regions of high quality resources rather than lingering to take advantage of a good resource patch as one would expect. This is in contrast to the classical view of resource selection considered at the individual level where animals should tend towards encampment in high quality patches and rapidly pass through low quality patches. One interpretation of these counter-intuitive results is that resources in high quality patches are consumed more rapidly by large groups, thereby forcing individuals to eat rapidly and move on to the next patch in order to remain close to the leading edge of the grazing front.

This example illustrates some of the challenges in revealing the drivers of movement decisions that are influenced by multiscale environmental and social factors. Different drivers may lead to similar observed behaviour [58] and novel statistical methods [59] are required to distinguish socially driven movements from movements driven by common external cues [60] and for assessing social structure and the differing leadership roles individuals adopt [61, 62]. Identifying how the subtle nuances and interactions between covariates can lead to totally different responses remains one of the largest challenges in the field.

4. Scaling across time and space

4.1. Observation scale and hierarchical approaches

When we observe animal movement we necessarily do so at a certain range of scales. Often there is no single correct scale [2] at which to observe ecological phenomena. In some cases a scale is arbitrarily chosen, while in others it is imposed. How data are collected will influence the phenomena that are observed, the questions addressed, and thus, possibly, the conclusions that are drawn [63].

As an example consider attaching a programmable GPS collar to a wildebeest. The collar has a finite battery life and so may produce a fixed number of reads at a controllable interval. If we are interested in how the animal responds to local cues, such as vegetation gradients we require an interval on the order of seconds or minutes. If we want to know how the animal responds to larger scale features we would select an interval of a day or more. If our question relates to whether the herds track seasonal variation we would require an interval of weeks, and finally if we wish to know about site fidelity and the annual return of individuals to particular areas we would require monthly, or less frequent, fixtures extending over as many years as possible, or even across generations. As we move from one end

of the spectrum to another we sacrifice fine scale detail for temporal range, breadth for depth. When a process has self-similarity we may extrapolate straightforwardly from fine scale observations to longer distance movement properties [64] however for species such as wildebeest, different mechanisms drive behaviour at different scales [35], and no universal scaling law exists [65].

To understand these various multiscale and overlapping drivers it is necessary to integrate data from different sources. Remote data from GPS collars can provide insight into long-term movement dynamics, the relocation of collared animals and repeated observations will reveal individual characteristics, while observations from aerial platforms provide information on fine scale second by second interactions. Through an iterative process where observations at one scale help to design observations at another in a hierarchical fashion, a holistic picture of movement can be created.

4.2. Decision points and behavioural states

Much of the difficulty in understanding the different scales of movement arise from variability. Individuals within the herd are not identical, so models that assume homogeneity fail to capture core details about individual variation in response to certain factors, or apply the unique characteristics of a few collared animals to the entire population. Similarly it is not possible to make detailed observations over the course of a few hours and extrapolate to movement over weeks or months, since behavioural variation or behavioural modes [66], such as ‘foraging’ or ‘encamped’ [67], have to be considered. Switching between these modes may be intermittent or occur multiple times a day as in the case of wildebeest alternating between grazing and marching bands. State-space models [68] [69] and hidden Markov models [67] have been used to detect these different modes from individual trajectories. Research has shown these modes exist and that switching between them depends on environmental conditions [70] [71]. While within these different states, animals are still responding to local cues and one another, the presence of these transition points indicate that there are some periods of time that more significantly impact overall movement patterns.

The first stage in an integrated multiscala approach is to identify the presence of behavioural states from long term tracking data [59]. Covariates, such as landscape features or temporal drivers, associated with the transition from one behavioural state to another, may be inferred from higher resolution positional and environmental data (see Fig. 3 for data relating to the landscape level movements of the wildebeest herds). Finally, armed with information on the presence and pre-

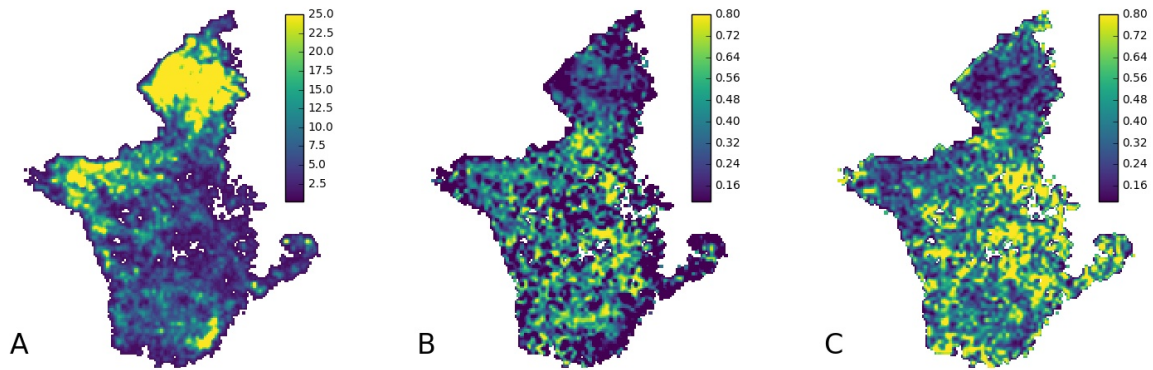


Figure 3: Landscape level movement patterns of the Serengeti wildebeest. GPS collar data taken from 55 wildebeest in the period 2005 to 2016. (A) Wildebeest density over time. The heat map displays the regions where wildebeest are most concentrated throughout the year. (B) Individual directness. Plotted is the average dot product of previous heading with current heading for each individual. High values indicate wildebeest are travelling more directly through these regions. (C) Population-level coordination. The degree of alignment for all individuals in each region is plotted. This reveals the spatial locations where the population as a whole tends to move in the same heading (South-East of the region).

dicators of transitions, fine scale observations can be made. In order to reveal the mechanisms underlying collective decision-making [72], these targeted, fine-scale observations require data collection methods akin to those associated with lab-based studies of movement [50, 51, 73] to be employed, from which detailed information about the interactions between individuals and their environment can be used to infer patterns of collective behaviour.

4.3. *Feedbacks between movement and the environment*

While social feedbacks can rapidly reinforce fast time-scale processes such as startle responses [74] or departure events [75], the interaction between the environment and animal movement patterns creates a longer time-scale feedback. The constant migration of animals across a landscape creates a system of trails that reinforce and even dictate movement patterns. Trails are created through a process of positive feedback [5] and once formed can have a significant effect on the movement decisions of individuals [34, 76].

Animal trails are found throughout the Serengeti and clearly influence the movement decisions of wildebeest (see Figure 4). The tendency of wildebeest to follow these pathways presents both opportunities and difficulties when studying the migration. The effect of trails on fine-scale behaviour is hard to distinguish from social effects. Following a trail is an energy efficient strategy so will encourage wildebeest to form travelling lines, hence the spatial structure of herds, shown in Figure 2, may well be a result of maintaining cohesion and trail

following. When attempting to detect signatures of collective behaviour, changes in orientation that are caused by meandering paths may be interpreted as imitation. Care must be taken to include landscape features into movement models at this scale [60].

Trail networks may also be interpreted as a form of cultural memory [77]. The lifetime of these spatial patterns may well extend beyond the lifespan of individual wildebeest and likely provide indicators of optimal routes for less experienced individuals. The trails represent a form of stigmergy, usually associated with social insects [78], as they represent an indirect interaction between wildebeest that is mediated by the environment. In fact, wildebeest have scent glands on their hooves, and the continuous passage of individuals along trails has been hypothesized to facilitate navigation [79] as wildebeest are able to follow social cues without maintaining visual contact. Explicit incorporation of trails has been shown to improve the predictive power of movement models in other species such as baboons [34], hence trails are likely a significant factor that may be followed by individuals due to efficiency savings or as a navigational aide [80].

Greater resolution satellite imagery combined with automated computer vision techniques now offer the potential to remotely detect and monitor these trails, offering the possibility to detect features of the migration even in the absence of wildebeest.

4.4. Memory, fidelity and spatial scale

Memory is a ubiquitous component of animal movement, influencing individual decision-making at various scales [81]. Memory's relative effect on movement can be difficult to distinguish from those of other sensory cues such as local forage quality, predation risk and conspecific attraction. In wild populations, inferences about memory are typically based on observing where individuals and conspecifics move in the past, and assuming that these locations (or prominent features there within) represent a known spatial reference [34, 82]. For instance, relocation data suggests that a variety of organisms exhibit strong loyalty to specific sites or routes at the individual level (i.e. 'site fidelity') [83]. Site fidelity, however, is not necessarily memory-driven, and can arise because of either innate navigational programs or because the set of available sites is small. Stronger evidence that memory shapes recursive movements comes from experimental work that involves relocations or introductions to novel landscapes. Memory effects can be separated from other navigational mechanisms, such as those based on compass bearing or celestial orienting [80].

Memory shapes movements in social animals in a number of ways. Navigational success appears to improve when groups are composed of older, more experienced individuals (e.g. [84, 85]), presumably because experienced animals transfer information about sites or routes to inexperienced members [86]. This learning also appears to enable adaptive route changes in response to environmental change [87]. An animal's social context may determine whether memory-based movements decisions are the most profitable or efficient in the short term [88]. For instance, strong fidelity across years is hypothesized to facilitate the use of the most efficient routes or the sites with the most predictable resources [89]. However, spatial fidelity can come at the cost of food intake or predator avoidance when the quality of the site/route changes [90, 91], and for animals moving in large groups, site fidelity may represent a particularly costly strategy because local resources become depleted quickly.

For migratory species, these conflicts play out across their annual cycles. Migration in wildebeest (and other larger herbivores) is classically described as an adaptive movement strategy enabling individuals to exploit ephemeral resource patches, such as those occurring after recent rainfall [15, 29, 36, 92]. The large group sizes extend wildebeest perceptual ranges for locating high quality forage up to 70km [29]. However, even wildebeest exhibit spatial fidelity at annual scales. In a multi-year mark-recapture study involving several thousand



Figure 4: Trail following behaviour of wildebeest. This image was taken from an aerial survey of the wildebeest population undertaken in 2009.

individuals, adult wildebeest in the Tarangire Ecosystem, Tanzania returned with high frequency to the same wet season ranges each year (82-100%) [30]. Notably, despite mixing within herds with wildebeest from other ranges in the dry season, individuals tended to return to the same wet season range each year [30]. Thus, fidelity may play a stronger role in inter-annual movement decisions than social-group membership in wildebeest. Whether this same pattern holds in groups as large as the ones found in Serengeti, where the population is 100-fold larger than in Tarangire, remains to be tested.

5. Conclusions

The primary goals of movement ecology may be divided into two broad categories; first, to understand the drivers and mechanisms underlying patterns of movement, and second, to evaluate the consequences of movement for individuals, populations, and communities [93]. The past several years have seen a rapid increase in the data available for addressing these questions. These data come from field observations and sampling, radio telemetry and satellite tracking [7], camera traps [94], aerial surveys, and video footage. In the context of understanding the causes of movement and the mechanisms underlying spatiotemporal movement patterns, research efforts have focused on connecting movement trajectories with local cues and drivers, examining temporal variation and behavioural modes, and understanding the role of social interactions and leadership. For broad-scale consequences of animal move-

ment, the concept of mobile links [95] has been introduced and increasingly movement patterns are seen as equalizing or stabilizing forces within ecosystems [18].

While there have been advances in data collection and analysis methods, the next major challenge for movement ecology lies in integrating data from different sources and developing comprehensive descriptions of movement that encompass both its drivers and its consequences. Inevitably this is a problem of scale. Data collection methods impose constraints on the nature of the observations that can be made and controlled experiments are often impossible. This means that extrapolation must be made from one scale (the scale of observation) to another (the scale of the phenomena of interest).

There remain gaps in our knowledge of both the drivers and the consequences of the Serengeti wildebeest migration. The synchronised mass movement of thousands of wildebeest returning to the same locations on an annual basis raises questions about how this level of organization is achieved. On one hand, the mass migration could be the result of animals moving in response to an oscillating underlying abiotic gradient such as seasonal rainfall or soil fertility that determines the cyclical availability of grass. However, behavioural observations illustrate wildebeest are unpredictable, responding to environmental cues at multiple scales, and not operating as independent migrants but instead part of a complex social structure [14].

Efforts to disentangle the various drivers of the migration are focused on increasing the number of individuals that are monitored and gaining higher resolution data on environmental covariates. As the number of GPS tracking collars deployed on wildebeest increases, a picture of individual and temporal variation can be developed. Combining these data with statistical models and inference techniques will reveal the competing time-varying drivers that influence decisions. To complement these individual-based data, observations of collective behaviour are required. Aerial filming and computer vision methods are now providing the tools needed to collect and process these observations. Integrating these studies of collective movement with individual tracking [53] will allow us to detect which individuals are influencing decisions and understand how wildebeest herds collectively respond to their environments.

As in many studies of animal migration, the aim of understanding the Serengeti wildebeest migration is driven by the significant impact it has on the local ecosystem. The wildebeest affect every facet of the ecology in the region [18]. The migration facilitates other species of herbivore through successional grazing,

migrants are transporters of disease, they impact vegetation dynamics and fire regimes, and are vital prey for carnivores [14, 96]. Movement allows the population of wildebeest to persist at high levels and this vast biomass has huge impacts as it moves around the park [20]. In the Serengeti region, as elsewhere, greater understanding of the mechanisms that drive keystone ecological processes is vital due to increased human activity and the need to make informed and effective management decisions [97, 98].

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