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Author for correspondence:

Chloe Bracis

e-mail: chloe.bracis@gmail.com

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Memory, not just perception, plays an important role in terrestrial mammalian migration

Chloe Bracis^{1,2} and Thomas Mueller^{1,2}

¹Senckenberg Biodiversity and Climate Research Centre, Senckenberg Gesellschaft für Naturforschung, Frankfurt (Main), Germany

²Department of Biological Sciences, Goethe Universität Frankfurt, 60438 Frankfurt (Main), Germany

CB, 0000-0003-4058-7638

One of the key questions regarding the underlying mechanisms of mammalian land migrations is how animals select where to go. Most studies assume perception of resources as the navigational mechanism. The possible role of memory that would allow forecasting conditions at distant locations and times based on information about environmental conditions from previous years has been little studied. We study migrating zebra in Botswana using an individual-based simulation model, where perceptually guided individuals use currently sensed resources at different perceptual ranges, while memory-guided individuals use long-term averages of past resources to forecast future conditions. We compare simulated individuals guided by perception or memory on resource landscapes of remotely sensed vegetation data to trajectories of GPS-tagged zebras. Our results show that memory provides a clear signal that best directs migrants to their destination compared to perception at even the largest perceptual ranges. Zebras modelled with memory arrived two to four times, or up to 100 km, closer to the migration destination than those using perception. We suggest that memory in addition to perception is important for directing ungulate migration. Furthermore, our findings are important for the conservation of migratory mammals, as memory informing direction suggests migration routes could be relatively inflexible.

1. Introduction

Seasonal variation in resource availability drives most large-scale movements of terrestrial mammals, including many iconic migrations [1–3]. However, underlying behavioural mechanisms of these movements are less well understood [4]. This is problematic because the underlying behavioural mechanisms are crucial for effective conservation measures, and many terrestrial migrations are currently threatened or have already disappeared [2,5].

One key area of uncertainty is the navigational mechanisms migrating mammals use to inform their decision of where to go [5]. Two fundamental behavioural mechanisms that could direct movements are perception and memory. Perception allows animals to adjust to current conditions and thus facilitates gradient following [6,7]. This can lead to long-distance migration but limits movement decisions to information acquired within an animal's perceptual range. By contrast, movement decisions based on memory generally refer to past information animals use to predict conditions at temporally or spatially distant locations [8]. Both genetic or social transmission of memory-based migratory information are possible, meaning either inherited information (e.g. route, departure cues or directional preferences) or juveniles learning from parents or other group members [9]. Movement decisions based on memory are not restricted to perceptual ranges but allow predictions with broad spatial extent and, importantly, also make forecasting future conditions based on past information possible. Thus, in principle, memory can be particularly advantageous for movement decisions across broad scales and in landscapes with regular seasonal dynamics [1,10] but cannot take advantage of or adjust to current conditions.

A challenge to studying these mechanisms in large terrestrial mammals is that they are less amenable to experimental manipulation compared with other taxa such as birds [4,11]. Most studies addressing navigation mechanisms of long-distance mammalian migrations thus rely on models [12,13], and researchers often simulate navigation mechanisms and determine which model best fits trajectory data of real animals. Most research to date in mammalian migration has examined perception-based mechanisms and relatively little work has been done to explore the potential importance of memory.

Much research has tackled large herbivore migrations in savannahs where perception-based proximate following of rainfall gradients could allow herbivores to access higher nutrition grasses in arid areas during the growing season [9,14–16]. Movements based on a proximate response to local environmental conditions explained the migratory pattern of wildebeest (*Connochaetes taurinus*) [16], recreated wildebeest migratory trajectories [15] and predicted Thomson's gazelle (*Gazella thomsoni thomsoni*) distributions [14]. However, a large perceptual radius may be necessary to escape local optima and match observed migration patterns at larger scales [9], such as the large perceptual range (80–100 km) necessary to match model outputs to observed migration patterns [16].

By contrast, memory-related mechanisms for long-distance migration have been relatively little studied. While on smaller scales, such as foraging-related movement, ample evidence suggests that memory is important [17–21], we know extremely little about how memory could be important for broader scale migratory movements in terrestrial mammals. Recent evidence from migrating red deer (*Cervus elaphus*) demonstrates they appear to jump ahead of vegetation green up rather than track it [22]. Though the mechanism enabling this is unexplored, it suggests that perceptual cues alone may not be sufficient and that possible mechanisms could include memory. Several transmission mechanisms of memory are possible, most prominently genetic or cultural transmission of information. Work is underway to better understand the genetic underpinnings of migration, including inherited migratory timing and direction [23]. In terrestrial migration, there is likely a learned or cultural component, though this has not been well studied [9,24]. However, it is possible for both genetic and social transmission mechanisms to be present [11,25]. It is also possible, though less common, that the memory is embedded in the landscape, whether through vegetation characteristics, geomorphological features or other cues, and animals are thereby able to sense long-term average conditions as well as predict future conditions. The idea of ecological memory has been explored in the context of fire [26], scent marking [27] and vegetation and soil characteristics [28].

In principle, both mechanisms—perception and memory—are important in terrestrial migrations. To the best of our knowledge, no study has yet undertaken a comparative approach for memory versus perception in the same system. We seek here to answer whether memory could play an important role in long-distance migration of terrestrial mammals. As a case study, we examined migratory movements of zebra (*Equus burchelli antiquorum*) tagged with Global Positioning System (GPS) collars from the Okavango Delta to the Makgadikgadi grasslands [29]. While the migration timing and speed of this population has been previously modelled as following perceptual cues [30], the migratory direction has not yet been examined.

We created a spatially explicit individual-based model for zebra's migratory movements to examine what mechanisms

could successfully direct them to the migration destination. Movement decisions in the model use dynamically changing resource landscapes based on remotely sensed vegetation data. Movement mechanisms differ in what informs the direction choice: perceptually guided migrants use currently sensed resource values within hypothesized perceptual ranges, while memory-guided migrants use long-term averages of past resource values to forecast future conditions. For the perception mechanism, we assume that the zebras detect information within a defined perceptual range used to select a direction. For the memory mechanism, we assume that the zebras accumulate information over the entire landscape, potentially over a long time frame, and then transmit that information genetically or culturally. Our model does not make specific assumptions of how the spatial memory is encoded (genetic, cultural or landscape); we simply assume that zebra accumulated information over hypothesized past time frames over the entire landscape. We compared simulated movement paths using the perception and memory mechanisms against data from GPS-tagged zebras to evaluate which mechanism better matched the GPS-tagged zebras' migratory movements and destination.

2. Material and methods

(a) Study system

Zebras migrate from the Okavango Delta to the Makgadikgadi grasslands at the start of the rainy season (November–April), returning to the Okavango Delta for the dry season [29]. The apparent factor driving the migration is the better nutrient quality of the Makgadikgadi grasslands rather than resource abundance, and not all zebras undertake the migration [29]. The Makgadikgadi grasslands are only inhabitable by zebras during the rainy season after the watering holes have filled. The migration is very directed and approximately 250 km long. However, the migration was blocked from 1968 until 2004 by a veterinary fence erected to separate wild-life and cattle to halt the spread of disease. Zebras were first observed resuming this migration only 3 years after the removal of the fence (and possibly could have resumed migrating earlier). It is very unlikely that those zebras were alive before the fence was installed given that their average lifespan is only one-third as long [30].

We used data from seven adult female zebras tagged in 2007 and 2008 available from the Movebank Data Repository [31] to model the Okavango–Makgadikgadi migration (figure 1). We focused on the Okavango–Makgadikgadi migration and not the return Makgadikgadi–Okavango migration because habitat in the dry season is limited by water availability for which we did not have good data. The GPS collars provided hourly location data with some periods of 15 min data [29,30]. Differences in travel speed as well as significant back and forth movements in 2007 (with individuals completing most or nearly all of the migration before retreating back to the start and departing again) mean the zebras accomplished the Okavango–Makgadikgadi migration in about 34 days in 2007 but only 14 days in 2008.

(b) The model

We created a spatially explicit individual-based model focusing on the directional information migrating zebras use to locate their destination. We compared two information sources for resources: perception of current conditions or a memory of the long-term average past conditions forecasted into the future. We then investigated whether modelled zebras using perception or memory better agreed with the GPS-tagged zebra's migratory movements and destination. The key difference between

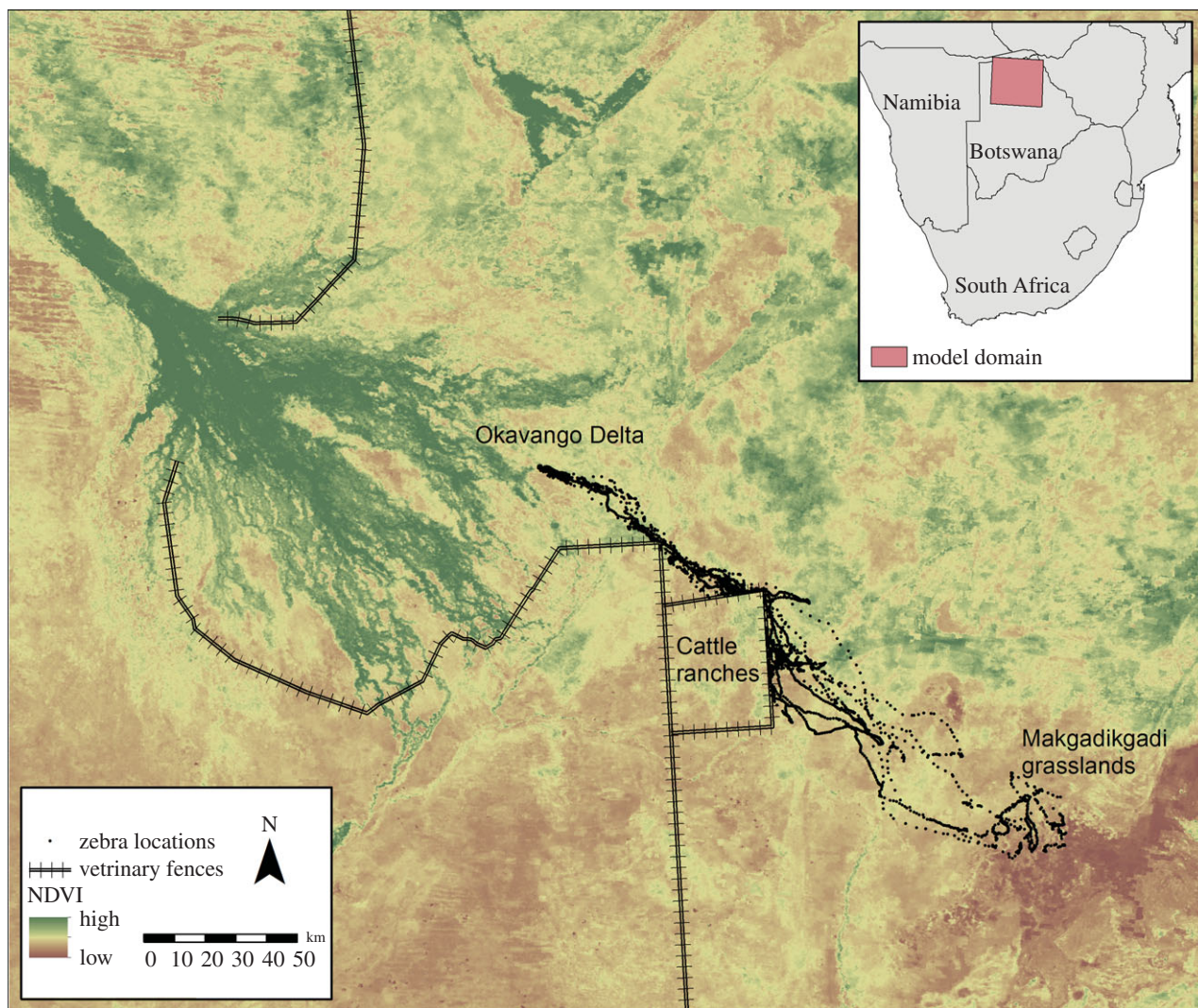


Figure 1. The model domain showing the GPS data for zebras making the Okavango–Makgadikgadi migration in 2007 and 2008. Normalized difference vegetation index (NDVI) values (range: -0.15 to 0.93) are averages of 2007 and 2008 on 1 November at the start of the migration. Zebra data from [31]. (Online version in colour.)

mechanisms is the time-scale of information: perception uses current conditions (at varying perceptual ranges, including omniscience) and memory uses long-term average past conditions. We use remotely sensed vegetation data to represent the habitat in both cases. The important driving variables to the model are thus the internal representation of habitat (current versus past average conditions), and the parameters central to translating these conditions into movement direction are the perceptual range and forecast horizon, i.e. how far into the future zebras forecast conditions to make movement decisions.

In the case of the memory mechanism, zebras could transmit migratory information through genetic or cultural means, and our model is flexible as to the specific details of how the spatial memory is encoded into a cognitive map [8]. We assume that at some point zebras exhaustively explored their environment and seek to test if memory is important to direct migrating zebras by determining whether this information can reproduce observed behaviour. In this, we break from most previous models incorporating memory based on individual experience (e.g. [32]) because of our focus on migratory behaviour. While our assumption that zebras have a memory of conditions for the entire landscape may seem extreme, this actually increases the degrees of freedom in the model by allowing modelled zebras to pursue alternative routes to the existing migration. For our model outcomes, a memory representing the entire landscape is thus conservative in permitting alternative destination options, although real zebras may indeed have a more limited spatial memory. Finally, we also

considered two versions of memory degradation: reducing the memory precision by smoothing the spatial map and reducing the memory accuracy by introducing noise.

We describe the model with the overview, design concepts, details (ODD) protocol [33,34] in the electronic supplementary material, appendix A, and here we provide a summary of the key concepts.

(i) Habitat

Our goal was to approximate as closely as possible the zebra's habitat usage from available remotely sensed data. We used the normalized difference vegetation index (NDVI), a satellite-derived product measuring global vegetation conditions [35], which is an index of primary productivity and has been used successfully in other models predicting herbivore movements [15,30,36,37]. For the perception mechanism, we used daily NDVI images for the 2007 and 2008 migration. For the memory mechanism, we created images of long-term average past conditions by averaging the 16-day composite NDVI images for each day of the year across the years 2000–2006 (the data extent prior to the zebra GPS migration data). A single averaged NDVI image was used for each simulation for a particular number of months ahead to forecast (electronic supplementary material, table A1). In order to replicate the habitat use of the GPS-tagged zebras, we transformed the NDVI values using the empirical probability distribution of values for used locations from the zebra GPS data (see the electronic supplementary material, appendix A *Input data* section).

(ii) Movement

Our movement submodel is based on the movement model of Bracis *et al.* [38], where velocity is a continuous correlated process with the direction informed by resource values in different directions. Our modelled zebras are free to wander in a two-dimensional landscape. Memory and perception processes differ in how the preferred direction is set, but we strove to keep all other aspects of the model the same between processes to focus the comparison on the different information used to make movement decisions. The speed component of the velocity process is identical between the perception and memory mechanisms and seeks to replicate distances travelled by the GPS-tagged zebras. Values are drawn from a distribution parametrized from the observed displacements of the GPS-tagged zebras for each year. The direction component of the velocity process is a combination of the previous direction (so movements are correlated) and the preferred direction (so movements are directed). The preferred direction is selected from a circular probability distribution created from the zebra's mental representation of habitat conditions, which differs between the memory and perception processes (see the electronic supplementary material, appendix A *Submodels* section). The key parameters driving the translation of habitat conditions to movement direction also differ between processes: perceptual range for the perception mechanism and the forecast horizon for the memory mechanism.

For the perception mechanism, the perceptual range, γ_R (see the electronic supplementary material, table A1) controls how far an individual can perceive its habitat. Modelled zebras sense the habitat conditions (i.e. transformed NDVI values) within their perceptual range perfectly (i.e. without measurement error) and without distance effects. Because the actual perceptual range of zebras is unknown, we compared several values to cover a range of modalities, the smallest (5 km) being the approximate distance to the horizon (though likely an overestimate of zebra's visual range, see [39]), a large sensory range (80 km) as has been suggested for wildebeest [16,40,41], and complete omniscience. The memory mechanism does not directly sense current habitat conditions, but instead relies on previously acquired information.

For the memory mechanism, the forecast horizon, κ , is the time of year that modelled zebras forecast conditions based using past average conditions. The time of year is expressed relative to the migration start, so $\kappa = 0$ days would mean past average conditions at the migration initiation while $\kappa = 30$ days would mean past average conditions a month after migration initiation and thus after arrival at the migration destination. Thus, the habitat conditions used to inform the movement direction are the transformed past average of NDVI values on a particular day of year κ days ahead of the migration start date. Again, we have no information on how far ahead zebra may forecast conditions, so we compared a range of values corresponding to approximately two, four and six months ahead.

Finally, we include a null random walk mechanism. In this case, the preferred direction angle is drawn randomly from a uniform distribution rather than informed by habitat conditions, then combined with the current direction so the movement process is a correlated random walk (see the electronic supplementary material, appendix A *Submodels* section).

(c) Simulations

We ran simulations of the perception, memory and random walk mechanisms for the years 2007 and 2008 according to the parameter values in electronic supplementary material, table A1. For each parameter value (spatial scale for perception and forecast horizon for memory), we ran 100 replicate simulations.

Model parametrizations were evaluated by comparing the simulated and observed trajectories (figure 1 and electronic supplementary material, figure B1). For each year, we calculated the

end location and date range (see the electronic supplementary material, appendix A *Initialization* section). We then compared the simulated trajectory locations for the end date range to the empirical migration destination in each year. We calculated effect sizes for the differences in distance to the migration end point at the end of the migration using Hedges' g statistic [42] using the R package *effsize* [43]. We also created kernel density plots of simulated trajectory locations in the end date range using the R package *adehabitatHR* [44].

3. Results

Memory played an important role in directing simulated migrants towards the empirical migration destination. The simulations using memory mechanism outperformed those using perception mechanism in terms of distance from the migration end point at the end of the migration across all parametrizations (figure 2 and electronic supplementary material, table B1). Memory using past average conditions was able to predict the migration destination of modelled zebras two to four times closer than even those with omniscient perceptual ranges: modelled zebras using the memory mechanism were an average of 30–50 km away from the real destination, whereas those with omniscient perceptual ranges averaged about 120 km away from final destination. Importantly, all results were consistent between the two study years. At the smallest perceptual range, the distance from the final destination was indistinguishable from the random walk mechanism. For the perceptual mechanism, performance improved as perceptual range increased from 5 km, to 80 km, to omniscience. For the memory mechanism, the four month forecast horizon outperformed both the two and six month forecast horizons.

The effect size comparing the distance to the migration endpoint at the end of the migration was always large for all parametrizations of memory compared with all parametrizations of perception (see the electronic supplementary material, tables B2 and B3), showing a clear difference in performance. The perceptual mechanism using the infinite perceptual range showed the biggest difference with both random walk and the other perceptual ranges. Among memory parametrizations, forecasting four months ahead consistently showed larger differences from forecasting six months ahead than two months ahead. The performance of memory mechanism was relatively insensitive to coarsening the spatial map, but did decline with added noise (electronic supplementary material, figures B2 and B3), meaning that a relatively accurate though imprecise spatial map is sufficient to guide simulated zebras to their migratory destination.

The kernel density estimate from the simulated trajectory locations for the period at the end of the migration for each year showed the distribution more focused on the migration endpoint for the memory mechanism than the perception mechanism across all parameter values (figure 3 and electronic supplementary material, figure B4). The memory mechanism distribution for four month forecast horizon were centred on the migration endpoint in both years, as was the distribution for the four month forecast horizon but with a wider spread. This was not the case for the perceptual mechanism at any perceptual range or the six month forecast horizon. Similar to the analysis of the final distance to the migration endpoint (figure 2), the distributions over the end date period were more centred on the migration endpoint in 2007 than 2008.

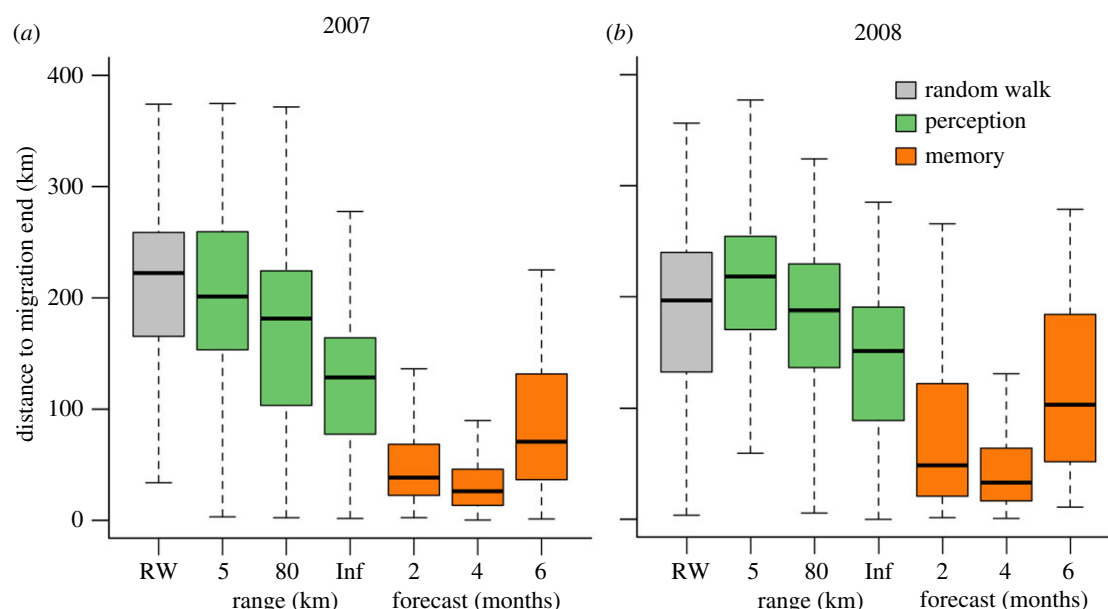


Figure 2. Distance from migration end point on the five day span when the GPS-tagged zebras ended their migration ((a) 27 November–1 December 2007 and (b) 15–19 November 2008). Random walk (RW), perceptual ranges (Inf indicates omniscience) and forecast horizon using past average conditions are compared. Outliers are omitted from the plot. (Online version in colour.)

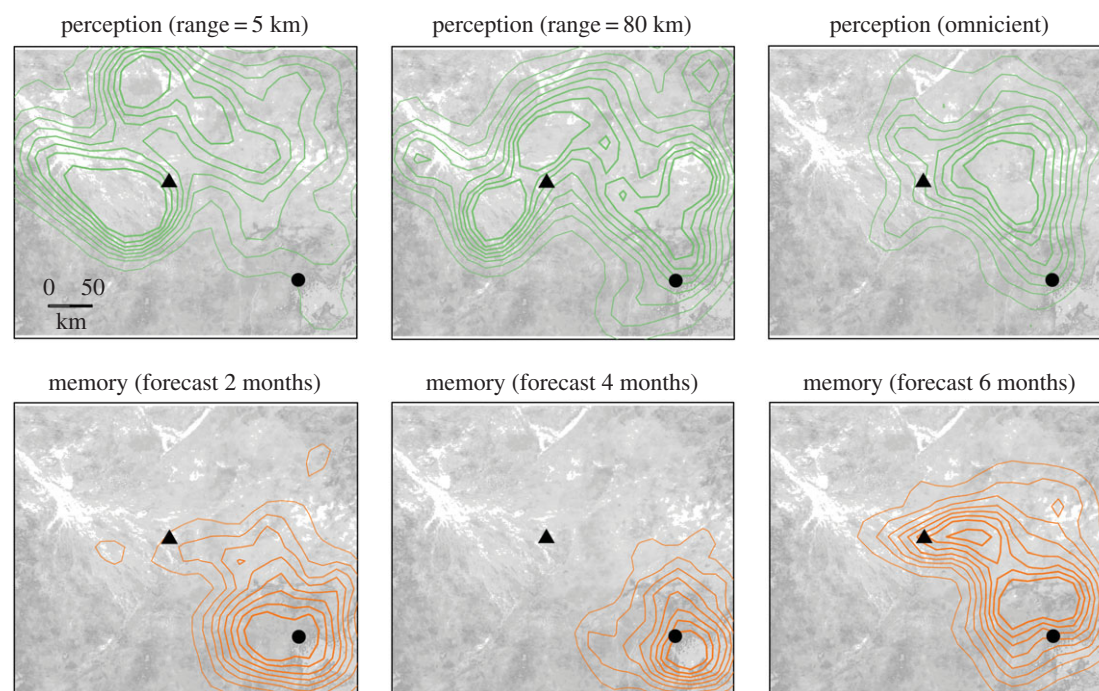


Figure 3. Locations of the modelled zebras at the time that the 2007 GPS-tagged zebras ended their migration. Contours show the 20th through 90th percentile using kernel density estimation. Migration start- and endpoints are marked with a triangle and circle, respectively. Perceptual ranges and forecast horizon using past average conditions are compared. Results for 2008 are broadly similar (see the electronic supplementary material, figure B4). (Online version in colour.)

4. Discussion

Our results show that information from past environmental conditions provided a clear signal that best directed zebras to the migratory endpoint compared to the perception mechanism at even the largest perceptual ranges. Most previous work has focused on perceptual cues when modelling ungulate migrations (e.g. [14–16,30]), and to our knowledge, this is one of the first studies to test a memory mechanism for long-distance mammalian migration. The overall evidence from the literature on behavioural mechanisms of mammalian migration is weak, which is perhaps unsurprising given the

inherent challenges in studying migratory mechanisms in large mammals [4]. Importantly, our results indicate that zebras performed the migration several months ahead of the phenological conditions that eventually determined the migration destination.

This is not to say that memory is the sole directional mechanism, nor that migrating mammals use memory to the exclusion of perception, though we considered them separately here. Rather, the relative success in using perceptual cues in previous studies [14–16,30], combined with the unique characteristics of large mammalian migrations, make it likely that both memory and perceptual cues are important.

Perceptual cues are plausible for some terrestrial migrations, such as short-distance elevational migrations where animals track the seasonal progression of green-up in montane environments to maximize nutrient intake [45,46]. However, memory playing a role in directing long-distance migrations makes intuitive sense, given the spatial memory capabilities known for large mammals in general and the resumption of a long-blocked migration by the zebras in this study in particular. Additionally, the spatial memory need not be exactly as we have implemented it here. A less precise spatial map with a more targeted spatial extent would also be sufficient to guide zebras to their migratory destination. We suggest that the timing and speed of the zebra migration in this study may be based on perception, as shown by previous research [30], and direction based on memory.

(a) Memory in terrestrial mammals

Evidence exists that ungulates use spatial memory in contexts other than migration: to revisit predictable, high-quality foraging locations. This includes experimental manipulations with domesticated ungulates [18,19], modelling feeding site selection for large herbivores [17], analyses of habitat selection [21] and movement behaviour [20]. Memory is also important for models of ungulate movement in the form of individual learning from experiences. For example, memory was shown to be important alongside perception in a seasonal model of caribou foraging [32]. Given this body of knowledge, and given that memory plays a crucial role in the migration of other taxa, such as avian migration [11,25,47,48], it may seem surprising that memory has been little studied as a navigation mechanism for large mammalian migration and that navigational and orientation mechanisms have been neglected in ungulates compared with smaller mammals and other taxa [4]. The clear evidence for spatial memory capabilities in large mammals, combined with the demonstration of the usefulness of memory over perception for route finding during migration, suggest that greater attention should be paid to the role memory plays in future studies of migration.

Much of the work related to understanding memory and movement in mammals has been via individual learning through exploration, e.g. in foraging. However, migration routes are unlikely to be individually learned, but rather either genetically inherited or socially transmitted. In some ungulates, offspring can learn migration routes from parents [24,49], though this is not a universal trait of mammalian migration [50]. The Okavango Delta zebra population resumed their migration after the removal of a fence that had been in place for several generations. This suggests a genetically inherited memory mechanism, although the social nature of herd behaviour means the social transmission of migratory information would also be possible. Alternatively, an intriguing possibility would be some form of ecological memory such that the average seasonal resource conditions are somehow encoded in the landscape according to some cue the zebras can perceive [28].

The temporal dynamics are also crucial to our implementation of memory. While other models have used memory to forecast current conditions in other locations, our model is unique in that animals forecast conditions several months into the future, rather than conditions at arrival. The timing and speed following current conditions identified by Bartlam-Brooks *et al.* [30] together with the importance of future conditions for direction may indicate a multi-stage

process whereby migration initiation follows different ecological forcing from directional choice. For example, motivation to initiate migration may stem from the motivation to leave the origin rather than to reach a specific target, whereas the destination may be determined as a location suitable for future months to come and therefore ultimately be controlled by future conditions.

(b) Green wave hypothesis

The 'green wave hypothesis', originally developed in the context of avian migration, predicts that migrants time their movements to take advantage of the progression of spring green-up and thus maximize the forage available at stopover sites along their migratory route [51,52]. Ungulates also use stopover sites, returning to the same sites in subsequent years and timing their usage with peak nutrition content [53]. Whether they surf or jump the green wave of forage availability has been examined in the context of elevational migrations. Red deer made rapid movements between seasonal habitats, jumping ahead of the green wave, though they also modified their habitat usage to track green-up on a small scale [22]. Here, we did not identify habitat dynamics independent of habitat use. Thus, in the context of our study, we cannot directly determine whether animals follow a green wave, but rather distinguish between current local conditions and future distant conditions as drivers for migration decisions. Furthermore, incorporating additional information, such as local scale water availability, could mediate resource quality for both memory and precipitation mechanisms.

Our results suggest that ungulate migrants may anticipate conditions at the migration destination. For the zebras in our study, local conditions modulated migration timing [30] (analogous to surfing the green wave), but habitat conditions four months ahead were the best directional cue (analogous to jumping the green wave). That means conditions considerably later than the arrival time are driving the zebra's migratory destination. One potential reason could be that the spatial extent of best habitat in the middle of the wet season (i.e. the four month forecast horizon) is potentially more limited than at the arrival time of zebras. The back and forth movements made by the GPS-tagged zebras in 2007 are reminiscent of surfing the wave, that is, with movement directly linked to the current environmental conditions. The directional signal based solely on habitat perceptual cues, however, led them in many directions, not efficiently to the migration destination. Instead, a memory cue based on future conditions, thus analogous to jumping the green wave, best directed the migrants to the destination. Furthermore, we present a possible mechanism for how migrants may jump the green wave: by using a spatial map of the average conditions at a critical point in the future to direct their migration.

(c) Perception in mammalian migration

Previous models of terrestrial migration have demonstrated that perceptual cues based on environmental variables such as precipitation, NDVI, tree cover and plant protein content [14–16] could provide useful information to model migration routes. However, most modelling efforts have assumed large perceptual ranges in order to generate model output resembling the actual data. For example, for a model of seasonal wildebeest migration, model fit improved up to a perceptual range of about 80–100 km [16]. While reports suggest that

wildebeest could track the localized rainstorms signalling new plant growth at distances of up to 80 km [40,41], there is no indication for how regularly and reliably animals could attain such information. Our results also showed better fit to the migratory endpoint with larger perceptual ranges. However, even if such large perceptual ranges are plausible, our results show, at least for our case study, that they are much less efficient at directing the simulated animals compared to a memory mechanism based on forecasting conditions in the future. Theoretical model results have also demonstrated that when migrants have information from memory, the behaviour of conspecifics and current resource conditions they rely on memory [54].

Perception could play a role in modulating migratory timing and progress to match internally derived predictions of resource conditions to the year-specific arrival and consistency of spring rains. In the zebra system, the years 2007 and 2008 differed dramatically in how quickly the animals proceeded along the migratory route, though the route itself was similar in both years. The migration averaged 34 days in 2007 but only 14 days in 2008, as seen in our results with the differing speeds between years (see *v* in the electronic supplementary material, table A1). Compared to 2008, the 2007 GPS-tagged zebras both moved more slowly on average and with large back and forth movements, including one individual returning to the starting point after nearly completing the migration before continuing a week later. This back and forth behaviour has not been successfully modelled, either in our work here or by Bartlam-Brooks *et al.* [30], who successfully modelled migration timing using local precipitation and NDVI. It appears that the zebras may be sampling conditions along the migratory route or even at the migration destination. In particular, the fact that one individual travelled nearly the entire route before returning implies that perceptual ranges, at least in this context, may be fairly limited.

(d) Conservation implications

A better understanding of how large terrestrial mammals make migratory decisions is crucial for conserving these often-threatened migrations [5]. Migrating animals face unique threats from climate change due to their particular habitat requirements, difficulties faced during migration and potential timing mismatch [55]. Attention has been paid to the problem of a mismatch between the timing of arrival of migrants and food availability (e.g. [56]), but conditions may also change along the migratory route [57]. Whether an animal's knowledge of its migration route comes from a basically invariant genetically inherited memory or instead from more plastic social learning could have direct implications for whether adaption of the route is possible. If migration direction and

route are primarily controlled by inherited directional information, as our results here suggest, this implies that migration routes might be relatively inflexible and important to protect before they disappear or are encroached on, whether by land use changes or climate change. This is in contrast to the apparent flexibility in this case for whether to migrate, as the zebras were able to resume a migration blocked for multiple generations [29], although blocked migration routes have often decimated populations [58].

Other species are known to have fixed migration routes, such as pronghorn (*Antilocapra americana*), which may have used migration routes unchanged for over 6000 years with low likelihood of adopting alternative routes [59,60]. On the other hand, if migration information is updated or transmitted through social learning, animals may be able to alter their migration routes or even destination, and social learning of migratory information is plausible given that large mammals frequently live in herds [9]. Migrating animals relying on inherited direction information, however, may not be able to detour around obstacles such as fences or respond to changing conditions. Fences can divide populations and are a particular threat to migrating species, with several documented examples in large mammals of the complete cessation of migration and resulting die-offs in the tens to hundreds of thousands in southern Africa [58]. While changing migration routes have already been observed in some non-terrestrial species [61,62], innovations in migration route may not be feasible for large terrestrial mammals, both because of inherited directional information and human-induced reductions in landscape permeability [63]. Our results suggest that even if perceptual cues may guide timing, they may not be sufficient to guide route finding. Protecting migration routes is crucial for conserving migratory species, and care must be taken if migration routes shift [55].

Data accessibility. The zebra location data are available from Movebank [31]. The NDVI data are available from NASA (<http://modis.gsfc.nasa.gov>). Source code is available upon request.

Author's contributions. C.B. and T.M. conceived the study, analysed the results and drafted the manuscript. C.B. designed and implemented the model.

Competing interests. We declare we have no competing interests.

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