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PERSPECTIVE

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Explaining and predicting animal migration under global change

Abstract

Many migratory species are declining due to global environmental change. Yet, their complex annual cycles make unravelling the impacts of potential drivers such as climate and land-use change on migrations a major challenge. Identifying where, when and how threatening processes impact species' migratory journeys and population dynamics is crucial for identifying effective conservation actions. Here, we describe how a new migration modelling framework – Spatially explicit Adaptive Migration Models (SAMMs) – can simulate the optimal behavioural decisions required to migrate across open land- or seascapes varying in character over space and time, without requiring predefined behavioural rules. Models of adaptive behaviour have been used widely in theoretical ecology but have great untapped potential in real-world contexts. Applying adaptive behaviour models across open environments will allow users to explore how migratory species may adapt their routes and usage of intermediate sites in response to environmental change. We outline how SAMMs can be used to model migratory journeys through aerial, terrestrial and aquatic environments, demonstrating their potential using a case study on the common cuckoo (*Cuculus canorus*) and comparing modelled to observed behaviours. SAMMs offer a tool to identify the key threats faced by migratory species, how they could adapt to future migratory journeys in response to changing environmental conditions and the consequences of not being able to adapt to change.

1 | INTRODUCTION

Animal migration is a global phenomenon. Every year, billions of animals – from butterflies and bats to wildebeest and whales – travel long distances in the pursuit of resources in different habitats around the world (Bauer & Hoye, 2014; Dingle, 2014; Wilcove & Wikelski, 2008; Figure 1). Populations of many migratory species are, however, declining more rapidly than their resident counterparts (Rosenberg et al., 2019; Wilcove & Wikelski, 2008). For example, the number of western monarch butterflies (*Danaus plexippus*) overwintering in Mexico is estimated to have dropped from millions in the early 1990s to two thousand by the winter of 2020. At the same time, resident populations in Californian urban gardens have become more abundant (Crone & Schultz, 2021). Similarly, since the 1970s there has been an estimated loss of 2.5 billion individuals of 419 native North American migratory breeding bird species, whilst over the same period populations of 100 native resident species have increased by 26 million individuals (Rosenberg et al., 2019). Conserving migratory species in the face of global change is now a priority for conservation scientists, practitioners and natural resource managers (Runge et al., 2015).

Identifying the specific causes of migrant population declines is challenging. Throughout their annual cycles, migratory animals rely on multiple landscapes, often in different geopolitical regions, where they may be exposed to a variety of threats (Kubelka et al., 2022). Climate and land-use change, overexploitation and the creation of obstacles and barriers such as fences and pipelines are all well-recognised threats to migratory animals (Kubelka et al., 2022). The mechanisms by which these threats affect migrants, however, are varied and not always clear, with reported impacts on fecundity, juvenile recruitment and adult survival (Wilson et al., 2018). To identify the specific drivers of migrant population declines and potential impacts of future environmental change, we need to ascertain both the processes that threaten species during their annual cycles and where and when in that annual cycle a population is critically limited

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(Flockhart et al., 2015; Sillett et al., 2000; Wilson et al., 2018). Understanding the processes that occur during migration requires an individual-based approach that considers the drivers of behavioural decisions, and the consequences of these decisions for fitness and population dynamics (Bauer & Klaassen, 2013). However, process-based models of the migratory journeys of real species are rare (Bauer & Klaassen, 2013; Howard et al., 2018). Many studies of the impacts of changing environmental conditions on migratory journeys have been static and correlative (Howard et al., 2018; Zurell et al., 2018), limiting insights into the biological and physical drivers of migratory behaviour and the responses of animal migrations to environmental change. Over the past few decades, rapid improvements in tracking technology and a proliferation of tracking studies have provided vast amounts of data on animal migration (e.g., https://www.movebank.org; Kays et al., 2022). With the empirical advances that high-resolution tracking data bring, we are now able to parameterise and scrutinise process-based models to understand the drivers of migratory behaviour and the impacts of changing environmental conditions on migratory journeys.

Classical individual-based models have become popular tools for understanding and simulating animal movements, including through open environments in which an animal can travel and refuel in any biologically plausible location (e.g. Bauer & Klaassen, 2013; Malishev & Kramer-Schadt, 2021). Typically, individual-based models require rules for animal behaviour to be defined a priori, requiring hypotheses about behavioural decisions underpinned by extensive empirical knowledge (Bauer & Klaassen, 2013). For example, an individual-based model might assume that an animal should depart on migration under a defined set of environmental conditions, once it has stored a pre-determined fuel reserve. However, behavioural rules are often context- and scale-specific, making it challenging to apply them to novel environmental scenarios and across different spatial scales (Feró et al., 2008; Malishev & Kramer-Schadt, 2021). Alternatively, behavioural decisions in individual-based models can be determined based on the perceived costs and benefits of a set of actions – without having to be predefined by the user – allowing models to be applied more readily to different contexts. Models of adaptive behaviour (also known as dynamic programming models or state-dependent optimisation models) assume that evolution has shaped behaviour and, thus, that animals make decisions that maximise expected fitness (Clark & Mangel, 2000; Houston & McNamara, 1999). Adaptive behaviour models compare the consequences of different sequences of state-dependent decisions on individual fitness (i.e., given their energy reserves and location, should they forage, rest or move on towards their destination) to determine fitness-maximising behaviour. Consequently, behaviour emerges from these models – optimised to the underlying environmental conditions and the internal state of animals. For example, a modelled animal will depart on migration with the level of fuel reserves and under the environmental conditions that maximise its likelihood of successfully reaching its destination to breed. This makes adaptive models well-suited to investigating how real migratory individuals might be expected to respond to novel environmental conditions (Stillman et al., 2015). Models of adaptive migratory behaviour are used increasingly in applied contexts, including to investigate the impacts of environmental change or management actions on the use

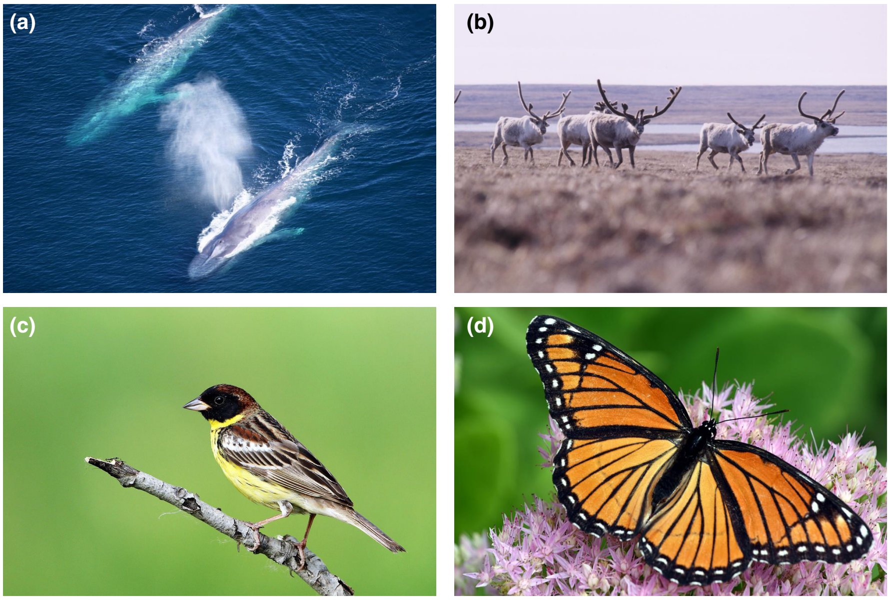

FIGURE 1 Examples of migratory animals for which SAMMs could be used to explain and predict their migratory journeys under changing environmental conditions. (a) Blue whales (*Balaenoptera musculus*, photo by Anthony Lombardi, PDM 1.0); (b) Barren-ground caribou (*Rangifer tarandus groenlandicus*, photo by National Oceanic and Atmospheric Administration (NOAA), U.S. Department of Commerce, CC BY 2.0); (c) Yellow-breasted Bunting (*Emberiza aureola*, photo by lonelyshrimp, CC BY 2.0); (d) Monarch butterfly (*Danaus plexippus*, photo by Chris Chow on Unsplash). The migrations of these species have been or are likely to be impacted by anthropogenic activities. SAMMs can provide insights into the determinants of current migratory journeys, how species may have to alter their journeys in response to environmental change and the implications for their population dynamics of not doing so.

of migratory refuelling and resting sites (Bauer et al., 2018; McHuron et al., 2021; Pirotta et al., 2019).

While classical individual-based models of animal movement and migration are often applied over open landscapes (e.g., Dodson et al., 2020; Merkle et al., 2019), adaptive behaviour models are typically used to model migratory journeys along predetermined routes. These are usually spatially restricted, for example, to discrete intermediate sites (Bauer et al., 2008, 2018; Weber et al., 1998) or single dimensions of space (McHuron et al., 2021; Pirotta et al., 2019). This limits the capacity of individuals to adapt their migratory journeys in response to environmental change (Alerstam & Bäckman, 2018). This application also lacks the flexibility required to model the migratory routes of species that do not use well-defined intermediate sites or routes, such as the many species that move more continuously through their environment. Applying adaptive behaviour models over real-world environments, comprising barriers and spatio-temporal variation in resources widens their applicability to populations and species that do not use clearly delineated intermediate sites. It also permits, for species currently using discrete intermediate sites, the selection of alternative sites as environments change over time.

Here, we propose a novel approach to individual-based modelling of migration, which unites the contextual realism of classical individual-based models with the long-term fitness focus of adaptive behaviour models. Spatially explicit Adaptive Migration Models (SAMMs) apply adaptive behaviour models over high-resolution gridded landscapes of varying environmental characteristics; the movement and stopping decisions of individuals are based on their body condition, landscape characteristics and the need to reach end goals in a timely manner. This approach takes advantage of recent increases in computational processing power and the consequent ability of adaptive behaviour models to find solutions for large regions of state space. SAMMs allow migrants to respond to environmental change experienced in different areas and to adapt their migration routes flexibly to changing conditions. Model landscapes can be characterised using spatially and temporally explicit environmental data, which may affect individuals indirectly, via effects on resource availability, or directly, via impacts on energy demands. Improvements in computational power also allow for a higher degree of biological complexity to be included in models. Here, we show how animal migration could be modelled over realistic landscapes, conditioned on the ecological and physiological attributes of real species and applied to contemporary and future scenarios to explore the primary threats to such species.

2 | MODELLING MIGRATORY JOURNEYS

2.1 | Model structure and assumptions

SAMMs require explicit consideration of state variables, constraints, behavioural decisions and a currency for optimisation (Clark & Mangel, 2000; Houston & McNamara, 1999) (see Figure 2). State variables represent the physiological, morphological or environmental characteristics that are relevant to decision-making. The most basic state variables in SAMMs are energy reserves and geographical location (Weber et al., 1998), but more complex models might consider other individual characteristics such as health status or age (Houston et al., 2007), feather condition (Barta et al., 2008) or reproductive stage (McHuron et al., 2021). The currency for optimisation is usually some measure of long-term fitness, such as expected reproductive success at the end of pre-breeding migration or expected survival during post-breeding migration. A terminal reward function – how the animal's state at the end of migration translates into expected fitness – is a crucial input to the model. The terminal reward typically varies as a function of the state variables, including energy reserves, location and time (Figure 2), with individuals generally only obtaining the terminal reward if they reach a particular location by a given date.

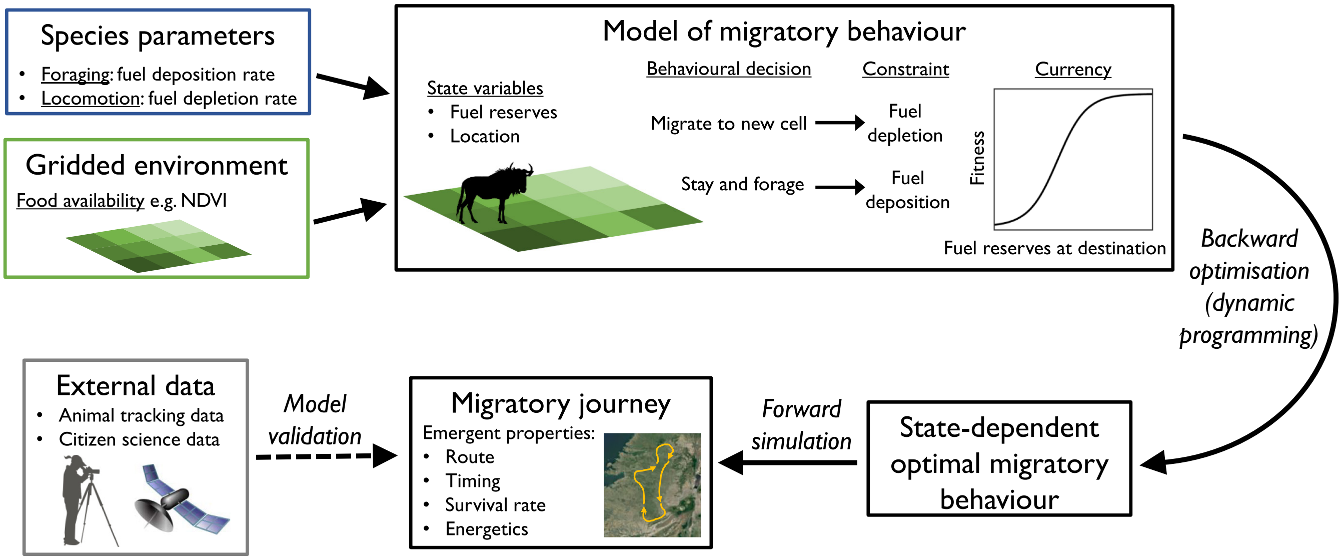

FIGURE 2 A conceptual diagram of a simple spatially explicit adaptive migration model.

SAMMs require information on internal and external constraints, such as the costs of locomotion and variation in food availability, and how these affect state variables; for example, how energy reserves deplete during locomotion (Figure 2). Based on the inter-relationships between state variables, constraints and expected fitness, the optimal behavioural decisions are determined for each time point (e.g., day) before, during and after migration, for all possible combinations of state variables (e.g., for each level of body reserves and location). This is achieved using a backward iterative procedure known as dynamic programming. Working backwards from the range of possible states of migrants at the terminal time-point, and the expected fitness associated with these states (the terminal reward function), this procedure iteratively identifies the optimal state-dependent decisions made at each previous time-point. In the simplest SAMMs, individuals decide between staying at a particular site and moving elsewhere (Figure 2). More complexity can be included by computing the fitness consequences of devoting different proportions of time or energy to foraging relative to other behaviours, such as resting and reproduction (Weber et al., 1998). Computational time increases with the number of state variables and their resolution, as more combinations of state variables become possible.

In SAMMs, there is also a trade-off between computational requirements and landscape complexity. As the resolution of the gridded environment is increased, and the number of potential sites increases, the breadth of possible behavioural options rises rapidly. Environment resolution may be selected based on the trade-off between the inferential gain from finer scale predictions and the computing power available. Other considerations are the resolution of data available for validation and the ecology of the focal species, such as their movement range.

Once the optimal state-dependent behavioural decisions are determined, the expected migratory behaviour of individual animals over time can be established either by Monte Carlo simulation or direct computation (Clark & Mangel, 2000; Houston & McNamara, 1999). Stochasticity could be explicitly included in these simulations, for instance, to represent animals experiencing variable foraging success (Houston & McNamara, 1993), or variation in the costs of locomotion, owing to environmental conditions (Weber et al., 1998). As with other individual-based approaches, a range of emergent properties of migration can be explored using SAMMs, including routes, timings of departure and arrival, the fitness and survival associated with individual strategies, the number, intensity of use and type of intermediate sites used during migration and seasonal dynamics in body reserves.

In contrast to approaches based on predetermined behavioural rules, the emergent characteristics of SAMMs represent ‘evolved’ migratory strategies adapted to the environmental conditions of the modelling landscape. As such, SAMMs are well suited to investigating the potential consequences of environmental change on migration, specifically: (1) determining the changes in migratory behaviour, such as timing, duration, length and routes, that would arise from responding optimally to novel environmental conditions and (2) estimating the consequences, for example on survival and fecundity, of not being able to respond optimally.

2.2 | Data requirements and challenges

The environmental variables used in SAMMs should be relevant to the migratory behaviour, state variables and fitness of the focal species. For example, for migrants that use terrestrial environments such as ungulates and many birds, spatial data on vegetation, land use, topography, climate and weather can be used to characterise environmental conditions across grid cells, much of which is widely available. One of the most important environmental inputs required in a simple SAMM is likely to be food availability, which will influence when and where animals can fuel up for migration and, consequently, the emergent timing and routes of their journeys. Remotely sensed indices of vegetation, such as the normalised difference vegetation index (NDVI), offer potential proxies for food availability for terrestrial species (La Sorte & Graham, 2021). Such indices are available globally at a fine spatial scale (down to 10 m) and temporal scale (weekly or bi-weekly). NDVI is commonly used to represent food availability for herbivores, such as wildebeest and zebra (Hopcraft et al., 2014), but may also be a suitable proxy for higher trophic level feeding guilds such as insectivorous birds (La Sorte & Graham, 2021). At some latitudes, rainfall may be a more suitable proxy for food availability, given the positive relationships that can occur between precipitation and insect emergence (Cumming & Bernard, 1997). Precipitation can also affect the availability of nectar plants, an important resource for migratory butterflies (Chowdhury et al., 2021). For marine species such as baleen whales, indices of chlorophyll concentration and marine upwelling have been used to represent food availability (Abrahms et al., 2019). The choice of proxies should be taken with care, based on knowledge of the system, because remotely sensed indices may not always provide good proxies for resource availability.

Relationships between measures of resource availability and fuelling rates could be determined by modelling how remotely sensed proxies for resource availability (e.g., NDVI) vary with spatio-temporal dynamics in body mass using large body mass datasets, such as from animal tagging studies (e.g., du Feu et al., 2016). Body mass dynamics before and during migration could either be quantified across individuals (e.g., Mason et al. (2012) or, where repeated measures are available, within individuals (see cuckoo case study, below). In the absence of observed data, allometric relationships could be used to provide baseline estimates of species-specific maximum fuelling rates (Lindström, 1991).

SAMMs require the relationship between locomotion and depletion of body reserves to be parameterised. For some taxa, including birds, bioenergetic models of locomotion exist that can predict species-specific movement parameters including rates of fuel depletion and maximum movement range (Alexander, 1999; Pennycuick, 2008). A variety of other constraints on how individuals use energy could be parameterised depending on the research question and the desired complexity of models. For instance, researchers might consider the potential effects of wind and atmospheric currents on the costs of locomotion (Kranstauber et al., 2015) or the influence of climatic conditions on metabolic rate (and, thus, background fuel depletion rates).

Parameterising the terminal reward function – how the animal's state at the end of migration translates into expected fitness – can use empirical data, such as the relationship between body condition at arrival on a species' breeding grounds and subsequent fecundity. Where such data are lacking, species-specific functions could be estimated from information on similar species and/or allometric relationships (Klaassen, 2003). For most migrations, the terminal reward is also usually time-dependent with, for example, successful breeding possible only within a specific time window of resource availability. Parameterising time dependence for such single-journey models requires empirical data on breeding phenology and outcomes, but the analysis may not be straightforward if differences in quality influence arrival time and breeding success. For studies focused on individual breeding populations, data on the timing of arrival and departure from field or tracking studies could be used for parameterisation (Bauer et al., 2018; Hewson et al., 2016). Alternatively, citizen science sightings providing data on migratory timing could be used for a range of taxa, including birds, terrestrial mammals, marine mammals and insects (du Feu et al., 2016; Pirotta et al., 2020; Swanson et al., 2015). Equally, such data could be retained from model parameterisation, to provide independent validation of simulated migrations (see below). The interpretation of data may not be straightforward if differences in an animal's quality influence its arrival time and breeding success. One way to proceed is to investigate the sensitivity of results to assumptions about the terminal reward. Ultimately, the time constraints associated with the terminal reward could be extended, with a view to modelling the annual routines – i.e., both the outward and inbound stages of migration, as well as time spent on the breeding and non-breeding grounds – of migratory species rather than single journeys (McNamara et al., 1998).

Validating migration simulations arising from SAMMs is important if the outputs from such models are to be regarded as plausible and useful for decision-making. Recent advances in animal tracking are making this increasingly possible (Figure 2). Various distance – and pattern-based approaches exist for comparing movement trajectories and could be refined into tools for validating simulated migrations against empirical migrations (Cleasby et al., 2019; Ranacher & Tzavella, 2014). Alternative empirical validations could use other emergent properties of simulations, such as relationships between simulated energetics and data on body condition, the location, timing and intensity of use of intermediate locations and the phenology of migrations (du Feu et al., 2016; Kays et al., 2022; Swanson et al., 2015).

2.3 | Case study: A SAMM of the Africa–Europe migration of common cuckoos

Declines in the populations of some trans-Saharan migrant birds (birds that breed in Europe and spend the non-breeding season in sub-Saharan Africa) have been attributed to threatening processes to which birds are exposed during their migrations, including climate and land cover change (Cresswell et al., 2007; Hewson et al., 2016; Vickery et al., 2014). The recent development of small platform transmitter terminals (PTTs) has enabled detailed tracking of some of the larger long-distance migrants, such as the common cuckoo (*Cuculus canorus*), whilst geolocators use light levels to enable tracking of smaller songbirds down to 10g (Kays et al., 2015). Available data on the migration routes and phenology of cuckoos provide an opportunity to demonstrate the efficacy of SAMMs for modelling migratory routes.

We illustrate a simple SAMM of spring migration strategies that maximise the reproductive success of cuckoos at their breeding grounds. We divided Europe and Africa into 309 equal-area hexagonal grid cells with centre points separated by 500km. Based on the tracking data for this species, we defined five grid cells within the Congo Basin as their non-breeding-grounds, and a grid cell in England as their breeding site (Figure 3). We defined the end of the migration period as the 14 May, a date that coincides with the end of cuckoo spring arrivals in England, and allowed birds 75days to prepare for and complete migration (Hewson et al., 2016).

We assumed that, at a given time point, expected reproductive success depended on a cuckoo's energy reserves and location. Energy reserves varied between 0, when an individual would die of starvation, and 10, which is an individual's maximum fuel load. At each time-point, until the cuckoo reaches the breeding site, it has three behavioural options: to forage, to rest, or, energy reserves permitting, to fly to another cell. We allowed the fuel deposition rate in foraging individuals to vary as a linear function of NDVI, used here as a proxy for food availability (La Sorte & Graham, 2021). For each grid cell, we estimated the mean daily NDVI by interpolating the weekly mean 2012–2016 NDVI values (Jiang et al., 2010). We used mass data from cuckoos captured for ringing to estimate the fuelling rate, based on a sample of data provided by the British Trust for Ornithology from their national ringing database. We considered data where there were repeated measures of individuals during the pre-migration fattening period (i.e., where individuals had been trapped more than once). The maximum observed intra-individual pre-migration mass gain recorded was 6.25g per day, which we assumed could be achieved in areas of maximum observed NDVI. The maximum potential flight range was estimated for any starting body mass using bioenergetic models of avian flight based on species-specific flight modes and measures of wing area, wingspan and fat-free body mass (Pennycuick, 2008). We assumed that the cuckoo's estimated maximum flight range (4284km) derived from these bioenergetic models could be achieved at maximum fuel load. Fuel depletion rates were assumed to be proportional to flight distance. The terminal reward was defined as a function of the date of, and energy reserves on, arrival at the breeding site.

We used dynamic programming to determine the optimal decisions for all combinations of grid cells and energy reserves, at each time-point. The optimal decision is the behavioural option – forage, rest or fly – that yields the highest expected future reproductive

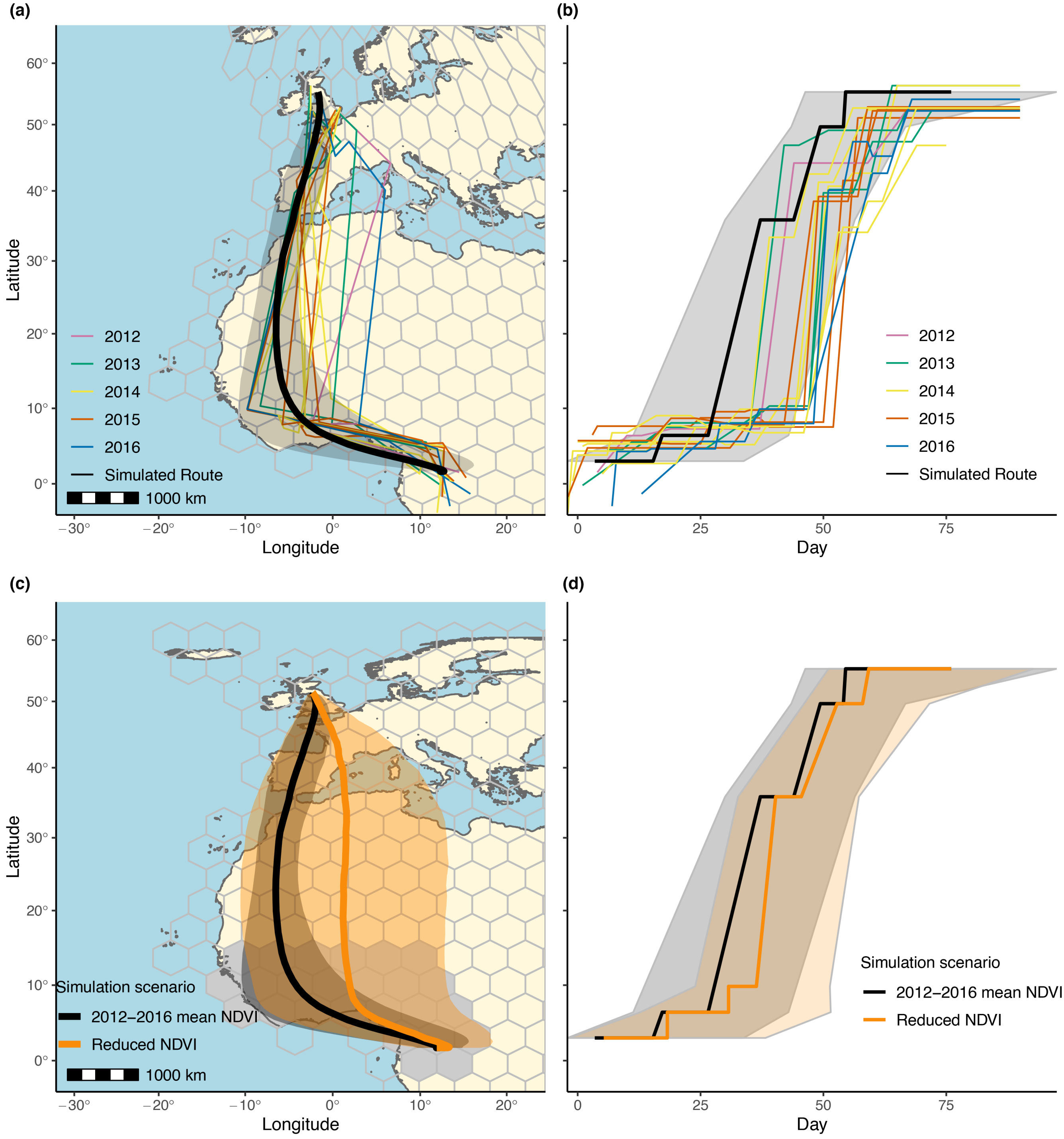

FIGURE 3 Comparing the routes and phenology of simulated and observed spring migrations of Common Cuckoo *(Cuculus canorus)*. (a) The mean simulated optimal spring migration routes of common cuckoos (black) from a SAMM and the observed spring migration routes of ten individual cuckoos tracked between 2012 and 2016. Lines for individual tracks are coloured by year. The mean is calculated for the 96.4% of 100,000 simulated individuals that arrived at the breeding ground by the end of the migration window. Grey shading indicates the standard deviation around the simulated mean. The modelling used a 500 km hexagonal equal-area grid, as illustrated. (b) The mean simulated relationship between day and latitude from the same simulated cuckoo migrations (black line) and the observed relationship between day and latitude for the same ten individually tracked cuckoos (lines colours and shading are as in Panel A). (c) The mean simulated optimal spring migration routes of common cuckoos using a SAMM fitted to average NDVI conditions between 2012 and 2016 (black) and a SAMM fitted to an environmental scenario with a 20% reduction in NDVI across West Africa (orange). Gray and orange shading indicates the standard deviation around the mean from the original SAMM and the reduced NDVI SAMM respectively. Grey-shaded hexagonal grid cells indicate the area of West Africa for which daily NDVI was reduced by 20%. (d) The mean simulated relationship between day and latitude from the same SAMMs shown in Panel C (line colours and shading as in Panel C). Days 0 and 75 are 28 February and 14 May, respectively.

success, given the state of the individual bird. Based on these optimal decisions, we simulated the fates of 100,000 individual cuckoos during their spring migrations. Individuals were randomly assigned a starting grid cell within the non-breeding range and a random starting level of energy reserve between 1 and 10. We modelled the migratory journeys of individuals through time and space until they either reached the breeding site, died (i.e., had an energy reserve of zero) or reached the end of the migration window in a grid cell other than the breeding site. For the 96.4% of individuals that reached the breeding site by the end of the migration window, we calculated the mean (and standard deviation) location at each time point and the mean latitude at each time point to summarise the simulated routes and phenology of spring migration (Figure 3). The simulated optimal migratory strategies had a good temporal and spatial match with the observed routes of ten individual cuckoos (Hewson et al., 2016) between 2012 and 2016 (Figure 3).

To illustrate how our approach could be used to understand the impacts of threatening processes on migratory journeys, we re-fitted the SAMM described above but using an NDVI layer that simulates a hypothetical scenario of habitat deterioration (Figure 3). We reduced NDVI by 20% across West Africa to simulate potential drought-like conditions (Tøttrup et al., 2012). All the other parameters in the SAMM remained the same. Here, we refitted both the dynamic programming and the forward simulation stages of the SAMM with the reduced NDVI layer. This approach assumes that individuals can alter their migratory strategies optimally to these changes in conditions and is useful for revealing which changes in migratory behaviour may be required in future, i.e., how individuals may change their migratory routes and use intermediate sites under various scenarios of environmental change. Alternatively, when the altered environmental scenario is only applied in the forward simulation, we assume that individuals lack the capacity to respond optimally to environmental change, revealing the likely fitness consequences of not doing so (cf. McHuron et al., 2021; Pirotta et al., 2019; Weber et al., 1999). We found substantial differences in the routes, phenology and survival rates of common cuckoos between the original SAMM and the reduced-NDVI SAMM (Figure 3). Specifically, we found that the mean arrival day on the breeding grounds in the original SAMM (day = 53, S.D. ±8.7), was substantially earlier than in the reduced-NDVI SAMM (mean arrival day = 59.4, S.D. ±8.7, see Figure S5 for the distribution of arrival dates). We also found that the mean departure day from the non-breeding grounds in the original SAMM (mean departure day = 15.5, S.D. ±6.3) was earlier than in the reduced NDVI SAMM (mean departure day = 18.7, S.D. ±7.0, see Figure S5 for the distribution of departure dates). Finally, survival rates were 4.1% lower in the reduced-NDVI SAMM (92.3%) than in the original SAMM (96.4%). Newly published analyses of cuckoo migration highlight the importance of conditions in West Africa as a constraint on spring migration to the UK (Davies et al., 2023), further validating the inference from our SAMM. This type of simulation could be produced for other threats or management scenarios. By comparing the outputs of these different simulations, we can identify which threat poses the greatest risk to populations or which management measures would be the most effective. For more details on the parameterisation of the SAMM and additional output metrics, see the Data S1 and Table S1.

2.4 | Extending the case study

The cuckoo case study presents a simple implementation of a SAMM under current environmental conditions and a simplified future scenario, which could be extended in a variety of ways to explore the impacts of environmental change on migratory journeys. For instance, the impacts of climate change-driven range shifts on migratory journeys could be investigated by using species distribution models to identify changes in climatic suitability and adjusting the SAMM's starting and destination cells, accordingly. This approach could be used to investigate the potential impacts of increasing migratory distances on the migration of birds such as cuckoos, as suitable breeding and non-breeding ranges shift towards the poles (Howard et al., 2018; Zurell et al., 2018). The interpretation would need to consider the potential propagation of bias if SDMs have been fitted under, for example, non-equilibrium conditions (Howard et al., 2023).

As demonstrated in our case study, SAMMs can also be used to explore the impacts of changes in resource availability experienced during migratory journeys, revealing the consequences of such changes on the ability of animals to, for example, successfully forage and refuel during migration. Climate change is leading to increased environmental variability, with extreme climate events such as droughts and flooding becoming more common (Diffenbaugh et al., 2017; Easterling et al., 2000). As in our cuckoo example, resource layers representing future scenarios of, for example, changing intra-seasonal resource variability or altered periods of resource scarcity could be developed. More sophisticated future NDVI scenarios could be developed by modelling the predicted impacts of future climate change on NDVI. The impacts of other changes, such as in the availability of water and habitat, could be considered using future landcover scenarios. Future environmental scenarios could be integrated with SAMMs in two ways. Firstly, comparing migrations simulated using SAMMs fitted under contemporary environmental conditions with those fitted under future scenarios would reveal the changes in migratory behaviour required to respond optimally to future environmental conditions, as in our case study. Secondly, determining optimal behaviour under a scenario based on current environmental conditions but simulating migrations under a future scenario could be used to reveal the fitness of 'naïve' individuals who are unable to respond optimally to environmental change (Klaassen et al., 2006). The relative importance of threatening processes, and the aspects of migratory journeys (e.g., routes, phenology, demographics parameters) on which they have the greatest influence, could then be identified by comparing the outputs of SAMMs fitted under different scenarios (cf. McHuron et al., 2021; Pirotta et al., 2019). Of course, SAMMs can only test the impacts and mechanisms of threats that have been incorporated into the structure of models.

Our case study could also be developed to investigate the impacts of other types of threats. Our simple SAMM of cuckoo migration only allows for mortality from starvation. Other sources of mortality, such as hunting/bycatch, collisions with artificial structures such as wind turbines and predation (Klaassen et al., 2006), could be incorporated as direct effects on the expected fitness of an individual. This would allow users to identify where in migratory journeys species may be critically limited by these sources of mortality and to predict the potential impacts of changes in the temporal and spatial distribution of these processes on migratory behaviour and expected fitness.

Our example SAMM was parameterised based on the ecology and physiology of the common cuckoo. It could be readily extended to other species by using data on species-specific resource availability, fuel deposition rate, cost of locomotion and life history characteristics (see 'Data requirements and challenges').

2.5 | Towards a better understanding of animal migration

SAMMs have clear applications for understanding and conserving migratory species in a changing world. They allow researchers to identify the key threatening processes that affect the migrations of different species and the points in migratory journeys where populations are critically limited, including the impacts of carry-over effects between different stages of their journeys. For example, they could be used to understand the impacts of resource extraction and associated features on migratory journeys, such as the Trans-Alaska Pipeline (TAP) on migratory Barren-ground caribou (*Rangifer tarandus groenlandicus*) (Carruthers & Jakimchuk, 1987). SAMMs also allow researchers to predict how migratory behaviours may adapt to changing environmental conditions, and to anticipate the emergence of new routes and strategies. Climate change is predicted to alter the abundance and spatial distribution of krill, the main prey base of some baleen whales, including Blue whales (*Balaenoptera musculus*) (Abrahms et al., 2019). Applying a SAMM approach could identify how whales would need to adapt their migratory journeys to accommodate a shifting prey base. With such information, it may be possible to predict key intermediate sites migratory populations will depend on during future migrations, revealing any changes in their coverage by, for example, protected area networks and any novel threats that may arise. Importantly, the approach could be extended to identify the potential consequences of environmental change for migratory populations that base decisions on a limited range of state variables e.g., species that use departure cues unrelated to environmental conditions, such as day length (Hewson et al., 2016). Thus, SAMMs could provide novel insights into the drivers of the global population declines of migratory species and, in turn, the proactive conservation measures that would stem or reverse these declines. Specifically, SAMMs could be used to explore the potential effectiveness of conservation actions, by assessing cost–benefit trade-offs under different management scenarios (Klaassen et al., 2008). In the case of caribou, SAMMs could be used to identify where the effects of future development and resource extraction will have the greatest impact on caribou survival and productivity, and where mitigation measures would be most effective (Carruthers & Jakimchuk, 1987).

In addition to the clear applications for conservation, SAMMs have the potential to address an extensive range of fundamental ecological and evolutionary questions. SAMMs facilitate the exploration of how different migratory routes and strategies have evolved, including how divisions may have arisen within species (Winger et al., 2019). Varying the environmental layers used to determine migratory behaviours in SAMMs (i.e., at the dynamic program stage), for example, using historic or current environmental conditions, could be used to investigate the mechanisms through which animals use information to guide their journeys, e.g., spatial memory, environment cues. SAMMs could also inform our understanding of the physiological drivers of migratory behaviour, such as identifying critically limiting environmental factors – such as energy availability – and how these might vary during migratory journeys. This could reveal previously unknown carry-over effects or predict where such effects are likely to occur in the future. Finally, they could be used to predict future changes in migration phenology, potentially revealing additional phenomena such as phenological mismatch and the effect of this on migratory and population processes.

3 | CONCLUDING REMARKS

The behaviour-based understanding of migratory journeys that can be gained from SAMMs has the potential to provide novel insights into the drivers of the global population declines of migratory species. Importantly, as the emergent properties of SAMMs represent evolved migratory strategies, SAMMs can be used to predict how migratory species could adapt their migratory journeys in response to future environmental change. These insights could help to identify key threats, both present and future, to migratory species and to inform both local management actions and broader conservation policy.

We have demonstrated that, even with very simple assumptions, SAMMs can effectively reproduce the complex migratory routes of a trans-Saharan migratory bird. Yet, there is clear scope to develop more complex models, incorporating additional biological parameters, to further refine predictions of species' responses to environmental change. Inevitably, there will be challenges to developing models that can realistically simulate migratory journeys. However, attempting to meet those challenges will yield a greater understanding of the processes and factors that underlie migration, from animal physiology to global weather patterns.

The approach we propose here is not restricted to any one system, and there is clear potential for investigating the impacts of global change on a wide range of migratory taxa, including aerial invertebrates such as butterflies, terrestrial herbivores such as caribou and wildebeest, and marine vertebrates such as sea turtles and whales (Figure 1). As the analytical framework is developed further, including validation metrics and more sophisticated parameterisation, SAMMs have the potential to open an extensive range of future research questions, in both fundamental and applied ecology.

KEYWORDS

animal migration, climate change, dynamic programming, global change, spatially explicit modelling

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The authors declare no conflicting interests.

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Cuckoo tracking data were taken from Hewson et al. (2016)). Cuckoo body mass data are available through the BTO at bto.org. The code used for the SAMM of the Africa–Europe migration of Common Cuckoos is available on Dryad (doi:10.5061/dryad.wdbrv15tn).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.