Animal Movement Strategies

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COLOPHON

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Thesis Abstract

MOVEMENT is a fundamental phenomenon in the natural world, and active movement in response to environmental drivers is key to animal ecology. Individuals' positions in a landscape determine what they perceive, and with which other animals they associate and how. These ecological interactions feed back into decisions on *where to go next*. Such fine-scale, individual-level decisions, made by each individual in a population or species, whether alone or in concert with others, scale up over time and space to affect large-scale ecological phenomena such as species distributions and interactions. Over the past twenty years, the field of *movement ecology*, driven by rapid advances in animal tracking technology, has revealed fascinating connections between animal movement and ecological drivers that were previously impossible to measure.

Now, movement ecology is advancing on new frontiers. This thesis is an episodic, personal account of developments on two of these frontiers, with which I have been involved: *(i)* the study of animal movements using massive datasets, and *(ii)* the exploration of the evolutionary causes and consequences of animal movement, using computer simulation models. These advances have been made possible by methodological innovations — such as new technologies for animal tracking, or by adopting new approaches — such as evolutionary individual-based simulations, and reflections on these methods are woven into this work. Organising this thesis into two parts, one for each of the themes above, I have tried to gain and present new insight, but also to lay the groundwork for future developments.

CHAPTER 1 provides a broad introduction to these two themes. I set out my view for how we could better understand the ecology and evolution of animal movement and spatial distributions by using mechanistic, individual-based simulation models. In brief, I cover why animals' foraging dynamics, rather than rare or sporadic events such as natal dispersal or annual migration, are especially suited to understanding the evolutionary causes and consequences of movement as an adaptive behaviour.

In **PART I**, I look at our advances in studying the fine-scale movement decisions of animals using *big data* collected with new *high-throughput* animal tracking systems. A useful primer to high-throughput tracking, with which I was involved, but which is not presented in this thesis, is a recent review in *Science*, "Big-Data

Approaches Lead to an Increased Understanding of the Ecology of Animal Movement"[1].

CHAPTER 2 lays out some practical aspects of dealing with the massive spatial datasets that are generated by *high-throughput animal tracking* systems, which can track the movement of hundreds of individuals at a very high spatio-temporal resolution (a few metres' accuracy, and a few seconds' interval). I cover data cleaning, aggregation, and first principles-based segmentation-clustering, as well as how to implement these methods in reproducible and efficient ways. Adopting computational best-practices from software development and other big-data fields such as genomics is the way forward for robust methods development and reproducible data-processing in movement ecology.

In INTERLUDE A, I include some thoughts on both the technical and aesthetic aspects of visualising animal movements, and show how I applied them while making a map that won the British Ecological Society Movement Ecology Special Interest Group's *Mapping Animal Movements* competition in 2021.

CHAPTER 3 combines high-throughput animal movement data with high-resolution data on the fine-scale, three-dimensional spatial structure of the biotic and abiotic environment. Specifically, I take a mechanistic look at the proximate drivers of the movement and habitat selection of moulting birds. I show how simple mechanistic aspects of a landscape — the visibility of one location from another, interacts with the physical determinants of movement — the surface area of birds' wings, to shape how individuals use their environment. A viewshed analysis approach that computes *fearscapes* — areas of high visibility — reveals that animal movements are a joint outcome of individuals' current physiological state (i.e., the condition of their wings), and individuals' likely perception of landscape risk, in terms of whether they could potentially be seen by *other individuals*.

In **PART II**, I look at how we can tackle questions about the evolutionary causes and consequences of animal movement strategies, using mechanistic *individual-based models* of movement decisions. These models, I suggest, are key to understanding the evolutionary ecology of movement, because they can incorporate both essential ecological detail as well as allowing evolutionary dynamics that are impossible to measure in natural systems.

In INTERLUDE B, I demonstrate how to implement conceptual models that link the ecology and evolution of animals' fine-scale movement strategies. Using

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[1] Nathan, R. et al. (2022), "Big-Data Approaches Lead to an Increased Understanding of the Ecology of Animal Movement," *Science*, 375/6582: eabg1780.

a prototype model that draws on principles laid out in the *Introduction*, I show a simple prototype of the mechanistic models used in this part of the thesis. I show how such models could lead to qualitatively and quantitatively different outcomes from those that would be obtained by structuring models according to classical assumptions — such as random or optimal movement — from evolutionary ecology.

CHAPTER 4 presents a mechanistic, individual-based model of the joint evolution of animal movement and foraging competition strategies. This is the first fully fleshed out study using the class of models I advocate in the *Introduction*. In this model, individuals' movement and foraging decisions depend on local environmental cues, and simultaneously, individual foraging decisions leads to a restructuring of the cues available in the environment. I show how movement strategies evolve to match individuals' competitive context as well as the availability of information on the resource landscape. Substantial individual variation is evolved in movement strategies among foragers, and furthermore, I find tight correlations between evolved movement and foraging strategies under some conditions. Modelling animal movement decisions in an eco-evolutionary context can help define the envelope of potential outcomes under different ecological scenarios in which there are complex feedback loops between individual movement and environmental cues.

In INTERLUDE C, I include a brief comment about the importance of attention to detail when building individual-based simulation models. That this comment had to be written in response to published work shows how it can actually be quite challenging to interpret and implement even a classic theoretical model (the Ideal Free Distribution; 'IFD') in terms of computational methods — specifically, as an individual-based simulation model. Such implementations therefore require both skill and care while coding, as well as a firm understanding of the biological processes (perception and movement) underlying phenomena such as the IFD.

CHAPTER 5 looks at the evolution of animal movement strategies following the introduction of an infectious, chronic pathogen, and examines how animals balance the benefits of social information on resource distributions, against the risks of pathogen transmission, and the consequences of this evolutionary change for animal sociality. I show that introducing a pathogen to a population that has evolved to use social information leads to very rapid changes in movement strategies; this leads to cascading outcomes including more movement overall, fewer individual associations, lower intake, but also reduced pathogen transmission compared to non-adapted ancestral populations. Mechanistically modelling the introduction and spread of a novel infectious pathogen, a scenario of increasing global concern, can help to predict the direct and indirect consequences for individual-level outcomes, as well as impacts on the spatial-social organisation of animal societies.

CHAPTER 6 uses simulated movement data from individuals in Chapter 4 to validate popular methods in the study of empirical animal movement data: repeatability analysis, and step-selection functions. I show that individual differences in movement strategies do not always result in differences in movement paths, and consequently, statistical tools including repeatability analysis and step-selection analysis, may not be able to detect often substantial underlying variation in animals' movement strategies. Applying statistical methods common in movement ecology to simulated movement data where the mechanisms controlling movement are known, can help reveal ecological and evolutionary scenarios which may confound these methods, enabling more precise inferences from tracking data.

Finally, in CHAPTER 7, I reflect on the findings in this thesis, and suggest how an energetics approach could be used to estimate some of the fitness consequences of animal movement.

* * *

Chapter 1

Introduction: Linking the Ecology and Evolution of Animal Movement

Pratik R. Gupte

Animal Movement as a Key Process in Ecology

MOVEMENT is key to animal ecology across spatial and temporal scales, as nearly all ecological processes have an explicit spatial context (Nathan et al. 2008). By moving, animals can track seasonal fluctuations in resources, as migrating blue whales (*Balenoptera musculus*) — among many other species — do, when tracking oceanic 'green-up' in the form of plankton growth and proliferation (Abrahms et al. 2019; 2021*a*). Animal movement can also facilitate or avoid ecological interactions; among these are both inter- and intra-specific competition. For instance, at very small spatial and temporal scales (on the order of minutes), competitive interactions including both scramble ('exploitation') and agonistic ('interference') competition (Birch 1957; Keddy 2001) are entirely determined by the relative positions of competing individuals and the resource to be gained (see also Chapter 4). At larger scales, such interactions can determine how species' distributions track environmental changes; in a classic example, competition for nesting spaces among Western bluebirds (*Sialia mexicana*) has led to a rapid expansion of their range across the north-western United States, leading to the displacement of their less aggressive congener, the mountain bluebird (*S. currucoides*; Duckworth and Badyaev 2007).

The importance of spatial limitations is also evident in other interactions, such as predation, as prey (in this case, North American elk, *Cervus elaphus*) attempt to minimise their likely overlap with predators (wolves, *Canis lupus*; Fortin et al. 2005; but see more recently Kohl et al. 2018); similarly, when facing parasitism, hosts attempt to avoid exposure to pathogens and parasites to prevent infection (Weinstein et al. 2018). Movement plays a key role in aspects of reproduction as well, such as in the sampling and selection of Arctic breeding sites in pectoral sandpipers (*Calidris melanotos*; Kempenaers and Valcu 2017). Finally, spatial proximity is also key to a number of transmission phenomena, including the spread of animal culture such as foraging techniques (e.g. opening garbage bins, among sulphur-crested cockatoos, *Cacatua galerita*; Klump et al. 2021) and migration routes (various ungulates across the United States; Jesmer et al. 2018), as well as the transfer of infectious pathogens (Stroeymeyt et al. 2018; Weinstein et al. 2018; Monk et al. 2022: see also Chapter 5).

Mobile animals do not only respond to their environments, but actively modify them as well. For example, small and medium-sized savanna herbivores (ungulates < 1,000 kg) in southern Africa, avoid closed and busy vegetation in order to lessen predation risk. In so doing, they transfer substantial nutrients to these areas through dung, altering the spatial distribution of suitable plant habitats, and thereby the future distributions of vegetated and open areas (Le Roux et al. 2018). The movement and behaviour of large herbivores can even facilitate the local, short-term growth of plants. In the United States (where many of these studies are performed), grazing by bison (*Bison bison*) seemingly induces local 'green-up' (the growth of plants) as plants respond to grazing damage (Geremia et al. 2019). This new growth is especially nutrient-rich, providing higher quality forage to bison and other animals than would be available without the presence of a bison herd.

The distributions of such 'ecosystem engineer' species can affect that of others in the same area; in the classic example, wolves cause an ecological cascade by reducing grazing by their prey, elk (Fortin et al. 2005). Conversely, changes in prey movements and distribution can alter the movement and behaviour of both their predators, and even that of scavengers (in Argentina; with Andean condor, *Vultur gryphus* scavenging on puma, *Puma concolor* kills of the vicuña, *Vicugna vicugna*; Monk et al. 2022). Often, species characteristics can determine how individuals structure their environment: in the example with southern African ungulates (Le Roux et al. 2018), megaherbivores that are relatively invulnerable to natural predators move across the landscape with no specific preference for open areas (where smaller herbivores are safer from ambush hunters). Consequently, they transfer nutrients more evenly against the small- and medium-sized herbivore nutrient transfer gradient (i.e., from open to more closed areas), thus modulating landscape vegetation structure.

Given the importance of animal movement to natural processes, it is important to note that animal movements as a whole are severely affected by human-induced global changes (Tucker et al. 2018). For example, the driver of changes in vicuña movements (and substantial mortality) discussed earlier (Monk et al. 2022) was the spread of Sarcoptic mange (*Sarcoptes scabiei*), which likely resulted from the artificial introduction into the region of a related species, llamas (*Lama glama*), which themselves were infected with mange. In addition to negative effects for animals themselves, perturbed natural regimes of animal movements (e.g. due to climate or land-use change), can severely impact humans too. One important example is the annual damage and injury resulting from direct human-animal conflict, especially in regions where megafauna persist or are recovering, but where they also have insufficient room to undertake natural movements (Abrahms et al. 2021*b*). Where mobile wildlife tends to interact, or even just overlap with humans, or with domesticated animals, there is a strong potential for the spillover and potential spread of zoonoses to humans, and epizootic diseases to animals such as poultry or livestock (Keeling et al. 2001; Carlson et al. 2022*a*; Wille and Barr 2022). Indeed, the past two and a half years (late 2019 – mid 2022) have been dominated by the Covid-19 pandemic, which should serve as a reminder of the perils of disregarding the potential of the natural world to intrude upon human societies which once thought themselves immune to ecological pressures.

The current and ongoing introduction of the little known tropical African disease monkeypox (primarily a rodent pathogen) to communities across the world, and the two-year long but relatively ignored outbreak of the H5N1 strain of avian influenza in bird populations worldwide (Wille and Barr 2022), should also serve as a clear example of the risks of shifting species range distributions due to climate change (Carlson et al. 2022*b*). Conversely, natural distributions of wildlife could aid climate mitigation by regulating key biotic and abiotic processes, such as the flow of soil carbon and nutrients (see Schmitz et al. 2018; Malhi et al. 2022; and recall Le Roux et al. 2018). While the studies presented here have examined relatively few individuals (compared to global populations, that is) and with relatively restricted geographical scope, it is individual-level movements and behaviours that scale up to influence species- and ecosystem-level phenomena. The rules governing animal movement are thus crucial to a sound understanding of ecological processes and patterns generally (Jeltsch et al. 2013; Schlägel et al. 2020; Costa-Pereira et al. 2022).

Movement in Eco-evolutionary Theory

Movement has long been recognised as an important process, but is often only implicitly included in the cornerstone models of eco-evolutionary theory. In these models, evolution is often not incorporated at all, but replaced by the assumption that individuals tend to make choices that maximize their fitness. An early example is the foundational foraging model of Fretwell and Lucas (1970) that predicts the distribution of fitness-maximising agents over patchily distributed resources ('ideal free distribution' or IFD). Here, individuals that are 'ideal' (having full knowledge of the distribution of resources and competitors) and 'free' (unconstrained in their movement) scan the whole landscape and immediately move to the location maximizing their resource intake. The idea underlying the assumption that individuals tend to move to fitness-maximising locations is that natural selection will have 'weeded out' all strategies that are not maximising fitness. Yet, there are serious problems with the assumption that well-adapted individuals are maximising fitness at all times.

First, 'fitness' is an intricate concept (Brommer 2000), and it is unlikely that individuals can judge the full fitness implications of their movement decisions. Instead, they are likely to be guided by other principles, such as the avoidance of predators or the amount of food available. Second, individuals will typically not be able to single out the best possible habitat patch, as they will only have knowledge on recently visited patches or the patches in their vicinity (Robira et al. 2021). More global knowledge may be obtainable, but obtaining this information will come at a (fitness) cost. Third, even if individuals are 'ideal' (i.e., omniscient) and 'free' (i.e., unconstrained in their movement, which in addition does not impose any costs), their distribution strongly depends on the mechanisms of movement (e.g. the sequence in which they move). Seemingly unimportant details of the movement process can result in quite different distributions in space, with different evolutionary implications (Houston and Lang 1998; Netz et al. 2022*a*). It is therefore essential to consider the movement process itself.

Yet we currently lack theory that explicitly considers the movement process itself, linking the short-term ecological drivers and outcomes of movement with its evolutionary causes — essentially, there is no evolutionary extension to the 'movement ecology paradigm' (Holyoak et al. 2008; Nathan et al. 2008). This hinders insight into how intensified selection on species due to global change would affect animal movement and related phenomena. Such selection is both rapid and currently ongoing, making the understanding of its potential consequences more than a purely academic exercise (Bonnet et al. 2022). For example, the unprecedented warming of their Arctic breeding grounds has caused body size shrinkage among red knots (*Calidris canutus*), including the development of shorter beaks. On their wintering grounds, this results in lower survival for shorter-billed individuals (e.g. Van Gils et al. 2016). Similarly, Sergio et al. (2022) demonstrate how selection winnows out black kites (*Milvus migrans*) with poor navigation capabilities during each annual migration, demonstrating how evolutionary forces can act very rapidly on even complex behavioural traits.

Eco-evolutionary theory, in order to provide general insights, must necessarily simplify biological reality down to essential processes. One such simplification has long been to consider movement to be a population-level property shared by all individuals. Work on consistent behavioural differences in animals, including differences in movement, suggests that this assumption is not well supported (Abrahms et al. 2017; Spiegel et al. 2017; Webber and Vander Wal 2018; Shaw 2020; Webber et al. 2020; Stuber et al. 2022). Yet it is not clear whether movement syndromes, in the sense of individual consistency and correlation in preferences for specific environmental conditions, truly exist (as suggested by Stuber et al. 2022), or whether researchers are instead identifying differences among spatial contexts that heavily influence animal movement (Spiegel and Pinter-Wollman 2022).

A consideration of movement in ecological theory should account for the fact that animals integrate many internal and external cues when making movement decisions (Nathan et al. 2008). Individual-based simulation models (IBMs) are well suited to representing movement as a decision made after integrating multiple cues in complex ecological contexts (Huston et al. 1988; DeAngelis and Diaz 2019). However, most IBMs in the study of animal movement do not tackle the ultimate evolutionary drivers of animal movement strategies (with a few exceptions: Getz et al. 2015; 2016; Netz et al. 2021*b*). In Part II, I develop and use a novel class of eco-evolutionary IBMs for broad conceptual insight into the evolution of animal movement strategies.

Evolutionary models of movement rules treat them as population properties (as in De Jager et al. 2011; 2020, or Morris 2011), whereas movement is an individual-level outcome, and it is on individual outcomes that selection acts. When individuals with different movement strategies have equivalent fitness, populations may show movement polymorphisms (Wolf and Weissing 2012; Getz et al. 2015; Shaw 2020). Including evolutionary dynamics in movement models could thus provide initial predictions for when individual variation (with its own consequences; Spiegel et al. 2017) should be expected. We could also gain insight into how movement strategies could possibly evolve under various ecological scenarios. This second aspect is often ignored, possibly because evolution is considered too slow to be relevant to the understanding and management of ecological dynamics over a few decades. This assumption is mistaken, as evolution can be both rapid and adaptive (Bonnet et al. 2022).

Animal movement behaviours are of many types, and span spatio-temporal scales, from migration to coordinated movement within a group. This makes it challenging to pick a behaviour common to all animals, and whose evolutionary aspects can be easily studied. For instance, although periodic migration (e.g. Guttal and Couzin 2010) and dispersal (e.g. Hillaert et al. 2018) away from the natal site in early life have received substantial attention from evolutionary biologists, these are not common to all or even a majority of taxa. Furthermore, such rare and sporadic events are especially prone to being genetically controlled, with only a smaller role for adaptive, fine-scale behavioural strategies. One scenario in which fine-scale strategies are important is the foraging context. All animals, as heterotrophs, require intake, making (active or passive) foraging a behaviour shared by nearly all animal taxa. Even among migratory species, foraging is a key behaviour that enables their journeys. This makes the foraging context a good *starting point* for models linking the ecology and evolution of fine-scale adaptive movement behaviours.

Proposing a New Method for Eco-evolutionary Models of Animal Movement

I propose models that *work forwards from plausible mechanisms to potential emergent outcomes* (Fig. 1.1). This first requires a change in perspective on individual-based models, from being highly detailed simulations of specific empirical systems (such as in Stillman and Goss□Custard 2010; Bocedi et al. 2014; Diaz et al. 2021), to being used to obtain broad conceptual insight into 'What if ...?' scenarios (see also Getz et al. 2015; 2016; White et al. 2018*b*; Gupte et al. 2021; Netz et al. 2021*b*; Gupte et al. 2022*a*). The key features of the simulation models we advocate is first, that they are *mechanistic, spatially explicit and individual-centric,* i.e., the functional unit of the model is the individual (animal) in a spatial context, and that interactions among individuals and their environment are based on plausible mechanisms (Fig. 1.1A). Second, that *individuals move in their spatial context using step-selection* based on the sensing of direct local cues, such as resource or conspecific counts (Fig. 1.1B). The way how an individual chooses its steps in relation to local cues forms the individual's movement strategy (see below). Third and finally, that the models *explicitly include both ecological and evolutionary timescales and dynamics*; we propose this be done by considering multiple generations, and conditioning an individual's number of offspring — to which it passes on its movement strategy — on its ecological performance in the simulation (Fig. 1.1C). This last means that ecological outcomes in one generation determine the population mixture of movement strategies in the next generation, linking the ecological and evolutionary timescales.

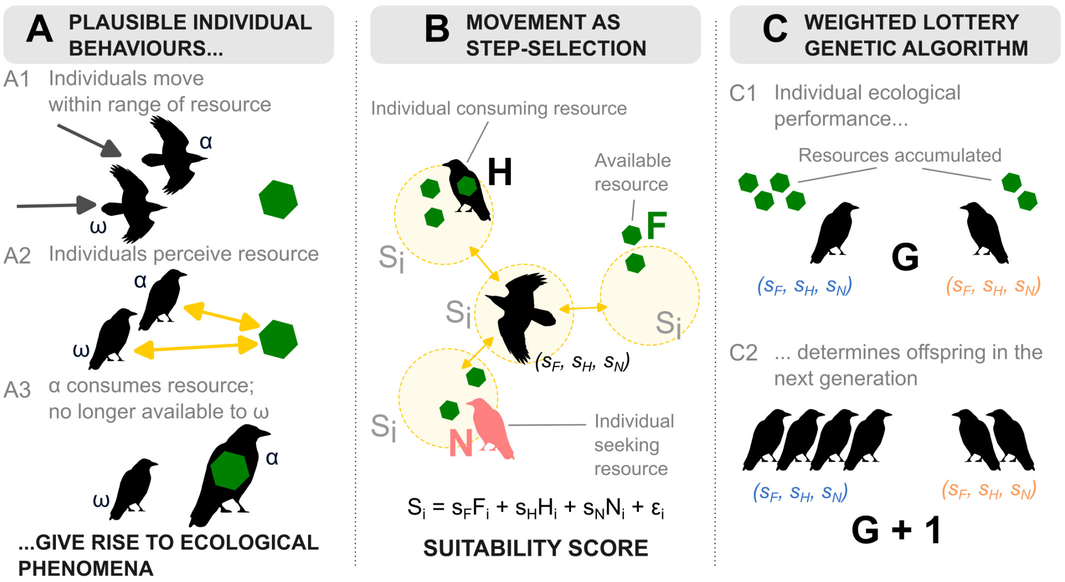

Figure 1.1: Key conceptual ingredients of a mechanistic, individual-centric model of the eco-evolutionary dynamics of animal movement strategies. **(A)** The model is individual-centric, and begins from first principles; model processes represent plausible, well supported animal behaviours, from which recognisable ecological phenomena may arise. Here, individuals' movement, perception, and consumption of resources leads to *exploitation competition*. **(B)** Animal movement is modelled as sequential step-selection. Individuals perceive local cues, and assign 'suitability scores' to potential destinations. Suitability at each location is calculated as the sum of the products of local cues (e.g. F, H, N) and the individual's cue preferences (e.g. s_F, s_H, s_N), with the optional addition of some small error in perception (ϵ). Individuals move to the location with the highest suitability, which may be their current location (thereby remaining stationary). Both the cue preferences and cue values, and thus the suitability scores, can take any positive or negative values. It is the value of the cue preferences *relative* to the other preferences, that determines the individual's *movement strategy*. **(C)** The model integrates both ecological and evolutionary timescales, by allowing the ecological outcomes of animal movement (here, resource intake), to have evolutionary consequences. In this example, the individual with more intake has more offspring. Individuals pass on their movement-determining cue preferences to offspring (with some rare mutations); thus individual movement strategies in one generation can determine the population-level mixture of movement strategies in the next generation, setting up a feedback loop between the ecology and evolution of animal movement. All individuals are conceptually represented by crows for convenience; crow silhouettes are copyright free images submitted to *PhyloPic*; see phylopic.org.

Mechanistic, Individual-Centric Simulations

The movement ecology paradigm recognises that animal movement is an individual-level process that integrates available external and internal cues into movement decisions (Holyoak et al. 2008; Nathan et al. 2008). Furthermore, the proliferation of animals' traits via reproduction — including cognitive traits such as movement strategies — is dependent on individuals' ecological performance, upon which natural selection acts (Hofbauer and Sigmund 1988). Consequently we advocate for simulation models that follow this individual-centric approach. Unsurprisingly, individual-based simulation models (IBMs) are ideal for this task, as they can include substantial ecological detail, including representing internal states, and interactions among hundreds of individuals and their environment (Huston et al. 1988; DeAngelis and Mooij 2005; DeAngelis 2018; DeAngelis and Diaz 2019).

While researchers may begin modelling with a phenomenon in mind, it is important to shift perspective to instead encode plausible, well supported individual-level processes (which we also call mechanisms) that could give rise to such phenomena. All ecological processes, including competition (Keddy 2001), signalling and signal perception (Torney et al. 2011), memory-based navigation (Bracis and Mueller 2017; Robira et al. 2021), and transmission processes (e.g. learning, pathogen transfer; see Cantor et al. 2021; Romano et al. 2021) have a strong spatial component. Thus models that study these phenomena should ideally also incorporate movement, and have an explicit spatial context.

For example, a model of exploitation competition would begin with the process that causes it: the depletion of discrete resource items due to individual foraging, which makes the resource unavailable to others (Keddy 2001: see Fig. 1.1A). This involves deliberately encoding a sequence of individual-level behaviours: movement that enables accessing a resource, perception of available resources, harvesting of the resource, and most importantly, removal of the resource from the landscape (see also Spiegel et al. 2017; Gupte et al. 2021; Gupte et al. 2022*a*). Here, the perspective shift lies in seeing that individual-level processes (movement, perception, foraging) could lead to the emergence of phenomena (exploitation competition), when local conditions are met (multiple individuals in the same vicinity going after the same discrete resource items).

Of course, any biological mechanism is an emergent outcome of constituent sub-mechanisms, down to the molecular level; some abstraction is therefore necessary. For simplicity, some ecological and evolutionary aspects will have to be set aside. This is not to say that issues such as sexual reproduction and non-random mating (included in Getz et al. 2016), detailed disease dynamics (seen in White et al. 2018*b*; Scherer et al. 2020), flexible population sizes (as in

Netz et al. 2021*b*), or animal memory (e.g. Bracis and Mueller 2017; Robira et al. 2021) are not important, but rather that researchers should focus on features of biological systems that are important to their study. Classical analytical models regularly make similar modelling choices to arrive at conceptual insight (see an examination in Van Der Meer and Ens 1997). Implementing these choices explicitly in simulation models' code helps bring these assumptions to the fore, promoting robust discussion of their importance to model conclusions.

Movement Strategies as Step-selection

We conceive of individual movement across the landscape to take the form of sequential step-selection (which we call 'movement decisions'; see Fig. 1.1B). Box A provides a primer to the idea of step-selection. In our models, when the individual moves, it chooses among a number of potential destinations in its neighbourhood, including its current location (in which case it remains stationary). Box B provides a brief overview of how step-selection has been used to encode movement in conceptual models. The step choice is made by assigning each potential step (including the current location) a step-selection score, which we call the 'suitability', such that every step i has a suitability $S = s_1X_{1i} + s_2X_{2i} + \ldots + s_NX_{Ni} + \epsilon_i$. Here, s_n where $n \in (1, 2, \ldots N)$ is the individual-specific weight or 'cue preference' for the cue n, and X_n is the value of the cue at the location i. We optionally include the small error term ϵ_i (typically drawn from a statistical distribution) to approximate individuals' error in assessing a location's suitability. The cue preferences, and thus the suitability, can have arbitrarily large or small (positive or negative) values. This is similar to step- and resource-selection coefficients β (see Box A Manly 2002; Fortin et al. 2005). Individuals are considered to move to the location with the highest suitability.

BOX A. STEP-SELECTION ANALYSIS: AN INTRODUCTION Step-selection analysis is a method developed from the study of empirical animal movement data, which seeks to determine the drivers of animal movement, with an early implementation in Fortin et al. (2005)'s study of the movement of deer in response to wolves, in Yellowstone National Park. In brief, step-selection analysis contrasts locations at which animals were observed, against locations that they could have used instead (Fortin et al. 2005). The locations that are considered to have been available to an animal are conditioned upon its current location — essentially, this avoids comparing used locations with distant regions that the animal could not have used at that time. In this sense step-selection analysis is essentially similar to conditional resource-selection analysis (see as general reference Manly et al. 2007). The difference is that in step-selection analysis, the available locations are sampled from a distribution (usually the Gamma distribution) fitted to the movement distances obtained from the tracking data, with relative headings ('turning angles'; see Calenge et al. 2009) drawn from a Von Mises distribution fitted to the animal's turning angles, again as seen in the tracking data (Thurfjell et al. 2014; Signer et al. 2019). The parameters determining the relative probability that a location is selected given its environmental attributes (the relative selection strengths, often denoted β) can be estimated via a maximum likelihood approach using common statistical software (see e.g. for R Therneau and Grambsch 2000). Overall, the step-selection method assumes that the probability that an animal will select a location is given by

$$\hat{w}(x) = \exp(\beta_1 x_1 + \beta_2 x_2 + \ldots \beta_n x_n)$$

where $\hat{w}(x)$ is the selection score for a step, β_i is the relative selection strength for (or against, if a negative value) the location attribute x_i.

Crucially, when individuals move by step-selection as in our models, the value of each cue preference s_n *relative* to the other cue preferences is more important than the absolute value of any cue preference by itself (see also the 'behavioural hypervolume' of Bastille-Rousseau and Wittemyer 2019). Thus individuals making movement decisions based upon three cues X_n for $n \in (1, 2, 3)$, that have relatively similar values of the corresponding cue preferences s_n may be thought of as weighing, or preferring each cue relatively equally (or indeed avoiding, if any $s_n < 0$). The relative values of each individual's cue preferences *taken together*, may be thought of as the individual *movement strategy*. Interlude B shows how these strategies can be visualised and interpreted when they are comprised of a small number of preferences.

In our models, we assume individuals have a constant instantaneous speed, which means that all steps have the same distance (see a similar implementation in Spiegel et al. 2017). This is different from step-selection analysis of empirical data, which draws steps from a movement kernel (Manly 2002; Fortin et al. 2005; Avgar et al. 2016). Drawing steps from a kernel (see e.g. 2018*b*) is *not* mechanistic, as the movement kernel idea derives from a phenomenological description of movements observed from animal tracking or relocation data (Fortin et al. 2005). Instead, our models allow movement kernels (and overall speeds, and ‘home ranges’) to emerge from individual movement decisions (yet see below for an alternative). Cues take the form of numeric values assigned to basic components of the individual’s local environment, such the number of food items or of conspecifics (both integer values), or some environmental property, such as temperature (which could be a decimal value). This allows individuals’ movement decisions to be interactions of intrinsic, heritable preferences, and different components of the environment. Spatio-temporal variation in cues can be externally forced (e.g. periodic fluctuations representing seasonality), but the much more interesting case is when such variation emerges from the movements and other behaviours of individuals.

There are two main mechanistic alternatives to our linear-function step-selection approach. First, suitability scores could be computed using more complex functions (e.g. quadratic functions to allow for avoidance thresholds; see White et al. 2018*b*) — but this could make movement strategies more challenging to understand. Second, the movement process could be based on separately generating a movement distance and relative heading (‘turning angle’; Calenge et al. 2009), rather than selecting from among steps (Mueller et al. 2011). In contrast with our approach where individuals have a fixed speed, the latter approach allows variable speeds. The drawback is that while movement distances are easily represented by linear functions, the turning angle is a circular measure that cannot be properly linearised. A complex function such as an artificial neural network (ANN) — standing in for an animal’s cognitive mechanisms — could generate both distances and valid turning angles, but the ANN parameters would be challenging to interpret as a movement strategy (Mueller et al. 2011; but see Bastille-Rousseau and Wittemyer 2019 for dimension reduction approaches). Nonetheless, this approach is the preferable mechanistic alternative to assuming a movement kernel, as it too allows phenomenological movement descriptors (e.g. home range, step-length distribution) to emerge from individual movement decisions.

Integrating Ecological and Evolutionary Timescales

The final feature of our model is the integration of ecological and evolutionary timescales. This can be done by adopting the mechanistic, individual-centric approach and modelling reproduction; this allows individuals to pass on heritable traits — including movement strategies — to their offspring. If individuals with

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BOX B. USING STEP-SELECTION IN CONCEPTUAL MODELS Step-selection analysis is now widely used in animal movement ecology, with specialised implementations for habitat-specific movement characteristics (Avgar et al. 2016), decision points identified from very high-resolution data (Munden et al. 2021); it can also be extended to estimate animals' utilisation distributions (Signer et al. 2017). Indeed, recall that step-selection analysis is used even in this thesis (Chapter 3). Despite its popularity and ease of implementation, step-selection has seldom been used in individual-based simulation models of animal movement. One good example of using a step selection approach is White et al. (2018*b*), who implemented a movement-disease model wherein individuals move across a grid, with their steps determined by their relative selection strengths (β_i) for cell attributes (x_i) such as resource levels or conspecific densities (in this sense they describe it as resource selection). In such models, individuals assign a selection score ($\hat{w}(x)$) to their current locations, and to neighbouring locations, and make the step with the highest score — this may mean staying in place! Furthermore, β_i values can be programmed to vary randomly or systematically in the population, to examine the effect of having individuals with a broad range of responses to similar cues (as White et al. 2018*b* do). In conceptual individual-based models such as mine, I refer to the selection score as 'suitability' $S = \Sigma\, s_i x_i$ where S, the suitability of the potential location, is simply the sum of the interaction of the individual's selection strengths (which I call a 'preference'; s_i) and the value of the corresponding cue at that location (x_i). In contrast with the step-selection approach, I assume that the individual moves in the direction of *maximal* suitability. Given that the 'cue preferences' are individual properties, they can be considered to be heritable between generations of a population, allowing the examination of evolutionary dynamics. This concept is examined further in the final scenario of my model, and models implementing this approach are described in Chapters 4 and 5.

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better ecological performance are considered to have more offspring, this would lead to the proliferation of their strategies. This would allow the mechanistic movement strategies to have evolutionary consequences, and in a scenario with discrete, non-overlapping generations, the ecological outcomes of individuals in one generation would determine the population-level mixture of behavioural strategies in the next generation. The same evolutionary dynamics could be applied to individual traits other than the cue preferences as well, to potentially examine the co-evolution of movement with behavioural or physiological traits (see e.g. Chapter 4). This approach, which we call the 'weighted lottery', derives from population genetics, and specifically from the replicator equation, which is fundamental to evolutionary biology (Hofbauer and Sigmund 1988). The replicator equation states that the expected frequency of a strategy in the next generation is proportional to its frequency in the present generation, times the average lifetime reproductive success of individuals using that strategy.

Here it is important to acknowledge that attempts to mimic biological evolution in individual-based models have previously been made, in the form of so-called 'genetic algorithms' (GAs: Hamblin 2013). Genetic algorithms have been applied to animal ecology, often coupled with individual-based models, but are relatively rare (see Beauchamp and Ruxton 2007; Hamblin et al. 2010; Hamblin 2013; Getz et al. 2015; 2016), possibly because their development and use is recognised as unsuitable for evolutionary biology. While GAs were conceptualised to find the best solutions to complex optimisation problems, many eco-evolutionary contexts have no single, stable solution; moreover, environmental heterogeneity may mean that multiple solutions are equally viable (Wolf and Weissing 2012). Furthermore, the GA conception of selection is often biologically unrealistic (e.g. truncation and tournament selection; Hamblin 2013). This is illustrated by Getz et al. (2015), which uses a specific form of truncation selection, called 'simulated annealing', wherein only the top 50% of individuals reproduce, and the frequency of variation (essentially, the rate of mutations) becomes smaller with each generation — neither of these are good representations of biological systems. Consequently, I do not believe that the GA approach is broadly suitable for models that seek to study relatively open-ended evolution (although some specific cases may be useful; see 'roulette wheel selection' in Hamblin 2013).

Versatility of Individual-Based Eco-evolutionary Models

I focus on three broad yet relatively distinct classes of scenarios that are amenable to investigation using our mechanistic, eco-evolutionary modelling approach. These are typically scenarios in which our current understanding of animal ecology suggests that multiple alternative or co-existing adaptive responses are possible. I stress that this is how such models should be considered: as tools that enable the broad exploration of hypothetical scenarios, some of which I lay out below. I caution against expecting eco-evolutionary dynamics known from analytical models; for instance, while steady-state eco-evolutionary equilibria may emerge in some models (e.g. Getz et al. 2015; 2016; Gupte et al. 2021; Gupte et al. 2022*a*), it is unrealistic to expect such dynamics from all models (see e.g. Netz et al. 2021*b*). Morever, an exploration of the parameter space, especially in terms of the environmental regime (e.g. environmental productivity, periodicity, or variation), could help generate broad predictive frameworks, with which empirical data could be compared. Finally, as an added feature, I suggest how eco-evolutionary IBMs can be used to investigate the performance of statistical methods commonly used in animal ecology.

Changes in the Environmental Regime

A key concern currently is knowing how the climate crisis is likely to affect animal spatial ecology, and I argue it is also important to know whether animal populations' evolutionary dynamics are likely to play a large role (e.g. Botero et al. 2015). For example, climate change is likely to induce greater variability in environmental conditions, thereby altering the spatial structure of resource landscapes (e.g. a transition from patchy to homogeneous resource landscapes). When resources are more homogenously distributed, direct resource cues (F in Fig. 1.1) are likely to be more widespread, potentially reducing the importance of social information (conspecific presence; H, N in Fig. 1.1), which could indicate a resource cluster. Yet with resources sparsely distributed, it may be important for animals to avoid conspecifics already at a resource cluster, to avoid exploitation competition — this would require social information to acquire a high (negative) weight for movement decisions. This scenario could be studied by building a model wherein the landscape spatial structure is altered after an initial (long) period of stability. Key questions that could be answered with such models are include whether a change in resource spatial structure — without a change in actual abundance — can lead to changes in movement strategies; whether movement strategies evolved to deal with changed spatial structure then also result in a non-ideal distributions of animals relative to resources (a test of Fretwell and Lucas 1970; Parker 1978); and whether different animal social structures could emerge (see Tanner and Jackson 2012; Webber et al. 2022).

Joint Evolution of Movement and Behavioural Strategies

Animal movement strategies alone are insufficient to explain individuals' ecological niches; individuals must combine these with other decisions, such as which resources to exploit (Pulliam 1974; Van Gils et al. 2015). In a scenario where there are two distinct types of prey, individuals could potentially prefer to use the locally more abundant prey (Emlen 1966; Pulliam 1974). Alternatively, individuals could specialise upon one of the two prey types; this could be on the prey type preferred by most other individuals (whereby social information on prey clustering could be useful; positive density dependence), or indeed upon the less preferred prey type, as this could reduce competition (negative density dependence). In this context, it is not clear how prey type preferences would evolve, but movement and foraging strategies could potentially be correlated, making it an ideal case for exploration with the class of models I advocate. This scenario could be explored with a model containing two overlapping prey type distributions, say A and B, and allowing individuals to sense and have a preference for these different prey types (s_A, s_B, instead of s_F in our Fig. 1.1). Simultaneously, it would be appropriate to consider prey choice to also be a flexible decision, and allow individuals to mechanistically choose, at each step, which prey type they want to target. Such a simulation could reveal the emergence of substantial individual variation in the preferences for the prey types, and potentially correlations with foraging movement strategies, forming a movement-behaviour syndrome (see e.g. Eckhardt 1979). More specific prey choice models could investigate how foraging individuals themselves may be a type of prey, through kleptoparasitism — this scenario is explored in Chapter 4. Models could also be extended to multiple trophic levels by including predators, in order to study the evolutionary arms-race of movement strategies between predators and prey (Netz et al. 2021*b*).

Introduction of New Eco-evolutionary Dynamics

The introduction to an environment of a novel biotic component could substantially alter existing eco-evolutionary dynamics; the introduction of a novel pathogen (or strain) to a population is a key example of current relevance (Carlson et al. 2022*a*; see also Monk et al. 2022 as a case study). Novel pathogen introductions should be expected to impose selection against animal sociality (e.g. Ashby and Farine 2022), but sociality emerges from an interaction of individual behaviour and the local environment, including the social environment (Tanner and Jackson 2012). To examine how a novel pathogen could affect the evolution of animal movement strategies, our modelling framework could be adapted into a movement-disease model following templates in White et al. (2018*a*). For instance, a pathogen could spread among spatially proximate individuals with some small probability p, and impose an energetic (and hence, fitness) cost δE. Such a model could reveal whether the novel pathogen introductions impose selective pressure against individual preferences for sociability as a proxy of transmission risk (Weinstein et al. 2018). Such a scenario, with special reference to social information use, is explored in Chapter 5. Recording and logging spatial associations and pathogen transmissions among simulation individuals could help provide useful expectations against which to compare transmission dynamics inferred from animal tracking data (Wilber et al. 2022; see Robitaille et al. 2019; Albery et al. 2021 for background).

Using Mechanistic Models to Probe Current Statistical Methods

Movement models are regularly used to simulate tracks with known features in order to examine and improve the performance of statistical tools (such as segmentation algorithms; see e.g. Gurarie et al. 2016; Michelot et al. 2016; Patin et al. 2020). One area which could benefit from a similar understanding of commonly used methods is the study of individual variation in movement; specifically, this could help determine whether studies are truly picking up ‘spatial personalities' from the confounding factors of environmental differences among tracked animals (Spiegel and Pinter-Wollman 2022; Stuber et al. 2022).

The class of mechanistic movement models I advocate could help explore whether current statistical tools can reliably detect individual differences in movement decision-making mechanisms. For instance, recording the movement paths of model agents, as well as their cue preferences and other traits (e.g. evolved prey-type preferences), and applying a repeatability approach, could help determine how the fitting of certain individual attributes as fixed effects could affect repeatability scores (*vs.* leaving them out). Similarly, recording the local cues available to individuals while making movement decisions would yield exactly the matched case-control data used in fitting step-selection functions (see Signer et al. 2019) Sub-sampling this data (to simulate low-resolution tracking), or using a static predictor such as landscape productivity (as is often used in empirical studies; e.g. NDVI: Pettorelli et al. 2011) could help demonstrate the benefits of using high-throughput tracking (Nathan et al. 2022), and the issues around using broad static predictors of landscape conditions. Overall, by treating a simulation model with simple movement strategies as one would empirical animal tracking data, one could explore the performance of popular statistical tools with data from known eco-evolutionary contexts — Chapter 6 explores this scenario.

Structure of this Thesis

In this Thesis, I take a broad approach to study both animal movement ecology, as well as presenting a framework for conceptual models to study the evolution of animal movement strategies. The thesis is divided into two parts, with five main chapter that are described here.

Modern movement ecology has become a 'big data' field (Nathan et al. 2022). In Part I I focus on studying animal movement ecology using tracking data and correlative statistical models, but from a strongly mechanistic perspective. In Chapter 2, I synthesise methods that can help overcome current limitations and issues in modern high-throughput tracking data. I present conceptual workflows to prepare high-throughput animal tracking data for further analysis, and may be seen as a more detailed explanation of the principles I contributed to Nathan et al. (2022). In brief, modern, high-throughput animal tracking increasingly yields 'big data' at very fine temporal scales, and 'cleaning' the data to reduce location errors is one of the main ways to deal with position uncertainty. Though data cleaning is widely recommended, robust guidance on how to organise the cleaning of massive datasets is relatively scarce. A pipeline for cleaning massive high-throughput datasets must balance ease of use and computationally efficiency, in which location errors are rejected while preserving valid animal movements. Another useful feature of a pre-processing pipeline is efficiently segmenting and clustering location data for statistical methods, while also being scalable to large datasets and robust to imperfect sampling. One major advantage when studying a particular species is that certain aspects of its biology are known — for example, the maximum speed it could realistically achieve. These physical constraints can be taken into account to filter data, and identify behavioural bouts in ways that are easy to interpret (Barraquand and Benhamou 2008). I show how taking this mechanistic view to filtering animal positioning data can be used with any high-throughput animal movement data in which the high data-volume combined with knowledge of the tracked individuals' biology can be used to reduce location errors.

In Chapter 3, I leverage the methods for improving and working with high-throughput tracking data that I developed in Chapter 2. I take an explicitly mechanistic view to studying the drivers of movement and habitat selection in a unique group of animals: moulting birds. The flight surfaces of bird wings require regular renewal through a process called moult — shedding worn out feathers and growing fresh ones — presenting birds with the dilemma of needing more resources for feather growth just when their flight capacity is reduced, making them more vulnerable to predation. I combine animal tracking and experimental approaches to present a first quantification of the direct effects of wing moult (in terms of reduced flight efficiency) on the movement and use of sheltered habitats, in four non-migratory passerine species. Rather than using a broad predictor such as vegetation productivity as a proxy for shelter (Pettorelli et al. 2011), I instead take a viewshed ecology approach (Aben et al. 2018), and directly quantified which areas of the landscape were visibile to potential predators (the 'fearscape': Olsoy et al. 2015). I use the methods, including the residence patch algorithm, developed in Chapter 2, to measure how non-moulting, naturally moulting, and artificially manipulated birds use sheltered areas. I apply both simple statistical models as well as step-selection analyses to analyse birds' habitat selection (Fortin et al. 2005; Avgar et al. 2016). Later, in Part II, I use the models described there to examine what we can learn about step-selection analysis, by using it to recover the mechanisms of simulation models (a better explanation of the links between the two is presented in Chapters 4).

In Part II, I demonstrate how conceptual insights can be obtained from mechanistic models of intermediate complexity that integrate both the ecological dynamics of animal movement, and their evolutionary causes and consequences. The key feature of such models is to let individual-level ecological outcomes in one generation influence which movement strategies are present in future generations, thus establishing a feedback loop between animals' evolutionary history and their current spatial ecology. Specifically, I advocate that movement be modelled as an individual response to local cues rather than a random walk or some ruleset shared by all individuals (see Mueller et al. 2011). I have taken this mechanistic in Chapters 4 and 5. In the models presented in those chapters, I used individual-based models, in which individuals have evolved *movement preferences* — these are explained below — and thus make quite different decisions when presented with similar cues (Getz et al. 2015; White et al. 2018*b*). Yet an open question when including such behavioural variation is whether the emergent outcomes may be transient phenomena that are quite different from the dynamics obtained on evolutionary timescales. Consequently, I additionally advocate for movement models to be embedded in an evolutionary context, with individuals' movement outcomes subject to selection, and their movement preferences subject to random change (mutation). I expand on this view further in this Introduction, and describe the three chapters comprising this Part in brief below.

In Chapter 4, I examine the joint evolution of movement and two different foraging strategies: searching for food items, and kleptoparasitism, an extreme form of interference competition. Although competition has an explicit spatial context, eco-evolutionary models rarely consider how competition strategies, including kleptoparasitism, might evolve alongside evolving movement strategies. I model movement strategies as heritable, individual-specific combinations of preferences for environmental cues, similar to step-selection coefficients (Manly 2002; Fortin et al. 2005). Step-selection coefficients have been used previously to cluster individuals with different preferences for local cues into discrete strategies (Bastille-Rousseau and Wittemyer 2019). I study the evolutionary dynamics of competition and movement strategies using individual-based simulations. I additionally, investigate the implications of this joint evolution for the distribution of consumers over the model landscape. Overall, this chapter lays the groundwork for a mechanistic approach to studying competition — and other behaviours — in a spatial context, and suggests how evolutionary modelling can be integrated with current work in animal movement ecology.

In Chapter 5, I aim to investigate a scenario that pre-occupied me over the course of the pandemic: the evolutionary consequences of the introduction of novel pathogens for animal social interactions, which are of course, outcomes of animal movement. Using a simulation model developed from the work I presented in Chapter 4, I examine how animals balance the risk of pathogen transmission against the benefits of public information about the location of ephemeral resource patches. Studying a scenario in which a fitness-reducing infectious pathogen is introduced into a population which has initially evolved movement strategies in its absence, I show how pathogen introduction changes host movement strategies, and how this determines the emergent structure of socio-spatial networks. The use of the deterministic step-selection framework borrowed from Chapter 4, which can be directly related to step-selection analyses conducted on empirical animal tracking data (Bastille-Rousseau and Wittemyer 2019), makes this a powerful modelling framework, with initial predictions for the evolutionary and ecological consequences of wildlife pathogen spillover scenarios.

In Chapter 6, I apply two popular statistical methods, repeatability analysis, and step-selection analysis, to the movement paths generated by agents from Chapter 4. Having encoded these agents to move using simplified step-selection, here, I examine what current statistical methods in movement ecology can tell us about individual variation in a population where the axes of variation are already fully known. I show how it is challenging, to recover the true causes of variation in animals' movement strategies from their actual movement paths (a major line of work in movement ecology). I demonstrate that statistical methods can yield quite different conclusions when applied to data in which underlying movement strategies are not accounted for, and therefore caution practitioners analysing empirical data to be careful with potential sources of behavioural variation.

Finally, in Chapter 7, I reflect upon the findings of this thesis, and upon potential future work.

* * *

Part I

A MECHANISTIC PERSPECTIVE ON ANIMAL MOVEMENT ECOLOGY

The central challenge of the study of animal movement is knowing where animals actually are, with a high degree of spatial and temporal accuracy. Harnessing the massive datasets generated by modern tracking systems for robust ecological inferences requires computational methods that are informed by the biology of the systems to which they are applied. Additionally, taking a mechanistic view can reveal the world as animals see it.

In the first part of this thesis, I demonstrate how to deal with large spatial datasets to investigate the direct drivers of animal movement.

* * *

Chapter 2

Pre-processing High Throughput Animal Tracking Data

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Spatial is special.

– A common maxim in data science.

Abstract

Modern, high-throughput animal tracking increasingly yields ‘big data’ at very fine temporal scales, and ‘cleaning’ the data to reduce location errors is one of the main ways to deal with position uncertainty. Though data cleaning is widely recommended, inclusive, uniform guidance on this crucial step, and on how to organise the cleaning of massive datasets, is relatively scarce. A pipeline for cleaning massive high-throughput datasets must balance ease of use and computationally efficiency, in which location errors are rejected while preserving valid animal movements. Manual methods being prohibitively time consuming, and to boost reproducibility, pre-processing pipelines must be automated. We provide guidance on building pipelines for pre-processing high-throughput animal tracking data to prepare it for subsequent analyses. We apply our proposed pipeline to simulated movement data with location errors, and also show how large volumes of cleaned data can be transformed into biologically meaningful ‘residence patches’, for exploratory inference on animal space use. We use tracking data from the Wadden Sea ATLAS system (WATLAS) to show how pre-processing improves its quality, and to verify the usefulness of the residence patch method. Finally, with tracks from Egyptian fruit bats *Rousettus aegyptiacus*, we demonstrate the pre-processing pipeline and residence patch method in a fully worked out example. To help with fast implementation of standardised methods, we developed the R package *atlastools*, which we also introduce here. Our pre-processing pipeline and *atlastools* can be used with any high-throughput animal movement data in which the high data-volume combined with knowledge of the tracked individuals’ movement capacity can be used to reduce location errors.

Introduction

Animal movement is an adaptive, integrated response to multiple drivers, including internal state, life-history traits and capacities, biotic interactions, and other environmental factors (Holyoak et al. 2008; Nathan et al. 2008). The movement ecology framework links the drivers, processes, and fitness outcomes of animal movement (Nathan et al. 2008), and remotely tracking individual animals in the wild is the methodological mainstay of movement ecology (Wikelski et al. 2007; Nathan et al. 2008; Hussey et al. 2015; Kays et al. 2015). A key challenge with observed tracks is to extract information on the behavioural, cognitive, social, ecological and evolutionary processes that shape animal movement. Addressing this challenge requires investigating the relationships between movement and its drivers at the fine scales at which animals sense and respond to variation in their environment. Tracking data, which are observations of a continuous process (animal movement) at discrete timesteps, reveal useful information about the movement process when the tracking interval is considerably shorter than the typical duration of a movement mode (Getz and Saltz 2008; Nathan et al. 2008; Noonan et al. 2019). This can be accomplished by wildlife tracking systems that collect position data from many individuals at high temporal and spatial resolution (i.e., high-throughput tracking) relative to the scale of the movement mode of interest (Getz and Saltz 2008).

High-throughput tracking technologies include GPS tags (Strandburg-Peshkin et al. 2015; Harel et al. 2016; Papageorgiou et al. 2019; Klarevas-Irby et al. 2021), tracking radars (Horvitz et al. 2014), and computer vision methods for tracking entire groups of animals from video recordings (Pérez-Escudero et al. 2014; Rathore et al. 2020). Furthermore, high-throughput wildlife tracking is routinely provided by terrestrial reverse-GPS systems such as ATLAS (Advanced Tracking and Localization of Animals in real-life Systems: Toledo et al. 2014; 2016; Weiser et al. 2016; Toledo et al. 2020) — see also (MacCurdy et al. 2009; MacCurdy et al. 2019) — and underwater acoustic reverse-GPS tracking of aquatic animals (Jung et al. 2015; Baktoft et al. 2017; 2019; Aspillaga et al. 2021*a*,*b*). Finally, low resolution tracking over a long duration may also capture important aspects of animal behaviour at certain time-scales (e.g. migration, long-range dispersal; Getz and Saltz 2008), thereby being ‘relatively’ high-throughput.

Although high-throughput tracking provides a massive amount of data on the path of a tracked animal, these data present a challenge to ecologists. When tracking animals at a high temporal resolution, the location error of each position may approach or exceed the true movement distance of the animal, compared to low-resolution tracking with the same measurement error. This leads to an over-estimation of the true distance moved by an animal between two discrete time-points, leading to unreliable behavioural metrics ultimately derived from movement distance, such as speed and tortuosity (see Calenge et al. 2009; Hurford 2009; Ranacher et al. 2016; Noonan et al. 2019). Additionally, the location error around a position introduces uncertainty when studying the relationship between animal movements and either fixed landscape features (e.g. roads), or mobile elements (e.g. other tracked individuals), as well as confounding estimates of habitat selection.

Users have two main options to improve data quality, *(i)* making inferences after modelling the system-specific location error using a continuous time movement model (Jonsen et al. 2003; 2005; Johnson et al. 2008; Patterson et al. 2008; Fleming et al. 2014; Fleming et al. 2020; Aspillaga et al. 2021*b*), or *(ii)* pre-processing data to clean it of positions with large location errors (Bjørneraas et al. 2010). The first approach may be limited by the animal movement models that can be fitted to the data (Fleming et al. 2014; Noonan et al. 2019; Fleming et al. 2020), may result in unreasonable computation times, or may be entirely beyond the computational capacity of common hardware, leading users to prefer data cleaning instead. Data cleaning reveals another challenge of high-throughput tracking: the large number of observations make it difficult for researchers to visually examine each animal's track for errors (Weiser et al. 2016; Toledo et al. 2020). With manual identification and removal of errors from individual tracks prohibitively time consuming, data cleaning can benefit from automation based on a protocol.

Pre-processing of movement data — defined as the set of data management steps executed prior to data analysis — must reliably discard large location errors, also called outliers, from tracks (analogous to reducing false positives) while avoiding the overzealous rejection of valid animal movements (analogous to reducing false negatives). How well researchers balance these imperatives has consequences for downstream analyses (Stine and Hunsaker 2001). For instance, small-scale resource selection functions can easily infer spurious preference and avoidance effects when there is uncertainty about an animal's true position (Visscher 2006). Ecologists recognise that tracking data are imperfect observations of the underlying movement process, yet they implicitly consider cleaned data equivalent to the ground-truth. This assumption is reflected in popular statistical methods in movement ecology such as Hidden Markov Models (HMMs) (Langrock et al. 2012), stationary-phase identification methods (Patin et al. 2020), or step-selection functions (SSFs) (Barnett and Moorcroft 2008; Avgar et al. 2016; Signer et al. 2017), which expect minimal location errors relative to real animal movement (i.e., a high signal-to-noise ratio). This makes the reproducible, standardised removal of location errors crucial to any animal tracking study. While gross errors are often removed by positioning-system algorithms in both GPS and reverse-GPS setups, 'reasonable' errors often remain to confront end users

(Fischler and Bolles 1981; Ranacher et al. 2016; Weiser et al. 2016). Further, as high-throughput tracking is deployed in more regions and for more species, standardised pre-processing steps should be general enough to tackle animal movement data recovered from a range of environments, so as to enable sound comparisons across species and ecosystems.

Despite the importance and ubiquity of reducing location errors in tracking data, movement ecologists lack formal guidance on this crucial step. Pre-processing protocols are not often reported in the literature, or may not be easily tractable for mainstream computing hardware and software. Some tracking data, such as GPS, are autonomously pre-processed without user access to the raw data (using error estimates and Kalman smooths; Kaplan and Hegarty 2005: and substantial location errors may yet persist). However, filtering out positions using estimates of location error alone may not be sufficient to exclude outliers which represent unrealistic movement but have low error measures (Ranacher et al. 2016; Weiser et al. 2016). When tracking systems do make their raw data available to researchers, this can enable users to better control the data pre-processing stage, and to substantially improve data quality while ensuring that cleaning does not itself lead to unrealistic movement tracks (e.g. Kalman smooths which distort tracks, Kaplan and Hegarty 2005). This makes identifying and removing biologically implausible locations from a track an important component of recovering true animal movement (Bjørneraas et al. 2010).

Even after removing unrealistic movement, a track may be comprised of positions that are randomly distributed around the true animal location (Noonan et al. 2019). The large data-volumes of high-throughput tracking allow for a neat solution: tracks can be 'median smoothed' to reduce small location errors that have remained undetected (e.g. Bijleveld et al. 2016). Large data volumes may also need to be thinned, for example, examining environmental covariates as predictors of prolonged residence in an area (see e.g. Aarts et al. 2008; Bijleveld et al. 2016; Harel et al. 2016; Bracis et al. 2018; Oudman et al. 2018) might require thinning of high-resolution movement data to match the lower spatial resolution of environmental measurements. Data thinning and clustering are also required to avoid non-independent observations due to strong spatio-temporal autocorrelation, or to examine the effect of sampling scale on movement metrics and resource-selection (Fleming et al. 2014; Noonan et al. 2019).

When dealing with datasets that contain many millions of positions, reseachers may run into computational limits when trying to apply pre-processing steps to their full dataset. For instance, the size of working memory (RAM) limits the size of datasets that can be loaded into *R*, the programming and statistical language of choice in movement ecology (Joo et al. 2020*a*,*b*; R Core Team 2020). Data-rich fields such as genomics inspire a possible solution: to break very large data into smaller subsets, and pass these subsets through automated computational 'pipelines' (Schadt et al. 2010; Peng 2011). Pre-processing pipelines for animal tracking data — the set of steps that users apply to prepare the data for a specific analysis — come with some additional concerns: *(i)* identifying which pre-processing steps are necessary, and *(ii)* ensuring that these steps reproducibly operate on the data as expected, and as efficiently as possible.

While exploratory data analysis and visualisation can help determine how to pre-process the data to maximise the signal to noise ratio (Slingsby and Van Loon 2016), standardising implementations of pre-processing techniques into robust, version controlled software packages (Wickham 2015: e.g. in *R*, see), can increase the reliability and reproducibility of animal movement ecology (Haddaway and Verhoeven 2015; Lewis et al. 2018; Powers and Hampton 2019; Archmiller et al. 2020). Overcoming hard computational constraints on speed and memory usage for very large data will often require a combination of programming strategies, such as using tools optimised for tabular data, or parallelised processing.

Here, we present guidelines for reproducibly pre-processing high-throughput animal tracking data (Fig. 2.1), with a focus on simple, widely generalisable steps that help improve data quality (Fig. 2.2). We take two important considerations into account, that *(i)* the pre-processing steps should be easily understood and reproduced, and *(ii)* our implementations must be computationally efficient and reliable. Consequently, formalising tools as functions in an *R* package would improve portability and reproducibility (Wickham 2015; Marwick et al. 2018). Using simulated movement tracks, we demonstrate simple yet robust implementations of the pre-processing steps we recommend, conveniently wrapped into the *R* package *atlastools* (Gupte 2020), with a discussion of features that make these steps more reproducible, and more efficient. We also suggest one potential application of high-throughput tracking in studies of animal movement and space use, illustrated by the first-principles based synthesis of 'residence patches' from clusters of spatio-temporally proximate positions (*sensu* Barraquand and Benhamou 2008; Bijleveld et al. 2016; Oudman et al. 2018).

In two fully worked out examples using our package on real tracking data, we show how to apply basic spatio-temporal and data quality filters, how to filter out unrealistic movement, and how to reduce the effect of location error with a median smooth. In the first example, using calibration data from an ATLAS system, we show how the residence patch segmentation-clustering method can be used to accurately identify areas of prolonged residence under real field conditions. Finally, in our second example, we use ATLAS data from Egyptian fruit bats (*Rousettus aegyptiacus*) tracked in the Hula Valley, Israel, to show a fully worked out example of the pre-processing pipeline and the residence patch method. While our approach to high-throughput tracking data, and our package of pre-processing functions was developed with reverse-GPS ATLAS systems in mind, both are broadly suitable to a wide range of high-throughput animal tracking data sources, from underwater acoustic reverse-GPS (Jung et al. 2015; Baktoft et al. 2017; 2019; Aspillaga et al. 2021*a*,*b*), high-resolution GPS (Strandburg-Peshkin et al. 2015; Harel et al. 2016; Papageorgiou et al. 2019; Klarevas-Irby et al. 2021), tracking radars (Horvitz et al. 2014), and visual video tracking (Pérez-Escudero et al. 2014; Rathore et al. 2020).

Best-Practices for Pre-Processing Workflows

Exploratory data analysis should be the first step towards pre-processing movement data (see Fig. 2.1; Slingsby and Van Loon 2016). Researchers with very large datasets of perhaps millions of rows should ideally select a representative subset of these data for exploratory data analysis, including individuals of different species, sexes, or seasonal cohorts. Examples of exploratory data analysis include plotting heatmaps of the number of observations per unit area across the study site (Fig. 2.1). Histograms of the location error estimates, plotting the linear approximations of animal paths between observations, and histograms of the sampling interval can help determine how data need to be treated so as to minimise location errors and improve computational tractability (Fig. 2.1). While pre-processing steps required for datasets will differ between studies and tracking technologies, we elaborate upon candidate steps and their parameterisation in following sections (see also Fig. 2.2).

Following exploratory data analysis and the parameterisation of data cleaning steps, the specific implementation of these steps should be made reliable and reproducible. Since reproducing pre-processing steps can be challenging when using only written descriptions from published articles, providing the code to implement pre-processing steps reduces ambiguity and increases reproducibility (Haddaway and Verhoeven 2015). For technically advanced users, the best-practices here are *(i)* to implement pre-processing steps as 'functions', *(ii)* to collect related functions — e.g. for similar kinds of data — into a software 'package', *(iii)* to 'test' that the functions handle input as expected, and *(iv)* implement 'version control' throughout, such that the process of development is documented (Fig. 2.1; Wickham 2015; Perez-Riverol et al. 2016; Alston and Rick 2020).

As an example, our *atlastools* package incorporates these best-practices, and may be used as a reference (Gupte 2020). We have written each pre-processing step as a separate function, and each of these functions is tested, usually on simulated data, but in some cases also on empirical data (Wickham 2015: see the directory *tests/* in the associated Zenodo repository). Finally, logging error messages is crucial when passing data through a pipeline, helping determine

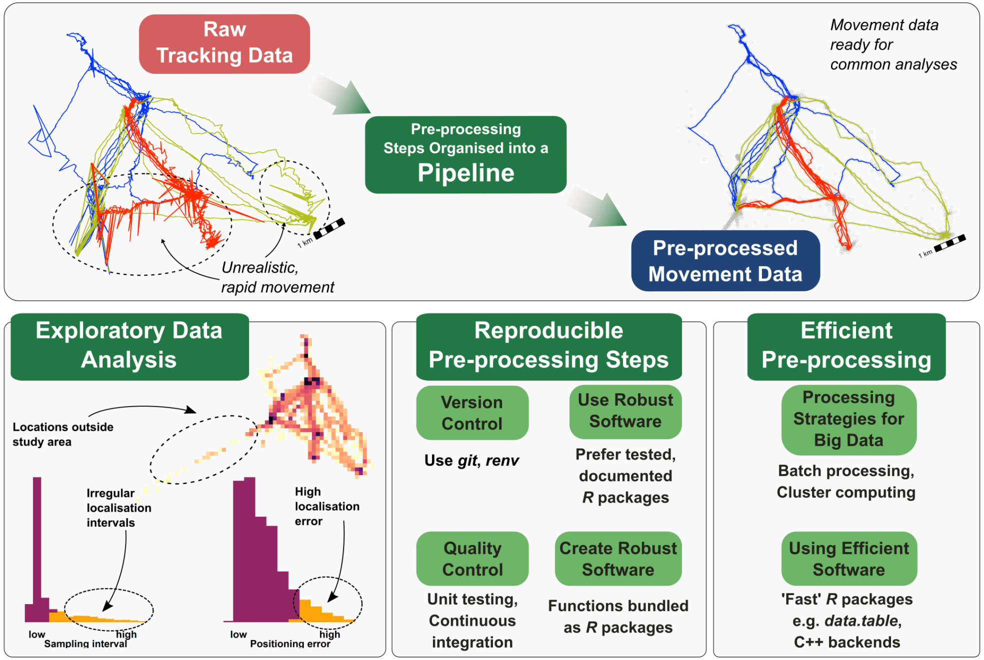

Figure 2.1: Some best-practices for pre-processing high-throughput tracking data. Simple pre-processing of animal tracking data can improve the quality of animal tracking data, and the inferences that are drawn from it. Exploratory data analysis of representative subsets of the data can help to identify common issues with data quality, and to determine which pre-processing, steps such as filters and smooths, might be necessary (*see also Fig. 2.2*). Pre-processing steps implemented as programming code can be made reproducible and shareable by following best-practices for software development: (i) tracking changes to the steps, and the software used, using version control (e.g. *git*, *renv*), (ii) preferring pre-existing tools, such as *R* packages, which are well documented and tested, (iii) encapsulating custom-written code as functions, and bundling related functions into a package, and (iv) checking the quality of both custom-written code (e.g. by testing functions), and the overall pipeline (e.g. data visualisation). The efficiency of pre-processing steps can be increased by using strategies for dealing with large datasets, such as batch processing, or using a computing cluster. The use of existing tools optimised for large datasets, or by writing code in a 'fast' language such as *C++*, can also speed up the pre-processing of large datasets (see main text for examples).

which data subsets could not be handled as expected, and why. Users who would prefer to rely on pre-existing toolsets and methods can use *R* packages that follow these best-practices, such as *move* (Kranstauber et al. 2011), and *sftrack* (Boone et al. 2020). The large size of modern, high-throughput animal tracking data means that the computational challenge can often be *the* main challenge in working with these data. For beginning users, organising their workflows so that they process subsets of the data (such as one individual) at a time can help overcome limitations on working memory. Animal tracking data stored in a relational database (e.g. SQL databases Codd 1970), for example, can be broken into meaningful subsets based on individual identity and tracking season. These smaller subsets can then be loaded into working memory, pre-processed, and saved in a separate location (see Supplementary Material 1, Section 2 for a worked out example on an SQL database). Using existing tools optimised for tabular data, such as the *R* package *data.table* (Dowle and Srinivasan 2020), can also speed up computation; *atlastools* is built using *data.table* for this reason.

More advanced users seeking substantial speed gains might wish to look into parallel-processing, and process each subset of the data independently of the full dataset, for example by using a computing cluster (see also Dai 2021: for an alternative). Finally, another advanced method, used by popular packages such as *move* (Kranstauber et al. 2011) and *recurse* (Bracis et al. 2018), is to write one's own methods in a 'fast' low-level language, such as *C++*, and link these to *R* (Eddelbuettel 2013); see also *adehabitatLT*, which is written partially in *C* (Calenge 2006). Beginning practitioners can organise their workflows around these packages to benefit from the features they incorporate.

Pre-processing Steps, Usage, and Simulating Data

An Overview of Pre-processing Steps and `atlastools'

In the sections that follow, we lay out pre-processing techniques for raw high-throughput tracking data, and demonstrate working examples of these techniques, which we have collected in the *R* package *atlastools* (see Fig. 2.2). Our package is aimed at getting 'raw data' to the 'analysis' stage identified by Joo et al. (2020) in their review of *R* packages in movement ecology. The package is based on *data.table*, a fast implementation of data frames; thus it is compatible with a number of data structures from popular packages including *move*, *sftrack*, and *ltraj* objects, which can be converted to data frames (Calenge et al. 2009; Kranstauber et al. 2011; Boone et al. 2020). Our package functions are suitable for use with both regularly sampled data, as well as data with missing observations.

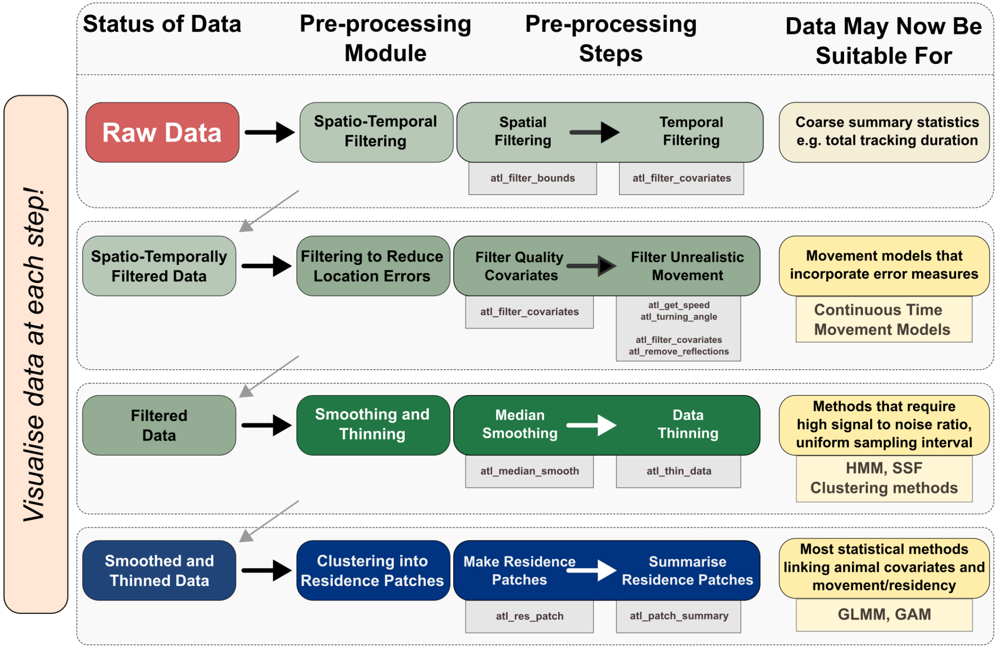

Figure 2.2: An example of a modular pipeline for pre-processing high-throughput tracking data from raw localisations to cleaned data, and optionally into residence patches. Users should apply the appropriate pre-processing modules and the steps therein until the data are suitable for their intended analysis, some of which are suggested here. The *atlastools* function that may be used to implement each pre-processing step is shown in the grey boxes underneath each step. Popular statistical methods are shown underneath possible analyses (yellow boxes). Users are strongly encouraged to visualise their data and scan it for location errors as they work through the pipeline, always asking the question, could the animal plausibly move this way?

We cover, first, the use of simple ***Spatio-Temporal Filters*** to select positions within a certain time or area. Next, we show how users can ***Reduce Location Errors*** by removing unreliable positions based on a system-specific error measure, or by the plausibility of associated movement metrics, such as speed and turning-angle (Calenge et al. 2009; Seidel et al. 2018). We then show how users can tackle small-scale location errors by applying a ***Median Smooth***, and users who need uniformly sampled data, can undertake ***Data Thinning*** by either aggregation or subsampling. At this stage, the data are ready for a number of popular statistical treatments such as Hidden Markov Model-based classification (Langrock et al. 2012; Michelot et al. 2016). Finally, we show how users wishing simple, efficient segmentation-clustering of points where the animal showed prolonged residence, can classify their data into 'residence patches' (Barraquand and Benhamou 2008; Bijleveld et al. 2016) based on the movement ecology of their study species, after filtering out travelling segments (see ***System-Specific Pre-Processing Tools***).

These pre-processing techniques and package were designed with ATLAS systems in mind, motivated to meet the rapid growth of studies using this high-throughput system worldwide: in Israel (Toledo et al. 2014; 2016; Corl et al. 2020; Toledo et al. 2020; Vilk et al. 2021), the UK (Beardsworth et al. 2021*a*,*b*), and the Netherlands (Bijleveld et al. 2021; Beardsworth et al. In press). However, the principles and functions presented here are ready for use with other massive high-resolution data collected by GPS (e.g. Papageorgiou et al. 2019), reverse-GPS (e.g. Aspillaga et al. 2021*b*) or any other high-throughput tracking system . Users may construct a pre-processing pipeline comprising of all the techniques we cover, or implement the modules most suitable for their data. Users are advised to visualise their data throughout their workflow, and especially to perform thorough exploratory data analysis, to check for evident location errors or other issues (Slingsby and Van Loon 2016).

Simulating Data to Demonstrate Pre-Processing Steps

To demonstrate pre-processing steps, we simulated a realistic movement track of 5,000 positions using an unbiased correlated velocity model (UCVM) implemented via the *R* package *smoove* (Gurarie et al. 2017: see Fig. 2.3.a). We added four kinds of error to the simulated track: (i) normally distributed small-scale offsets to the X and Y coordinates (small-scale error), (ii) normally distributed large-scale offsets to a random subset (0.5 %) of the positions (spikes), (iii) large-scale displacement of a continuous sequence of 300 of the 5,000 positions (prolonged spikes; indices 500 – 800), and (iv) we removed 10% of the canonical track to simulate missing data (see Fig. 2.3.a). To demonstrate the residence patch method, we obtained data, in the form of 1,000 positions, from a mechanistic, individual-based simulation model, in which agents move using simple decision making rules, and can find high-productivity patches using only ephemeral cues, such as the density of prey-items and other competitors (Gupte et al. 2021; Netz and Gupte 2022). The emergent, complex track structure is analogous to the foraging movements of animals, and provides a suitable challenge for the residence patch method and helps to demonstrate its generality.

Spatio-Temporal Filtering

Spatial Filtering Using Bounding Boxes and Polygons

First, users should exclude positions outside the spatial bounds of a study area by comparing position coordinates with the range of acceptable coordinates (the bounding box), and removing positions outside them (Fig. 2.3.a). A bounding box filter does not require a geospatial representation such as a shapefile, and can help remove unreliable data from a tracking system that is less accurate beyond a certain range (Beardsworth et al. In press). In some special cases, users may wish to remove positions *inside* a bounding box, either because movement behaviour within an area is not the focus of a study, or because positions recorded within an area are known to be erroneous. An example of the former is studies of transit behaviour between features which can be approximated by their bounding boxes. Instances of the latter are likely to be system specific, but are known from ATLAS systems. Bounding boxes are typically rectangular, and users seeking to filter for other geometries, such as a circular or irregularly-shaped study area, need a geometric intersection between their data and a spatial representation of the area of interest (e.g. shapefile, geopackage, or *sf*-object in *R*). The *atlastools* function *atl_filter_bounds* implements both bounding box and explicit spatial filters, and accepts X and Y coordinate ranges, an *sf*-polygon or multi-polygon object (Pebesma 2018), or any combination of the three to filter the data. When both coordinate ranges and a polygon are provided, the data is first filtered by the ranges and then the polygon. The boolean function argument *remove_inside* determines whether positions inside the bounds are retained (*FALSE*) or removed (*TRUE*).

Temporal and Spatio-temporal Filters

Tracking data might fail to properly represent an animal's movement at certain times, for instance, data recorded before release, or data from shortly after release when the animal is still influenced by the stress of capture and handling. Periods of poor tracking quality may result from system malfunctions and unusual disturbances, and users may wish to exclude these data as well. Temporal

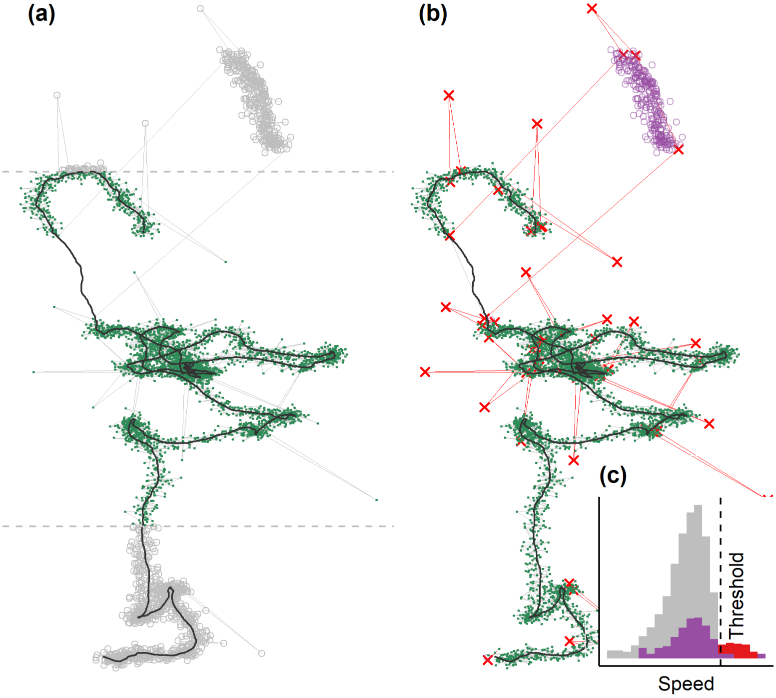

Figure 2.3: Simulated movement data showing four kinds of artificially added errors. (i) Normally distributed small-scale error on each position, (ii) large-scale error added to 0.5% of positions, (iii) 10% of positions removed to simulate missing data, and (iv) 300 consecutive positions displaced to simulate a gross distortion affecting a continuous subset of the track. **(a)** Tracks can be quickly filtered by spatial bounds (dashed grey lines) to exclude broad regions (green = retained; grey = removed). **(b)** location error may affect single observations resulting in point outliers or 'spikes' (red crosses and track segments), or continuous subsets of a track, called a 'prolonged spike' (purple circles, top right), and both represent unrealistic movement. **(c)** Histograms of speed for the track (grey = small-scale errors, red = spikes), and the prolonged spike (purple) show that while spikes could be removed by filtering out positions with both high incoming and outgoing speeds and turning angles, prolonged spikes cannot be removed in this way, and should be resolved by conceptualising algorithms that find the bounds of the distortion instead. Users should frequently check the outputs of such algorithms to avoid rejecting valid data.

filtering can exclude positions from intervals when data are expected to be unreliable for ecological inference, either due to abnormal movement behaviour or system-specific issues. Temporal filters can be combined with spatial filters to select specific time-location combinations. For example, studies of foraging behaviour of a nocturnal animal would typically exclude tracking data from the animal's daytime roosts (see *Worked Out Example*). Users should apply filters in sequence rather than all at once, and visualise the output after each filtering step ('sanity checks'; see Supplementary Material Section 2). The atlastools function *atl_filter_covariates* allows convenient filtering of a dataset by any number of logical statements, including querying data within a spatio-temporal range. The function keeps only those data which satisfy each of the filter conditions, and users must ensure that the filtering variables exist in their dataset in order to avoid errors.

Filtering to Reduce Location Errors

Filtering on Data Quality Attributes

Tracking data attributes can be good indicators of the reliability of positions calculated by a tracking system (Beardsworth et al. In press). GPS systems provide direct measures of location error during localisation (Ranacher et al. 2016: Horizontal Dilution of Precision, HDOP in GPS), while in reverse-GPS systems, a measure referred to as Standard Deviation (SD in many datasets), can be calculated from the variance-covariance matrix of each position as: $\mathrm{SD} = \sqrt{\mathrm{Var\ X} + \mathrm{Var\ Y} + \mathrm{Cov\ XY}}$ (see details in MacCurdy et al. 2009; Ranacher et al. 2016; Weiser et al. 2016; MacCurdy et al. 2019). Tracking data can also include indirect indicators of data quality. For instance, GPS systems' location error may be indicated indirectly by the number of satellites involved in the localisation. In reverse-GPS systems too, the number of base stations involved in each localisation is an indirect indicator of data quality, and positions localised using more receivers are usually more reliable (the minimum required for an ATLAS localisation is 3; see Weiser et al. 2016; Beardsworth et al. In press). A location error measure associated with each coordinate pair (similar to GPS HDOP) can be calculated and assigned to a new column *SD* using the formula for the sum of correlated random variables

$$SD = \sqrt{VARX + VARY + 2 \times COVXY}$$

Unreliable positions can be removed by filtering on direct or indirect measures of quality using *atl_filter_covariates*. While filtering on direct quality attributes and unrealistic movement speeds (see below) will often be sufficient, filtering on indirect quality indicators is a strategy to consider when direct error measures are not available.

Filtering Unrealistic Movement

Filtering on system-generated attributes may not remove all erroneous positions, and the remaining data may still include biologically implausible movement. Users are encouraged to visualise their tracks before and after filtering point locations, and especially to 'join the dots' and connect consecutive positions with lines (Fig. 2.3.b). Whether the resulting track looks realistic is ultimately a subjective human judgement, but any decision to filter-out data must remain independent of the hypothesised movement behavior. This basic principle does not preclude explicitly integrating prior knowledge of the movement ecology of the study species to ask, 'Does the animal move this way?'. Segments which appear to represent unrealistic animal movement are often obvious to researchers with extensive experience of the study system (the non-movement approach; see Bjørneraas et al. 2010). Since it is both difficult and prohibitively time consuming to exactly reproduce expert judgement when dealing with large volumes of tracking data from multiple individuals, some automation is necessary. Users should first manually examine a representative subset of tracks and attempt to visually identify problems — either with individual positions, or with subsets of the track — that persist after filtering on system-generated attributes. Once such problems are identified, users can conceptualise algorithms that can be applied to their data to resolve them.

A common example of a problem with individual positions is that of point outliers or 'spikes' (Bjørneraas et al. 2010), where a single position is displaced far from the track (see Fig. 2.3.b). Point outliers are characterised by artificially high speeds between the outlier and the positions before and after (called incoming and outgoing speed, respectively; Bjørneraas et al. 2010), lending a 'spiky' appearance to the track. Removing spikes is simple: remove positions with extreme incoming and outgoing speeds. Users must first define plausible upper limits of the study species' speed (Calenge et al. 2009; Seidel et al. 2018). Here, it is important to remember that speed estimates are scale-dependent; high-throughput tracking typically overestimates the speed between positions where the animal is stationary or moving slowly, due to small-scale location errors (Ranacher et al. 2016; Noonan et al. 2019). Even after data with large location errors have been removed, it is advisable to begin with a liberal (high) speed threshold that excludes only the most unlikely speeds. Estimates of maximum speed may not always be readily obtained for all species, and an alternative is to use a data-driven threshold such as the 90th percentile of speeds from the track. Once a speed threshold S has been chosen, positions with incoming *and* outgoing speeds $> S$ may be identified as spikes and removed.

Some species can realistically achieve speeds $> S$ in fast transit segments when assisted by their environment, such as birds with tailwinds, and a simple filter on incoming and outgoing speeds would exclude this valid data. To avoid removing valid, fast transit segments while still excluding spikes, the speed filter can be combined with a filter on the turning angles of each position (see Calenge et al. 2009; Bjørneraas et al. 2010). This combined filter assumes that positions in high-throughput tracking with both high speeds and large turning angles are likely to be due to location errors, since most species are unable to turn sharply at very high speed. Users can then remove those positions whose incoming and outgoing speeds are both $> S$, and where $\theta > A$ (sharp, high-speed turns), where θ is the turning angle, and A is the turning angle threshold. Many other track metrics may be used to identify implausible movement and to filter data (Seidel et al. 2018). At this early stage in pre-processing, track metrics should be considered provisional — it is not until after smoothing and potentially resampling to a regular interval (see below), that calculated track metrics should be used for ecological inference.

Sometimes, entire subsets of the track may be affected by the same large-scale location error. For instance, multiple consecutive positions may be roughly translated (geometrically) away from the real track and form 'prolonged spikes', or 'reflections' (see Fig. 2.3.b). These cannot be corrected by targeted removal of individual positions, as in Bjørneraas et al.'s approach (2010), since there are no positions with both high incoming and outgoing speeds, as well as sharp turning angles, that characterise spikes. Since filtering individual positions will not suffice, algorithms to correct such errors must take a track-level view, and target the displaced sequence overall. Track-subset algorithms are likely to be system-specific, and may be challenging to conceptualise or implement. In the case of prolonged spikes, one relatively simple solution is identifying the bounds of displaced segments, and removing positions between them. This identification can be based on relatively simple rules — for example, the beginning of a prolonged spike could be identified as a position with a high *incoming* speed, but a low *outgoing* speed, while the end of such a spike would have a low incoming, but a high outgoing speed. We have implemented an illustrative example of such an algorithm in the form of track-subset filtering for prolonged spikes using the *atlastools* function *atl_remove_reflections* (see the *atlastools* documentation for details on the algorithm). Users are strongly encouraged to visualise their data before and after applying such algorithms; as these methods are not foolproof, and data that are heavily distorted by errors affecting entire track-subsets should be used with care when making further inferences.

Smoothing and Thinning Data

Median Smoothing

After filtering out large location errors, the track may still look 'spiky' at small scales, and this is due to smaller location errors that are especially noticeable when the individual is stationary or moving slowly (Noonan et al. 2019). These smaller errors are challenging to remove since their attributes (such as speed and turning angles) are within the expected range of movement behaviour for the study species. The large data volumes of high-throughput tracking allow users to resolve this problem by smoothing the positions. The most basic 'smooths' work by approximating the value of an observation based on neighbouring values. For a one-dimensional series of observations, the neighbouring values are the K observations centred on each index value i. The range $i - (K - 1)/2 \dots i + (K - 1)/2$ is referred to as the moving window as it shifts with i, and K is the moving window size. A common smooth is nearest neighbour averaging, in which the value of an observation x_i is the average of the moving window K. The median smooth is a variant of nearest neighbour averaging which uses the median rather than the mean, and is more robust to outliers (Tukey 1977). The median smoothed value of the X coordinate, for instance, is

$$X_i = \text{Median}(X_{i-(K-1)/2} \dots X_{i+(K-1)/2}).$$

Users can apply a median smooth with an appropriate K independently to the X and Y coordinates of a movement track to smooth it (see Fig. 2.4.a – e). The median smooth is robust to even very large temporal and spatial gaps, and does not interpolate between positions when data are missing. Thus it is not necessary to split the data into segments separated by periods of missing observations when applying the filter (see Fig. 2.4).

Some data sources, such as GPS, provide tracks that have already been smoothed in quite sophisticated ways, such as with a Kalman filter, making a median smooth unnecessary (Kaplan and Hegarty 2005). Furthermore, smoothing is not a panacea for data quality issues, and has its drawbacks. Smoothing does not change the number of observations, but does decouple the coordinates from some of their attributes. For instance, smoothing breaks the relationship between a coordinate and the location error estimate around it (VARX, VARY, and SD in ATLAS systems). Since the X and Y coordinates are smoothed independently, the smoothed coordinates of an observation will likely differ from all the coordinates used to compute the smoothed value. Any position covariates (e.g. environmental values such as landcover or elevation) obtained before smoothing should be replaced with the covariates obtained at the smoothed coordinates. Similarly, instantaneous track metrics, such as speed and turning angle, should also be updated at this stage to reflect the smoothed coordinates. Furthermore, the location error estimate around each coordinate, and around the localisation overall, become invalid and should be ignored. This makes subsequent filtering on measures of data quality unreliable, and smoothed data are unsuitable for use with methods that model location uncertainty (Fleming et al. 2014; Calabrese et al. 2016; Noonan et al. 2019; Fleming et al. 2020). Thus, when applying location error modelling methods, users should ensure that the error measure bears a mechanistic relationship with the location estimate (see Noonan et al. 2019; Fleming et al. 2020: for more details). Additionally, excessively large K may result in a loss in detail of the individual's small-scale movement (compare Fig. 2.4.e with 2.4.a). Users must themselves judge how best to balance large-scale and small-scale accuracy, and choose K accordingly. Median smoothing is provided by the *atlastools* function *atl_median_smooth*, with the only option being the moving window size, which must be an odd integer.

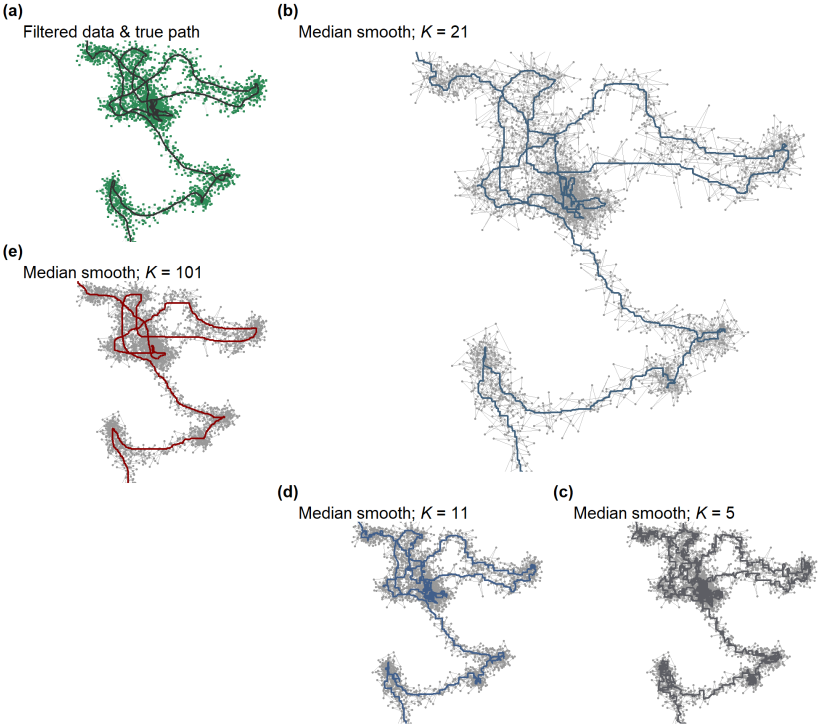

Figure 2.4: Median smoothing position coordinates reduces small-scale location error in tracking data. The goal of this step is to approximate the simulated canonical track (black line, **(a)**), given positions with small-scale error that remains after filtering in previous steps (green points). **(b)** Median smoothing the position coordinates (green points, in **(a)**) over a moving window (K) of 21 positions gives a good approximation (blue line) of the canonical track, and is a significant improvement on the unsmoothed track (grey lines and points). While K should usually be at least two orders of magnitude less than the number of positions in the track, users are cautioned that there is no correct K, and they must subjectively choose a K which most usefully trades small-scale details of the track for large-scale accuracy. Here, smoothing with a K of **(c)** 5 (dark grey line) and **(d)** 11 (blue line), leads to a jagged track, compared to the true path in (a), and the distance moved by the animal would be overestimated. **(e)** Using extremely large values of K (101) may lead to a loss of both large and small scale detail (red line). Across panels, grey lines and points show the track without smoothing.

Thinning Movement Tracks

Most data at this stage are technically ‘clean’, yet the volume alone may pose challenges for lower-specification or older hardware and software if these are not optimised for efficient computation. Thinning data i.e., reducing their volume, need not compromise researchers’ ability to answer ecological questions; for instance, proximity-based social interactions lasting 1 – 2 minutes would still be detected on thinning from a sampling interval of 1 second to 1 minute (Aspillaga et al. 2021*a*). Thinning data also does not imply that efforts to collect high-throughput movement data are ‘wasted’, as rich movement datasets enable more detailed and more accurate representation of the true track, as elaborated above. Indeed, some analyses require that temporal auto-correlation in the data be broken by subsampling the data to a lower resolution; these include traditional kernel density estimators for animal home-range, as well as resource selection functions (Manly et al. 2007; Fleming et al. 2014; Dupke et al. 2017). Furthermore, a number of powerful methods in movement ecology, including Hidden Markov Models and integrated Step-Selection Analysis recommend uniform sampling intervals (Langrock et al. 2012; Avgar et al. 2016; Michelot et al. 2016). Finally, subsampling data may be an important strategy in exploratory data analysis; for instance, it allows researchers to determine whether computationally intensive methods, such as distance and speed estimates from continuous time movement model fitting, are required for their data, or whether the movement metrics stabilise at a certain time scale (Noonan et al. 2019). Two plausible approaches here are subsampling and aggregation, and both approaches begin with identifying time-interval groups (e.g. of 1 minute). Subsampling picks one position from each time-interval group while aggregation involves computing the mean or median of all system-generated attributes for positions within a time-interval group. Here again, users should repeat the extraction of any environmental covariates for the thinned data, and may wish to obtain the mean values in a radius aroung the locations, rather than point estimates alone. Both approaches yield one position per time-interval group (Fig. 2.5.a). Categorical variables, such as the habitat type associated with each position, can be aggregated using a suitable measure such as the mode. We caution users that thinning causes an extensive loss of small-scale detail in the data, and should be used carefully.

Both aggregation and subsampling have their relative advantages. The aggregation method is less sensitive to selecting point outliers by chance than subsampling. However, to account for location error with methods such as state-space models (Jonsen et al. 2003; 2005; Johnson et al. 2008) or continuous time movement models (Fleming et al. 2014; Calabrese et al. 2016; Gurarie et al. 2017; Noonan et al. 2019; Fleming et al. 2020), correctly propagating the location error is important, and subsampling directly propagates these errors without further processing. In reverse-GPS systems systems the location error is calculated from the variance-covariance matrix of the coordinates of candidate positions considered by the location solver (Weiser et al. 2016); this is equivalent to GPS systems' HDOP (Ranacher et al. 2016). In the aggregation method, the location error around each coordinate provided by either GPS or reverse-GPS systems can be propagated — assuming the errors are normally distributed — to the averaged position as the sum of errors divided by the square of the number of observations contributing to each average (N):

$$\text{Var}(X)_{\text{agg}} = \left(\sum_{i=1}^{i=N} \text{Var}(X)_i \right) / N^2$$

Similarly, the overall location error estimate for the average of N positions in a time-interval can be calculated by treating it as a variance. For instance, the ATLAS error and GPS error measures (SD and HDOP, respectively) can be aggregated as:

$$\text{SD}_{\text{agg}} \; or \; \text{HDOP}_{\text{agg}} = \sqrt{\left(\sum_{i=1}^{i=N} \text{SD}_i^2 \; or \; \text{HDOP}_i^2 \right) / N^2}$$

Users may question why thinning, which can obtain consensus positions over an interval and also reduce data-volumes should not be used directly on the raw data. We caution that thinning prior to excluding unrealistic movement and smoothing (Fig 5.b) can lead to preserving artefacts in the data, and estimates of essential metrics — such as straight-line displacement (and hence, speed) — that are substantially different from the true value (see Fig. 2.5.c; Noonan et al. 2019). In our example, the data with errors would have to be thinned to $\frac{1}{30}^{\text{th}}$ of its volume for the median speed of the thinned data to be comparable with the overall median speed — this is an undesirable step if the aim is fine-scale tracking. Additionally, the optimal level of thinning can be difficult to determine, especially if there is wide individual variation in movement behaviour, and the mis-estimation of track metrics from inappropriately thinned data could have consequences for the implementation of subsequent filters based on detecting unrealistic movement. However, thinning before data-cleaning has its place as a useful step before exploratory visualisation of the movement track, since reduced data-volumes are easier to handle for plotting software. Thinning is implemented in *atlastools* using the *atl_thin_data* function, with either aggregation or subsampling (specified by the *method* argument) over an interval using the *interval* argument. Grouping variable names (such as animal identity) may be passed as a character vector to the *id_columns* argument.

System-Specific Pre-processing Tools

When researchers' pre-processing requirements exceed the functionalities of existing tools, they might have to conceptualise and implement their own methods. For instance, an important and common analysis with animal tracking data is to link space use with environmental covariates. This is difficult even with smoothed and thinned high-throughput data, as these may be too large for statistical packages, or have strong autocorrelation. Users aiming for such analyses can benefit from segmenting and clustering the data into spatio-temporally independent bouts of different behavioural modes (Patin et al. 2020). Treating these as the unit of observation also conveniently sidesteps pseudo-replication and reduces computational requirements. While numerous methods of segmenting and clustering data are in use, they may not be scalable to very large or gappy datasets (Langrock et al. 2012; Michelot et al. 2016; Patin et al. 2020). As an alternative, a first-principles approach that segments data based on the movement capacity (top speed, etc.) of tracked animals, could provide a fast, yet useful way to cluster data. Here, as a working example that may be suitable for some systems, we present a simple segmentation-clustering algorithm to make 'residence patches', identified as bouts of relatively stationary behaviour (Barraquand and Benhamou 2008; Bijleveld et al. 2016; Oudman et al. 2018). Details of the implementation may be found in the package code, and examples are provided in the Supplementary Material.

Conceptualising a Simple Segmentation-Clustering Algorithm: The Residence-Patch Example

Before implementing the algorithm, users should identify positions where the animal is relatively stationary, for instance on its speed or first-passage time (Barraquand and Benhamou 2008; Bracis et al. 2018). Our suggested algorithm begins by assessing whether consecutive stationary positions are spatio-temporally independent, and clusters them together into a residence patch if they are not. This clustering could be based on a simple proximity threshold — points farther apart than some threshold distance are likely to represent two different residence patches. In cases where animals visit multiple sites in sequence (such as traplining: Thomson et al. 1997), and which researchers might wish to consider as a single residence patch, a larger-scale distance threshold can help cluster nearby residence patches together, and this can also be applied to cluster together patches artificially separated due to missing data. Our algorithm separates two observations at a similar location, but at two very different time points, by comparing the intervening time-lag against a time-difference threshold, which can also apply to patches that would otherwise be clustered by the large-scale distance threshold.

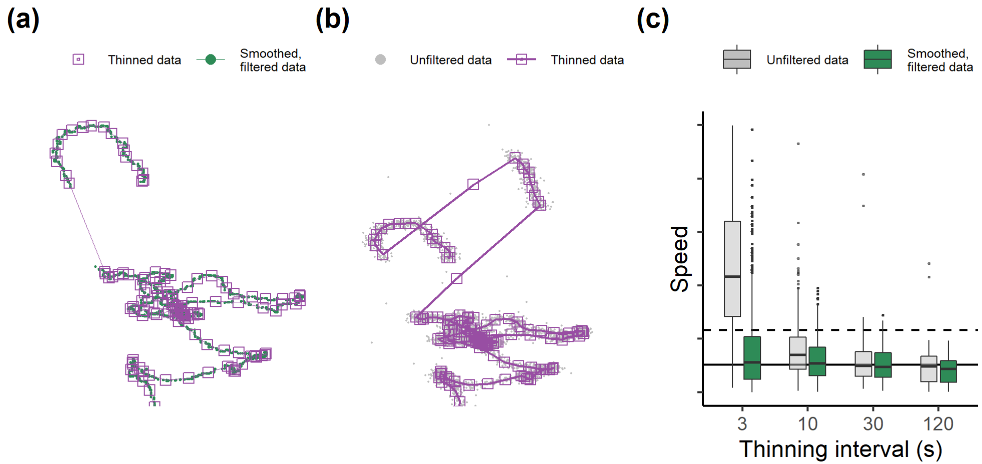

Figure 2.5: Thinning tracking data can aid computation but must be approached carefully. Aggregating a filtered and smoothed movement track **(a)** preserves track structure while reducing data-volume, but **(b)** aggregating before filtering gross location errors and unrealistic movement leads to the persistence of large-scale errors (such as prolonged spikes). **(c)** Thinning before data cleaning can lead to significant misestimations of essential movement metrics such as speed at lower intervals. Boxplots show the median and interquartile ranges for speed estimates of tracks aggregated over intervals of 3, 10, 30, and 120 seconds. For comparison, the median and 95th percentile of speed of the canonical track are shown as solid and dashed horizontal lines, respectively.

Users are encouraged to base these thresholds on the movement habits of their study species (see the *Worked Out Example*).

We have implemented a working example of the simple clustering concept presented here as the function *atl_res_patch* (see Fig. 2.6.b), which requires three parameters: (i) the distance threshold between positions (called *buffer_size*), (ii) the large-scale distance threshold between clusters of positions (called *lim_spat_indep*), and (iii) the time-difference threshold between clusters (called *lim_time_indep*). Clusters formed of fewer than a minimum number of positions can be excluded. Our algorithm performs well when movement modes are clearly separated, and is capable of correctly separating positions that are close together in space and time, but which comprise different behavioural sequences (see Fig. 2.6). While the algorithm may not cover all possible use-cases and study species, we provide it here as an example of a user-built exploratory method for animal tracking data. It is important to systematically test such custom-made algorithms, to ensure reproducibility and reliability (Wickham 2015; Marwick et al. 2018). Simple examples of such tests for the residence patch method and other functions in *atlastools* may be found in the *tests/* directory in the associated Github repository.

A Real-World Test of User-Built Pre-Processing Tools

We applied the pre-processing pipeline using *atlastools* functions described above to an ATLAS dataset to verify that the residence patch method could correctly identify known stopping points (see Fig. 2.7). We collected the data (n = 50,816) on foot and by boat, with a hand-held WATLAS tag (sampling interval = 1s) around the island of Griend (53.25°N, 5.25°E) in August 2020 (WATLAS: Wadden Sea ATLAS system Bijleveld et al. 2021; Beardsworth et al. In press). Since the data were intended to test the accuracy of the WATLAS system, we were able to log stops in the track as waypoints using a handheld GPS device, and manually annotate the WATLAS data with the timestamp of each waypoint (Garmin Dakota 10; see Beardsworth et al. In press). We estimated the real duration of each stop as the time difference between the first and last position recorded within 50m of each waypoint, within a 10 minute window before and after the waypoint timestamp (to avoid biased durations from revisits). Stops had a median duration of 10.28 minutes (range: 1.75 minutes – 20 minutes; see Supplementary Material). We cleaned the data before constructing residence patches by (i) removing a single outlier (> 15 km away), removing unrealistic movement (≥ 15 m/s), smoothing the data ($K = 5$), and (iv) thinning the data by subsampling over a 30 second interval. The cleaning steps retained 37,324 positions (74.45%), while thinning reduced these to 1,803 positions (4.8% positions of the smoothed track). Details and code are provided in the Supplementary Material (see *Validating the Residence Patch Method with Calibration Data*).

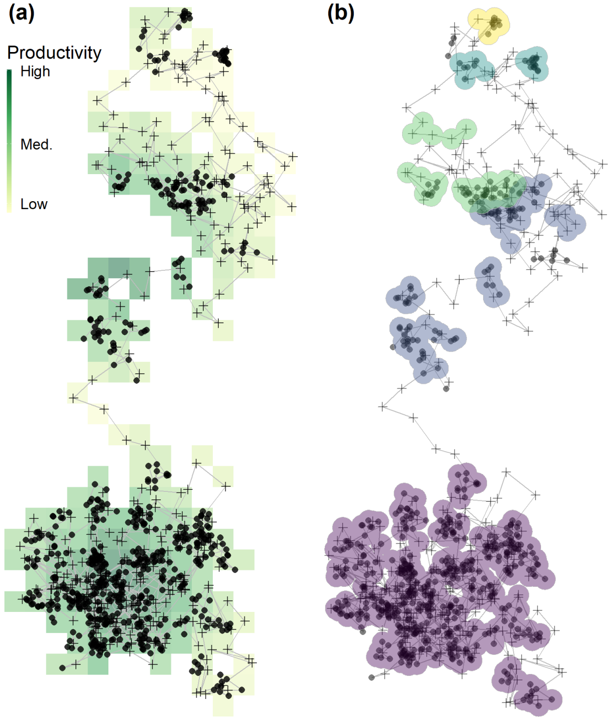

Figure 2.6: Movement tracks can be classified into residence patches, while leaving out the transit between them. (a) A simulated animal movement track from Gupte et al. 2021, where an agent uses local cues to make movement decisions to maximise intake. The agent tends to stop (solid circles) on high-productivity areas of the landscape, as these are more likely to generate prey-items. Transit points between stationary phases are shown as crosses. **(b)** Our simple, first-principles based clustering algorithm classifies the track into five residence patches. Some transit points are erroneously classified as being part of a residence patch (top, yellow), illustrating why is it important to remove such data before applying this method. Simultaneously, some points where the animal is not stationary for long are not picked up by the method. While the large purple patch (bottom) is composed almost entirely of consecutive positions, the subsequent patches are composed of multiple parts. This is because our method was designed to be robust to missing data from empirical tracks; the spatial and temporal limits of splitting and lumping can be controlled using the arguments passed to *atl_res_patch*, and can be adjusted to fit the study system. Users are cautioned that there are no 'correct' options, and the best guide is the behavioural biology of the tracked individual.

We began by visualising the data to check for location errors, and found a single outlier position approx. 15km away from the study area (Fig. 2.7.a). This outlier was removed by filtering data by the X coordinate bounds using the function *atl_filter_bounds*; X coordinate bounds ≤ 645,000 in the UTM 31N coordinate reference system were removed (n = 1; remaining positions = 50,815). We then calculated the incoming and outgoing speed, as well as the turning angle at each position using the functions *atl_get_speed* and *atl_turning_angle* respectively, as a precursor to targeting large-scale location errors in the form of point outliers. We used the function *atl_filter_covariates* to remove positions with incoming and outgoing speeds ≥ the speed threshold of 15 m/s (n = 13,491, 26.5%; remaining positions = 37,324, 73.5%; Fig. 2.7.b). This speed threshold was chosen as 5 m/s faster than the known boat speed, 10 m/s. Finally, we targeted small-scale location errors by applying a median smooth with a moving window size $K = 5$ using the function *atl_median_smooth* (Fig. 2.7.c). This step does not reduce the number of positions.

We identified stationary positions as those where the median smoothed speed ($K = 5$) was < 2m/s, as people or a boat moving any faster are likely to be in transit. We clustered these positions into residence patches with a buffer radius of 5m, spatial independence limit of 50m, temporal independence limit of 5 minutes, and a minimum of 3 positions per patch. Inferred residence patches corresponded well to the locations of stops (see Fig. 2.7.c). However, the residence patch algorithm detected seven more stops (n = 28) than there were waypoints (n waypoints = 21). One of these was the field station on Griend where the tag was stored between trips (red triangle, Fig. 2.7.c), while another patch was formed of positions recorded while waiting for the boat; such unintended stops, not recorded as waypoints, likely accounted for the remaining five 'extra' residence patches. Our analysis also did not detect two stops of 105 and 563 seconds (1.75 and 9.4 minutes) since they were data poor and were cleaned away during pre-processing (n positions = 6, 15), highlighting that the quality of the raw data (as in the rest of the track) is still a limiting factor on the inferences that are possible after pre-processing. To determine whether the residence patch method correctly identified the duration of detected stops in the calibration track, we first extracted the patch attributes using the function *atl_patch_summary*. We then matched the patches to the waypoints by their median coordinates (rounded to 100 metres). We assigned the inferred duration of the stop as the duration of the spatially matched residence patch. We compared the inferred duration with the real duration using a linear model with the inferred duration as the only predictor of the real duration. Inferred duration was a good predictor of the real duration of a stop (linear model estimate = 1.021, t-value = 12.965, $p < 0.0001$, $R^2 = 0.908$; see Supplementary Material Fig. 2.1.7). This translates to a 2% underestimation of the stop duration at a tracking interval of 30 seconds. Finally, any classification algorithm will present users with a trade-off between over-sensitivity (erroneously finding stops where there were none), and under-sensitivity (missing stops where they are not local or long enough) — users should balance between these based on the broader questions sought to be answered.

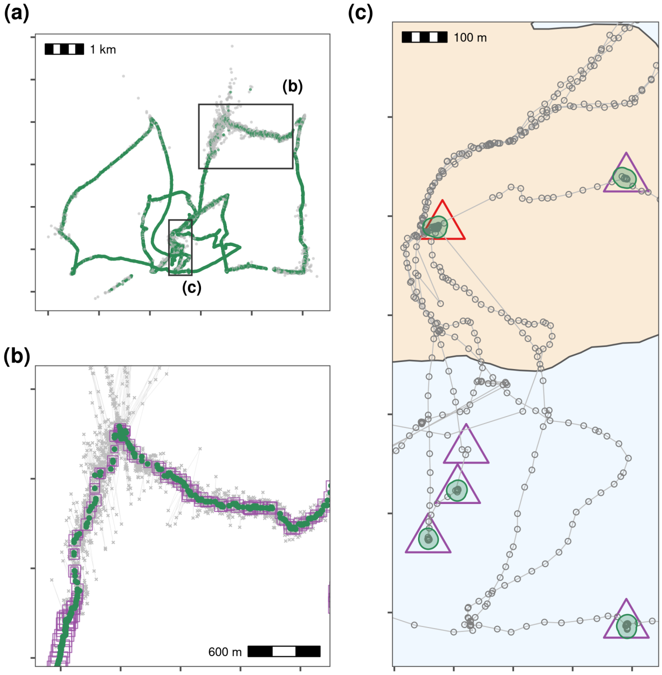

Figure 2.7: Pre-processing steps for WATLAS calibration data showing filtering on speed, median smoothing and thinning by aggregation, and making residence patches. **(a)** Positions with incoming and outgoing speed > 15 m/s are removed (grey crosses = removed, green points = retained). **(b)** Raw data (grey crosses), median smoothed positions (green circles; moving window $K = 5$), and the smoothed track thinned by aggregation to a 30 second interval (purple squares). Square size corresponds to the number of positions used to calculate the averaged position during thinning. **(c)** Clustering thinned data into residence patches (green polygons) yields robust estimates of the location of known stops (purple triangles). The algorithm identified all areas with prolonged residence, including those which we had not intended to be recorded, such as stops at the field station (n = 12; red triangle). Our analysis could not find two stops of 105 and 563 seconds duration (6 and 15 fixes, respectively), since these were lost in the data thinning step; one of these is shown here (purple triangle without green polygon).

A Worked-Out Example on Animal Tracking Data

We present a fully worked-out example of our pre-processing pipeline and residence patch method using movement data from three Egyptian fruit bats (*Rousettus aegyptiacus*) tracked using the ATLAS system in the Hula Valley, Israel (33.1°N, 35.6°E) (Toledo et al. 2020; Lourie et al. 2021). Code and data can be found in the Supplementary Material and Zenodo repository (see *Processing Egyptian Fruit Bat Tracks*). Data selected for this example were collected over three nights (5th – 7th May, 2018), with an average of 13,370 positions (SD = 2,173; range = 11,195 – 15,542; interval = 8 seconds) per individual. Plotting the tracks revealed potential location errors (see Fig. 2.1, see also Supplementary Material Fig.2.1), which we filtered out by removing observations with ATLAS SD > 20 (see Supplementary Material Section 2.5), as well as removing observations calculated using fewer than four base stations, altogether trimming 22% of the raw data (mean positions remaining = 10,447 per individual). Then, we removed unrealistic movement represented by positions with incoming and outgoing speeds > 20 m/s that exceed the maximum flight speed recorded in this species (15 m/s; Tsoar et al. 2011), leaving 10,337 positions per individual on average (98% of previous step). We median smoothed the data with a moving window K size = 5, and no observations were lost.

We aimed to study bats' night-time foraging on fruit trees by quantifying the duration of bats' residence patches. We began the construction of residence patches by finding the residence time within 50 metres of each position; this is the maximal radius of a 'cloud of points' around fruit trees (Bracis et al. 2018). Foraging bats repeatedly traverse the same routes (Tsoar et al. 2011; Toledo et al. 2020; Lourie et al. 2021) and this could artificially inflate the residence time of positions along these routes. To avoid confusing revisits with residence, we limited the summation of residence times at each position to the period until the first departure of 5 minutes or more. Thus, two nearby locations (≤ 50m apart) each visited for one minute at a time, but separated by an interval of some hours would not be clustered together as a residence patch. To focus on bats' night-time foraging behaviour, we also excluded positions during the day (5 AM – 8 PM), and at or near the roost-cave (see Fig. 2.8a) to focus on night-time foraging behaviour; 22,910 of 31,012 positions remained (73.9%). Since bats departed and returned to their roost at different times each night, we also excluded locations with a residence time > 200 minutes (approx. 3.3 hours), as this was more likely to represent daytime roosting than nighttime foraging; of 31,012 smoothed positions, 18,677 remained (60%). From these positions, we calculated that between leaving the roost to forage, and returning, bats had a mean residence time at each position of 95.64 minutes (SD = 119.23) — this value is still likely to be biased by some positions at the roost.

To determine the true duration of foraging, we opted for a first-principles approach and first selected only locations with a residence time > 5 minutes, reasoning that a flying animal stopping for > 5 minutes at a location should plausibly indicate resource use or another interesting localised behaviour. This step retained 5,736 positions per bat on average (17,208 total), or 72.4% of the nighttime positions. We then constructed residence patches with a buffer distance of 25m, a spatial independence limit of 100m, a temporal independence limit of 30 minutes, and rejected patches with fewer than three positions. These values are meant as examples; users should determine the sensitivity of their results to parameter choices. Bats spent 56.95 minutes at foraging sites (SD = 62.20), and were stationary in particular fruit trees and roosting trees during 83.8% of their foraging time (Fig. 2.8). Although all three bats roosted at the same cave during the day, and all their tracks are within the typical foraging area of bats roosting in this cave (Lourie et al. 2021), they used distinct foraging sites across the area at night (Fig. 2.8.a). The lack of overlap among individuals in tree use, obtained with the residence patch algorithm, shows that although co-roosting bats share the same cave-specific foraging area (Lourie et al. 2021), they often forage on different trees. Contrasting the actual movement path with the linear path between residence patches can help reveal details of how animal cognition affects space use (Toledo et al. 2020). Bats tended to show prolonged residence near known food sources (fruit trees), but also where no fruit trees were recorded (Fig. 2.8.b, 2.8.c), in line with previous evidence for their use of non-fruiting trees to rest, to handle and digest food, and presumably for social interactions (Tsoar et al. 2011).

Future Perspectives on Pre-processing Tracking Data

Recent technical advances in wildlife tracking have already yielded exciting new insights from massive high-resolution movement datasets (Tsoar et al. 2011; Strandburg-Peshkin et al. 2015; Harel et al. 2016; Baktoft et al. 2017; Harel and Nathan 2018; Oudman et al. 2018; Baktoft et al. 2019; Papageorgiou et al. 2019; Corl et al. 2020; Toledo et al. 2020; Aspillaga et al. 2021*a,b*; Beardsworth et al. 2021*a,b*; Lourie et al. 2021; Vilk et al. 2021), and high-throughput animal tracking is expected to become increasingly more common in the near future. Tackling the very large datasets that high-throughput tracking generates requires a different approach from that used for traditionally smaller volumes of data. We foresee that movement ecologists will have to adopt ever more practices from fields accustomed to dealing with 'big data', and that the field will become increasingly computational (Peng 2011).

Researchers have long used some of these approaches *ad hoc*, such as exploratory data analysis on small subsets before applying methods to the full data, using efficient tools, and basic batch-processing. Yet formally prescribing these steps can help practitioners avoid pitfalls and implement techniques that make their analyses quicker and more reliable. Standardised principles, implemented a basic pipeline, for approaching data cleaning promote reproducibility across studies, making comparative inferences more robust. While massive datasets make reliance on standardised pipelines necessary, the output of such pipeline should periodically manually double-checked to ensure 'realistic' output. The open-source *R* package *atlastools* serves as a starting point for methodological collaboration among movement ecologists, and as a simple working example on

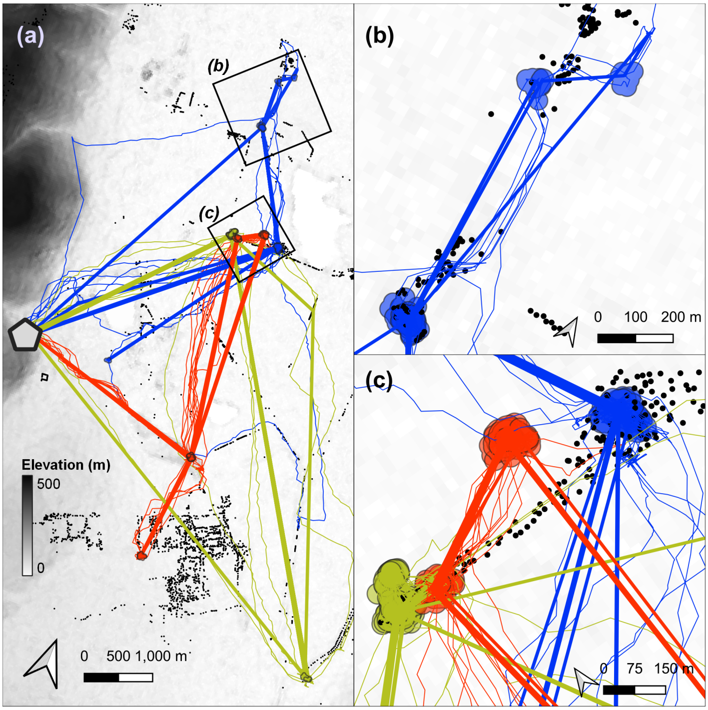

Figure 2.8: Synthesising animal tracks into residence patches can reveal movement in relation to landscape features, prior exploration, and other individuals. **(a)** Linear approximations of the paths (coloured straight lines) between residence patches (circles) of three Egyptian fruit bats (*Rousettus aegyptiacus*), tracked over three nights in the Hula Valley, Israel. Real bat tracks are are shown as thin lines below the linear approximations, and colours show bat identity. The grey hexagon represents the roost-cave at Gar Hershom. Black points represent known fruit trees. Background is shaded by elevation at 30 metre resolution. **(b)** Spatial representations of an individual bat's residence patches (green polygons) can be used to study site-fidelity by examining overlaps between patches, or to study resource selection by inspecting overlaps with known resources such as fruit trees (black circles). In addition, the linear approximation of movement between patches (straight green lines) can be contrasted with the estimated real path between patches (irregular green lines), for instance, to determine the efficiency of movement between residence patches. **(c)** Fine-scale tracks (thin coloured lines), large-scale movement (thick lines), residence patch polygons, and fruit tree locations show how high-throughput data can be used to study movement across scales. Patches and lines are coloured by bat identity.

which researchers may wish to model their own tools. Efficient location error modelling approaches (Fleming et al. 2020; Aspillaga et al. 2021*b*) may eventually make data-cleaning optional. Yet cleaning tracking data even partially before modelling location error is faster than error-modelling on the full data, and the removal of large location errors may improve model fits. Thus we see our pipeline as complementary to these approaches (Fleming et al. 2014; Fleming et al. 2020).

Finally, we recognise that the diversity and complexity of animal movement and data collection techniques often requires system-specific, even bespoke, pre-processing solutions. Though the principles outlined here are readily generalised to numerous data sources (including terrestrial radio-based reverse-GPS: e.g. Toledo et al. 2020, and marine acoustic reverse-GPS: e.g. Aspillaga et al. 2021*b*; high-resolution GPS such as Strandburg-Peshkin et al. 2015, and video-tracking: Rathore et al. 2020), users' requirements will eventually exceed the particular tools we provide. For instance, relational databases are the standard for storing very large datasets, and extending pre-processing pipelines to deal with various data sources is relatively simple, as we show in our Supplementary Material. We see the diversity of animal tracking datasets and studies as an incentive for more users to be involved in developing methods for their systems. We offer our approach to large tracking datasets, and our pipeline and package as a foundation for system-specific tools in the belief that simple, robust concepts are key to methods development that balances system-specificity and broad applicability.

* * *

Supplementary Information for Chapter 2

The supplementary material for this chapter is a worked out, step-by-step guide to using the *atlastools* package to clean data as described in preceding sections. Being primarily a tutorial for practitioners — and quite lengthy — it is not provided here, but may be found online as Supporting Information published along with the manuscript, Gupte et al. (2022*b*), "A Guide to Pre-Processing High-Throughput Animal Tracking Data," at: https://besjournals.onlinelibrary.wiley.com/doi/10.1111/1365-2656.13610.

* * *

Interlude A

Mapping Animal Movement in R

Pratik R. Gupte

MAPPING AS EXPLORATORY DATA ANALYSIS Mapping animal movements is a key component of exploratory data analysis. It is important to 'join the dots' of animal positions. Large tracking datasets can contain errors that are only evident to researchers when they look at an approximation of the animal's path and ask, "Does the animal move this way?" This map shows 'jumps': long, linear segments between points, indicating missing data for some periods.

Mapping can also reveal interesting behaviours that can only be observed after significant effort in the field. The 'looping' behaviour of *AM253* to water sources is the focus of this map. Seeing this looping behaviour allowed us to focus our study on elephant movements between visits to water sources.

MAPPING AS ART Growing up in early 2000s India, I read hard copies of National Geographic Magazine, which has long had fantastic graphics. *Where the Animals Go*[1] was a source of inspiration as well. I built up the image in layers, used colours that don't clash, and highlighted the phenomenon of interest. These approaches chime with the 'grammar of graphics' approach of *ggplot*, which I used to make this map.

MAPPING IN R R's great advantage over other languages is visualisaton, specifically the popular *ggplot* package. *ggplot*'s emergence as a mainstay of spatial visualisation is due to its *geom_sf* function, which can handle sf spatial objects.

One of *ggplot*'s advantages is its many extensions. Here, I used the *ggspatial* and *ggtext* extension packages to add the scale bars and north arrow, and to add the text box, respectively.

Plotting rasters is not straightforward in *ggplot*. There are two main options: the stars package and its associated *geom_stars*, or converting a

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[1] Cheshire, J. and Uberti, O. (2017), *Where the Animals Go: Tracking Wildlife with Technology in 50 Maps and Graphics* (W. W. Norton), 174 pp.

raster dataset into a dataframe with regular coordinate intervals and using *geom_tile*.

Here, I chose the second approach because I'm an infrequent stars user; since making the map I've tried *geom_stars* which works just as well, and is very convenient.

REPRODUCIBILITY IN R I adopted a relatively relaxed understanding of reproducibility: given the data, the code would be reproducible if it could produce the map I had entered for this contest. To do this, I set up a continuous integration pipeline using Github Actions (GHA).

Using the *usethis* package, I created a 'DESCRIPTION' file, which is usually reserved for packages. This file tricks GHA into reading its contents, especially the dependencies, i.e., the R packages required by the project.

GHA automatically reads the dependencies and installs them, as well as the programs required by those dependencies. For instance, GDAL (the Geospatial Data Abstraction Library) is key to nearly all spatial analyses, and is installed as a requirement of the *rgdal* package, which is itself key to *sf* and *raster*.

I used the R package *renv* to make sure that the packages (and the package versions) I used are available to the pipeline. *renv* creates a lockfile, a registry of packages the current project uses, from which those packages can be installed. Finally, to check whether the entire pipeline works, I used *bookdown* to sequentially execute the series of Rmarkdown files. An obvious alternative is *rmarkdown*.

GHA runs this pipeline and reports whether the code ran successfully, and if not, where it failed (you can see these reports here). GHA runs the pipeline on Linux, and Windows containers (Mac OS-x is also supported). This means that though I use Linux, I'm pretty sure that this code works for Windows users.

THE LIMITS OF REPRODUCIBILITY Reproducibility inevitably breaks down at certain scales in an ecological study. For instance, it would be impossible to reproduce the primary data collection of the study, such as which elephants were captured and fitted with transmitters. These data are taken on faith from the original researchers, highlighting the role of trust in the scientific community.

In ten years, code in R or another language may no longer be reproducible due to software and hardware changes, as many researchers found in the 10-year reproducibility challenge. Finally, entire services might become unavailable; for example, the raster processing using Google Earth Engine is dependent on Google maintaining this service.

Researchers then, should be pragmatic about reproducibility. Who is it for — the researchers themselves, the reviewers of their manuscript, their students, their funders? To whom this effort is owed, and by whom, and how the additional work required can be prevented from becoming a gatekeeping mechanism[2;3], are are issues that the ecology and evolution community will have to address.

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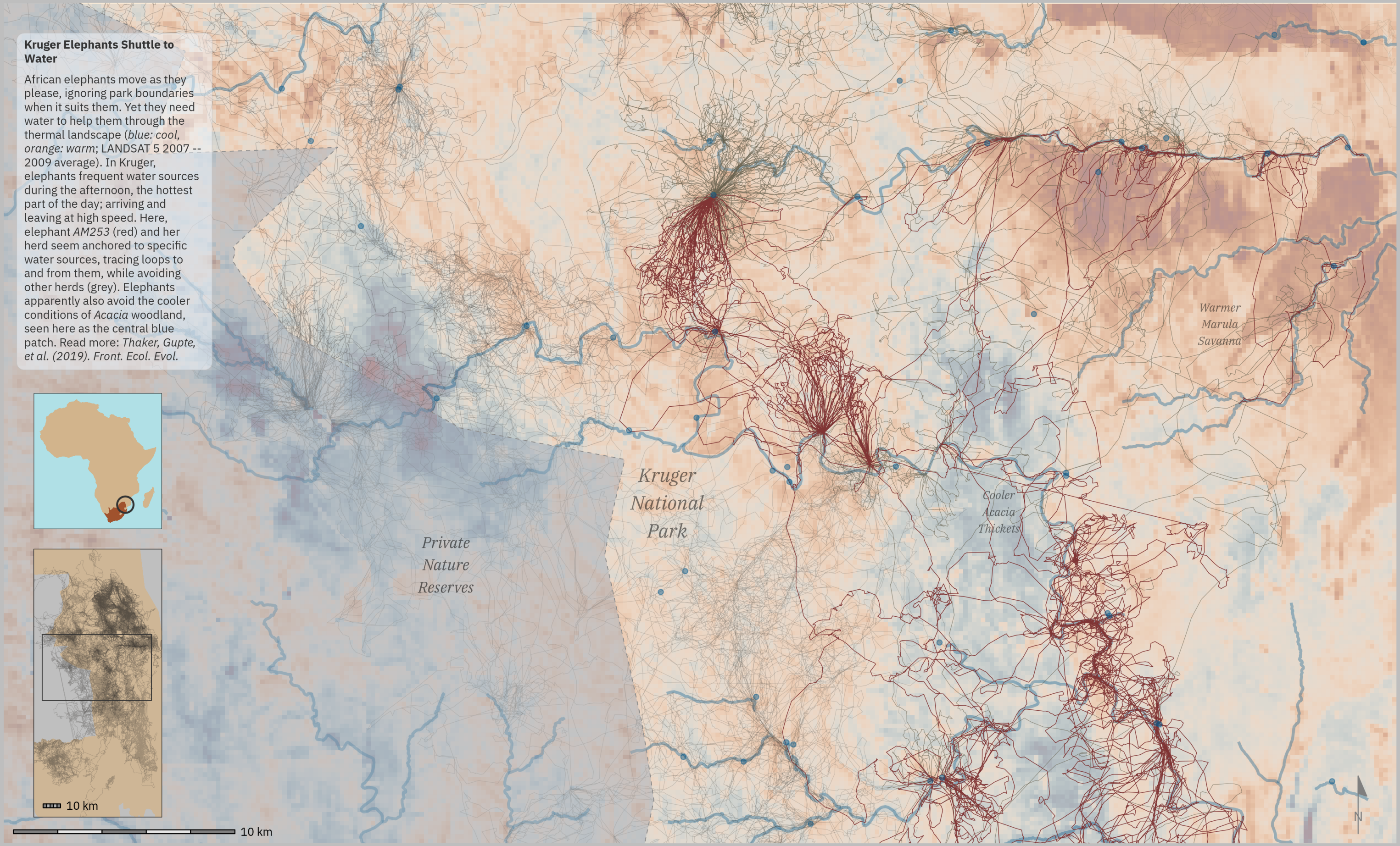
[2] Finley, K. (2017), "Diversity in Open Source Is Even Worse Than in Tech Overall," *Wired*.

[3] Murphy, M. C. et al. (2020), "Open Science, Communal Culture, and Women's Participation in the Movement to Improve Science," *Proceedings of the National Academy of Sciences*, 117/39: 24154–64.

Kruger Elephants Shuttle to Water

African elephants move as they please, ignoring park boundaries when it suits them. Yet they need water to help them through the thermal landscape (*blue: cool, orange: warm*; LANDSAT 5 2007 -- 2009 average). In Kruger, elephants frequent water sources during the afternoon, the hottest part of the day; arriving and leaving at high speed. Here, elephant *AM253* (red) and her herd seem anchored to specific water sources, tracing loops to and from them, while avoiding other herds (grey). Elephants apparently also avoid the cooler conditions of *Acacia* woodland, seen here as the central blue patch. Read more: *Thaker, Gupte, et al. (2019). Front. Ecol. Evol.*



About This Map

This map and text is adapted from a submission to the *Methods in Ecology and Evolution* blog, after my entry won the BES' Mapping Animal Movements Contest (2020 – 2021), in the reproducible "R Map" category. The map shows the movement of 14 female savanna elephants *Loxodonta africana* tagged in Kruger National Park, South Africa, with a focus on the elephant *AM253*. The study that inspired this map was published as Thaker et al. (2019) "Fine-Scale Tracking of Ambient Temperature and Movement Reveals Shuttling Behavior of Elephants to Water."

I coloured the temperature raster using the *scico* package's 'VikO' palette. I tried out a number of palettes from *scico*, pals (providing the Kovesi palettes), *RColorBrewer*, and *colorspace* packages. I chose a diverging palette to show heterogeneity in the thermal landscape, but this approach is not to be recommended for material that will be printed in grayscale.

Map text is set in two related typefaces designed by the Dutch type foundry *Bold Monday* for IBM: *Plex Serif* — for text on the map — and *Plex Sans* — for text in the box. While aiming to be text typefaces, I think both perform much better as 'display' faces; Plex Serif especially so.

* * *

Chapter 3

Direct Effects of Flight Feather Moult on Bird Movement and Habitat Selection

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4. Tel-Aviv University, Israel

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What is a bird if not a dinosaur persevering?

– Vinny Thomas, comedian.

Abstract

The flight surfaces of bird wings require regular renewal through a process called moult — shedding worn out feathers and growing fresh ones. Moult presents birds with the dilemma of needing more resources for feather growth just when their flight capacity is reduced due to feather loss, making them more vulnerable to predation. We combined mechanistic and experimental approaches to present a first quantification of the direct effects of wing moult on the movement and habitat selection of four non-migratory passerine species. We followed the movement of moulting birds using a high-throughput tracking system. Taking a viewshed ecology approach, we examined how birds used areas sheltered from observation by potential predators. We found that species' moult rate determined whether they adjusted their movement to their wing condition. Among species that adapted movement to moult rate, natural moult led to increased movement between habitat patches, whereas artificial feather removal led to shorter between-patch movements. Across moult rates, birds preferred lower visibility areas that are more sheltered from visual predators. Our study revealed that birds' fine-scale adaptive movement decisions are intertwined with their evolved physiological strategies, and they can adopt the spatial perspective of their predators at landscape scales, pre-emptively avoiding areas where they could be observed. Overall, we show how combining experimental and tracking approaches with mechanistic, biologically-grounded estimates of landscape attributes allows cross-species comparisons of movement strategies in response to moult dynamics.

Introduction

Birds are unique in moving mostly by powered flight on feathered wings. Feathers, unlike animal hair and claws, are dead proteinaceous structures, which cannot be renewed continuously as they suffer wear and tear (Rayner 1988; Jenni and Winkler 1989). As feathers mature, wing condition and consequently flight capacity gradually decreases (Lindström et al. 1994; Hedenström and Sunada 1999; Hedenström 2003). Moult — the shedding of old, worn-out feathers, and their replacement with freshly grown ones — is thus a key process in avian ecology (Ginn and Melville 1983; Rayner 1988). During wing moult, as one or more feathers are lost and new ones grow in their place, the flight surfaces of bird wings become smaller. The reduction in flight surface area during moult can be measured using a robust-cross species index of the size of the (temporary) wing gap (Lind and Jakobsson 2001; Kiat et al. 2016). Wider gaps lead to larger reductions in flight surface area, power output, and flight capacity and efficiency in captive birds (Tucker 1991; Swaddle et al. 1996; Swaddle and Witter 1997; Lind 2001; Lind and Jakobsson 2001; Williams and Swaddle 2003; Bowlin et al. 2009). In addition to these indirect costs, wing moult is among the most energetically demanding phases of a bird's annual cycle, as regrowing large flight feathers requires substantial resources (Lindström et al. 1993; Newton 2009; Kiat and Sapir 2017). Despite these mechanistic links between moult and movement, our understanding of moult's influence on birds' movement strategies and habitat selection is poor.

The direct influence of wing moult on the movement and habitat selection of birds has primarily been examined in a few small-scale, disconnected studies (Bell 1970; Haukioja 1971; Green and Summers 1975; Madsen and Mortensen 1987; Francis et al. 1991; Fox et al. 1998). Moving less, as some northerly species of finches and buntings do (Bell 1970; Haukioja 1971; Green and Summers 1975; Francis et al. 1991), could save energy required to regrow feathers. Avoiding predation risk during moult by sheltering in vegetation and rough terrain (Bell 1970; Haukioja 1971; Green and Summers 1975; Francis et al. 1991), or near water-bodies as geese and ducks do (Madsen and Mortensen 1987; Fox et al. 1998), could also lead to reduced movement during moult. Moult often coincides with migratory periods (Kiat et al. 2019), making it difficult to separate the effects of migration-related energetic requirements (Alerstam and Lindström 1990; Wikelski et al. 2003; Horvitz et al. 2014), such as preferences for high-quality resources (Madsen and Mortensen 1987; Fox et al. 1998), from moult-related considerations on habitat selection. Simultaneously, moult is influenced by bird physiology, with large-bodied species molting faster (Jenni et al. 2020; Kiat and Izhaki 2021), and also by birds' evolved movement strategies, as wide-ranging and aerial foraging species (e.g., swifts and swallows) moult more slowly to maintain movement capacity (Kiat et al. 2016).

The direct effects of moult could be robustly studied with a cross-species comparison of unrelated, non-migratory species that are not constrained by the short time available for moult in northern temperate regions (Ginn and Melville 1983; Jenni et al. 2020). Cross-species studies of movement and habitat selection in molting birds could benefit from dramatic advances in the high-throughput position tracking of small species (Toledo et al. 2020; Nathan et al. 2022). Birds, among other animals, can take the spatial perspective of visual predators, and avoid risky, exposed areas in favour of sheltered ones (Hampton 1994; Emery 2000; Krams 2001; Davidson and Clayton 2016; Krams et al. 2020). Shelter is often only proxied by correlated variables, such as vegetation growth (Pettorelli et al. 2011). Adopting a mechanistic, viewshed ecology approach (Olsoy et al. 2015; Aben et al. 2018; 2021) in habitat selection analyses could directly account for birds' visibility to potential predators (Olsoy et al. 2015; Aben et al. 2018; 2021).

We explore the direct effects of wing moult on the movement of birds, focusing on four sympatric, non-migratory species: barn swallows (*Hirundo rustica*), white-spectacled bulbuls (*Pycnonotus xanthopygos*), house sparrows (*Passer domesticus*), and clamorous reed-warblers (*Acrocephalus stentoreus*). Scoring the moult-related wing gap size of naturally molting birds (Lind and Jakobsson 2001; Kiat et al. 2016), we manipulated a subset of molting individuals by trimming a number of flight feathers. We tracked birds during a 4-month period using the high-throughput ATLAS system, which brings unprecedented temporal and spatial resolution to small bird tracking (Toledo et al. 2014; Weiser et al. 2016; Toledo et al. 2020; Nathan et al. 2022; Beardsworth et al. In press). We examined *(i)* how the size of the moult-related wing gap affected bird movement, and *(ii)* how the wing gap size influenced selection for more sheltered habitats. Overall, we show how birds' movement decisions, influenced by their immediate physiological condition, scale up to affect their space use, and how individuals' adaptive behavioral strategies have feedbacks with their evolutionary ecology.

Examining the Movement of Moulting Birds

We studied bird moult and movement in the Hula Valley of northern Israel (33.10°N, 35.60°E), which includes reconstructed wetlands and reedbeds as well as agricultural areas (crops, plantations and fishponds; see *Supplementary Information*).

Bird Capture, Wing Moult Scoring and Experimental Manipulation

We captured 86 individuals of four species in 2016: 16 barn swallows, 19 white-spectacled bulbuls, 35 house sparrows, and 16 clamorous reed-warblers, for which we also measured the wing gap index. All individuals were trapped after breeding was completed and before the molting season commenced, between June and October 2016.

We described the state of each primary feather on a scale of 0 to 5 using the primary score (PS) method (Ginn and Melville 1983). Both PS = 0 and PS = 5 indicate a fully mature feather, and hence no gap in the wing. A PS value between 1 and 4 indicates feathers in increasing stages of growth, with PS = 1 representing a large gap left by a recently molted feather. This method allows a cross-species estimate of the size of the moult-related gap in the wing, and is also strongly and negatively correlated with moult rate and duration (Rohwer et al. 2009). We scored the wing gap size due to any single feather molting as the inverse value of PS for each of the wing's nine primary feathers (P1 – P9; counted outward) such that when PS = 1, wing gap size = 4, and when PS = 2, wing gap size = 3, etc. However, for PS = 0, wing gap size is also 0 because there is no gap in both the PS = 0 and PS = 5 stages, as either an old, mature feather, or a new, freshly grown feather is present. To compare moult-related wing gap sizes across individual birds, we summed the wing gap size scores across all nine primary flight feathers, for each individual, into a single wing gap index (Kiat et al. 2016). This index is independent of the size of individual birds and their morphology, controls for the stage of wing feather moult, and allows for reliable cross-species comparisons (Bensch and Grahn 1993; Kiat et al. 2016).

We experimentally manipulated 29 individuals across species (bulbuls = 6, sparrows = 14, reed-warblers = 2, swallows = 7), and removed one to three primaries; the exact number was determined randomly for each bird. We varied this number to produce variation in the possible effect of wing gap size, and the manipulation was symmetrical, i.e., the same feather was removed in both wings. Primaries were removed by cutting the feather near its base, in addition to the primaries missing as part of natural moult; this procedure simulates an enlargement of the moult-related wing gap. Cutting the feather rather than tearing it out from the base, which is still innervated (Jenni et al. 2020), avoided excess trauma which could impact birds' behaviour, and allowed us to examine the effect of only the wing gap size on movement and habitat selection. For these experimentally manipulated birds, we calculated the wing gap size after the procedure described here. Bird capture and handling, the experimental manipulation procedure, and tagging for position tracking (see below) were conducted under a permit from the Israel Nature and Parks Authority (NPA permit 2016/41402) and from the ethics committee of the Hebrew University of Jerusalem, Israel (NS-16-14801-2).

Forecasting Daily Changes in the Wing Gap Size Index

The size of the moult-related wing gap decreases slowly and constantly as feathers regrow, yet as a mature feather is shed, the wing gap size may also increase in gradual jumps. Over our tracking period of about 7 days per individual (see below), this is expected to represent small changes in the wing surface area, which could further influence movement decisions. These changes in wing condition should be accounted for when relating movement characteristics to wing gap size. To do this, we calculated for each species the mean daily progress in the moult score, based on a sample of individuals documented twice during the moult process (bulbul = 0.45 ± 0.15, n = 17; sparrow = 0.40 ± 0.25, n = 10; reed-warbler = 0.69 ± 0.34, n = 24; swallow = 0.34 ± 0.18, n = 22). Then, we estimated for each bird included in the study the expected daily change based on the measurement we made at the time of tagging (see *Supplementary Information*).

Tracking Bird Movement Using ATLAS

We tracked the movement of individual birds using ATLAS (Advanced Tracking and Localization of Animals in real-life Systems), a state-of-the-art high-throughput radio-telemetry system capable of tracking dozens of individuals at intervals as low as 4 seconds (Toledo et al. 2014; Weiser et al. 2016; Toledo et al. 2020; Nathan et al. 2022). We glued ATLAS tags (0.9 – 1.6 g, depending on species) to birds' dorsal feathers after capture, and then released them (tag weights as percent of body mass: bulbuls = 3.85% ± 0.21%; sparrows = 4.21 ± 0.13; reed-warblers = 4.75% ± 0.19%; swallows = 4.9% ± 0.13%). Tags automatically drop off as these feathers are molted. Each individual was tracked for an average of 8.23 ± 3.24 days (bulbul = 9.8 ± 10.1 days; sparrow = 12.0 ± 13.4 days; reed-warbler = 5.9 ± 2.1 days; swallow = 5.1 ± 14.8 days). We collected 4.3 million position estimates overall, with 7,276 positions per individual per day, for an effective tracking interval of 5.05 ± 1.85 positions per minute on average (bulbuls = 6.14 ± 3.93; sparrows = 5.98 ± 5.57; reed warblers = 5.80 ± 3.16; swallows = 2.28 ± 1.42). Since we were interested in exploring movement patterns, and these species are diurnally active, we removed all nighttime positions, leading to an approximate halving of the total dataset.

Processing Tracking Data

ATLAS conservatively filters out location estimates that are clearly wrong (e.g., too far from the study area), letting users inspect most location estimates, which come with several measures of quality, and decide whether they want to retain the estimates or not. For this study, we aggressively filtered out location estimates, removing estimates for which we had indications that ATLAS failed to find a high-quality estimate (Gupte et al. 2022*b*) (see *log_preprocessing.log* in the analysis code). We began data cleaning by removing locations near a so-called attractor position (at (257000.0,780000.0), Israeli grid; see file *log_preprocessing.log*); these are locations for which the positioning system had defaulted to a (wrong) estimate. We identified and removed other attractor positions by removing positions sharing the exact same common coordinate pair. Since coordinates are resolved down to double-precision, it is very unlikely for two location estimates to have the same coordinate pair, and this rather indicates an error in location estimation. Each individual's track was pre-processed separately.

We first *(i)* filtered the data for large-scale errors by removing positions with a system-generated positioning-error estimate (SD) > 20m, and then *(ii)* split each individual's tracking data by calendar date, removing days with < 500 positions. Finally, we *(iii)* filtered the data for unrealistic movements, removing positions with both speeds > 20 m/s *and* a turning angle > 10°. We deliberately used larger thresholds than these species' maximum speeds to avoid removing valid, high-speed movements (Gupte et al. 2022*b*). Finally, we *(iv)* accounted for small-scale errors — noise around the true positions — by applying a median smooth with a moving window $K = 7$. After excluding night time data and all other data filtering and smoothing, we analyzed 1.1 million locations from 86 individuals, keeping high per-minute sampling rate for all species (bulbuls = 4.85 ± 3.3, sparrows = 2.73 ± 3.0, reed-warblers = 2.09 ± 1.44, swallows = 2.07 ± 1.14). Compared with current technologies for tracking small birds (< 50g) — primarily radio triangulation and geolocators, which have low temporal (a few fixes per hour or day) and spatial resolution (error margins up to 200 km) (Bridge et al. 2013) — ATLAS data represent an unprecedented sampling rate, with GPS-level accuracy (Beardsworth et al. In press).

Quantifying Large-scale Movements

We investigated the large-scale space-use of bulbuls, sparrows, and reed-warblers by summarising their processed movement paths into daily sequences of 'residence patches' using the *atlastools* package developed specifically with high-throughput ATLAS tracking data in mind (Gupte et al. 2022*b*). The residence patch algorithm uses simple distance and duration thresholds, chosen based on the movement ecology of the tracked species, to efficiently and rapidly cluster-segment individuals' non-travelling positions (Gupte et al. 2022*b*). We applied this algorithm to the date-specific tracks of each individual, considering consecutive positions less than 25m and 30 minutes apart to be part of the same cluster. We joined clusters (with at least 9 positions) less than 100m and 30 minutes apart together for bulbuls and sparrows, and less than 25m and 30 minutes apart for reed warblers, which typically fly only short distances (Kiat et al. 2016). Doing so, we obtained 4,373 residence patches overall and extracted environmental covariates (NDVI and visibility index; see below) for the positions clustered into each patch. We handled swallows differently, as these are highly aerial birds whose movement is not easily clustered into residence patches. Instead, and because the relatively higher-flying swallows are more accurately tracked by ATLAS, we simply calculated the total distances moved along daily tracks from the cleaned, processed data.

Visibility Analysis to Quantify Sheltered Habitats

Many animals can gauge the risk posed by predators by estimating a predator's field of view ('spatial perspective taking') (Emery 2000; Bruce et al. 2003; Davidson and Clayton 2016), and select for sheltered locations outside of a predator's view (Hampton 1994; Krams 2001; Watve et al. 2002). To assess the field of view of a hypothetical predator, and thus the estimated riskiness of the landscape, we took a viewshed ecology approach to determine how visible an area was from surrounding locations (Aben et al. 2018; 2021).

We first obtained a 50cm canopy height model (CHM) (Aben et al. 2021) of the majority of our study area (courtesy of the Survey of Israel). For each cell of the CHM, we calculated a *visibility index*, which is the proportion of surrounding cells from which the focal cell is visible, given that lines of sight can be blocked by intervening structures (also called cumulative viewshed analysis, or a 'fearscape') (Olsoy et al. 2015). Open areas, such as agricultural fields or water bodies, are likely to be visible from all directions and have a visibility score ≈ 1.0. In contrast, locations inside woodland or reedbeds are likely to be hidden from view, with a lower visibility index (see *Supplementary Information*).

Importantly, the visibility index depends upon the hypothetical observer's height above surface level; observers higher up may be able to see locations that are obstructed from a terrestrial viewpoint. We parameterised our visibility index calculations based on the hunting flight altitude of a raptor that commonly preys on small birds, the Eurasian sparrowhawk (*Accipiter nisus*). Sparrowhawks and other bird-preying raptors hunt by surprising their prey via low-level flight, as hovering or high-flying raptors are conspicuous and can be easily detected (Krams 2001; Krams et al. 2020). In line with experimental and observational work, we assumed an observer height of 1.5m above surfaces (tree canopy, fields, or other) (Seress et al. 2011; Krams et al. 2020), and an observer visual range of 50m. We used the 'Visibility Analysis' plugin v1.2 for QGIS v3.20 to calculate visibility scores over the study area (Cuckovic 2016).

Drawing Alternative Residence Patches to Examine Habitat Selection

In our landscape, it is mostly wooded areas that offer shelter from observation by aerial predators (see *Supplementary Information*). We examined the relative importance of the provisioning effects of vegetation (proxied by NDVI) (Pettorelli et al. 2011), and its sheltering effects (section F above), on birds' movement decisions at the patch scale. To do this, we combined our residence patch approach for bulbuls, sparrows, and reed warblers with a step-selection approach (Thurfjell et al. 2014; Avgar et al. 2016) using the *amt* package (Signer et al. 2019). While barn swallows could potentially make use of sheltering vegetation by flying very low (Warrick et al. 2016), we could not detect their altitude above the ground — a key component of shelter — and so did not include them in this analysis.

We first converted each individual's daily sequence of residence patches into steps, with each patch i as the starting point, and the following patch $i + 1$ as the end of the step. Then, for each such real step, we drew 9 alternative steps that the individual could have taken from patch i, and considered the end coordinates of these alternative steps to represent the median coordinates of a potential residence patch. The distances of these movements were drawn from a gamma distribution fitted to each individual's movements between patches, and turning angles were drawn from a Von Mises distributions fitted to the observed turning angles (Signer et al. 2019). For each alternative patch with median coordinates $(X_{\text{alt}}, Y_{\text{alt}})$, we drew 15 coordinate pairs from a normal distribution centred on $(X_{\text{alt}}, Y_{\text{alt}})$, with a standard deviation of 20 m.

To control for the resource-provisioning effect of vegetation, we also obtained the normalised difference vegetation index (NDVI) as a metric of vegetation growth (Pettorelli et al. 2011) across our study area, using Copernicus Sentinel-2 MultiSpectral Instrument, Level-1C data (10m resolution; June – October 2016). We sampled the NDVI and visibility index at real and potential patch coordinates, and calculated averages per patch. With between-patch movements as steps, we performed species- and moult-status specific step-selection analysis (SSA) to determine how these predictors affected habitat selection (Avgar et al. 2016: see *Supplementary Information*). The time intervals between patches were not fixed, but step lengths were not dependent on step duration, and so we implemented a simple SSA.

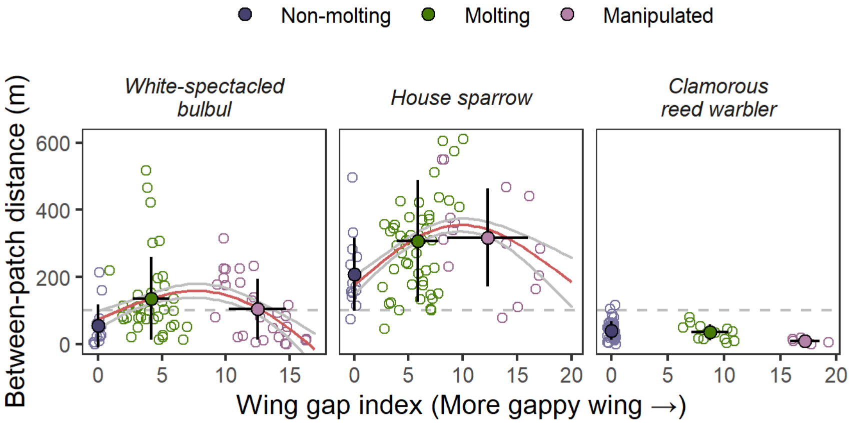

Figure 3.1: Naturally molting bulbuls and sparrows, but not reed-warblers, move farther between residence patches during natural moult than following experimental feather manipulation. White-spectacled bulbuls (*Pycnonotus xanthopygos*) and house sparrows (*Passer domesticus*) moved 251% and 150% as far between areas of prolonged use ('residence patches') when molting, compared to non-molting individuals (see text for statistics). However, when bulbuls' and sparrows' wings were heavily compromised by experimental manipulation (wing gap index ≥ 12), both species made shorter movements between residence patches. In contrast, clamorous reed-warblers (*Acrocephalus stentoreus*) did not show a significant difference in large-scale movements with increasing wing gap index, possibly because they are already restricted to small patches of reedbeds.

Effect of Wing Moult on Bird Movement and Habitat Selection

Moult-related wing gap size

Of the four species we studied, bulbuls and sparrows are relatively wide-ranging birds, reed-warblers are strongly range restricted to patchy reedbeds, and swallows are very wide-ranging, largely aerial foragers. Bulbuls and sparrows moult more slowly than reed-warblers, but more rapidly than swallows. Thus reed-warblers have the largest moult-related wing gaps, swallows the smallest, while bulbuls and sparrows are intermediate between them (wing gap index, mean ± SD: swallows = 4.3 ± 0.95, bulbuls = 4.95 ± 1.37, sparrows = 5.9 ± 2.1, reed warblers = 9.5 ± 1.38). All non-molting birds had a wing gap index score of zero.

Moult-related Wing Gap Size and Large-scale Movements

For bulbuls, sparrows, and reed-warblers, we quantified large-scale movements as both the displacements between areas of prolonged residence, called 'residence

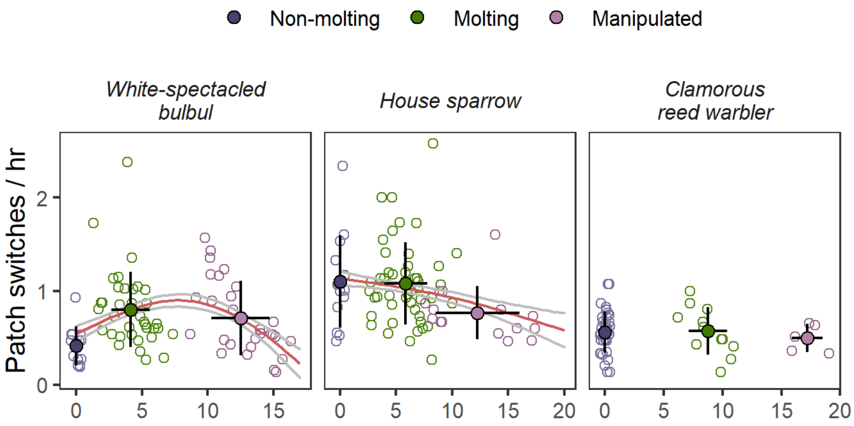

Figure 3.2: Patch-switching behaviour is affected by wing gap size in bulbuls and sparrows, but not in reed-warblers. Bulbuls switched between areas of prolonged use ('residence patches') more frequently when molting naturally than when not molting; however, bulbuls whose feathers had been artificially cut ('manipulated') switched less frequently between patches. Molting sparrows switched residence patches less frequently with increasing wing gap index; naturally molting birds switched less than non-molting ones, and manipulated birds least of all. Reed-warblers did not show a significant difference in patch switching with increasing wing gap index, possibly because they are already restricted to small patches of reedbeds.

patches' (Gupte et al. 2022*b*), as well as the frequency of these displacements. Since swallows constantly fly while foraging, we chose to quantify their large-scale movement by simply calculating the total distance moved, adjusting for the daily duration of daytime tracking. We related total large-scale movements (controlling for daily, daytime tracking duration) with wing gap size using generalised additive models (GAM). We fit one GAM for bulbuls, sparrows, and reed-warblers (species included as both fixed and random effect), and a separate GAM for swallows (see *Methods*; see *Supplementary Information* for model specification).

Distance Between Residence Patches

We found that bulbuls and sparrows, but not reed-warblers, adjusted their daytime large-scale movements between residence patches to their wing gap size (Fig. 3.1; GAM t-value = 2.13, p = 0.034; *Supplementary Information* Table 3.1). Compared with non-molting individuals (wing gap = 0), naturally molting bulbuls with moderately large moult-related gaps (3 < wing gap ≤ 10) actually moved 2.5 times as far per hour between residence patches (GAM estimate $F = 4.734$, p = 0.01; distance between patches: non-molting = 54.11 m, molting = 135.89 m). Similarly, naturally molting sparrows moved 1.5 times as far per hour between residence patches (GAM estimate $F = 11.58$, p = 0.00002; distance between patches: non-molting = 208 m, molting = 307 m). This is consistent with the idea that wing moult is an energetically demanding period that requires actively seeking out high-quality food sources (Madsen and Mortensen 1987; Fox et al. 1998).

Reed-warblers and swallows, which represent very rapid and very slow moult rates, respectively, showed no statistically significant change in large-scale movement with increasing size of the moult-related wing gap (Fig. 3.1: reed-warblers). Rapidly-molting reed-warblers moved similar distances between residence patches when molting or non-molting (GAM estimate $F = 0.055$, $p = 0.815$; Fig. 3.1). This is presumably because reed-warblers do not move between distant patches even when not molting (mean distance between residence patches: non-molting = 27.20 m, molting = 29.09 m, manipulated = 8.49 m) (Kiat et al. 2016). Slow-molting swallows also moved similar (large) distances per hour when they were either non-molting, molting, or artificially manipulated (GAM estimate $F = 0.129$, $p = 0.723$). Swallows' slow moult rate likely represents an adaptation to their aerial foraging habit, allowing them to maintain flight performance across moult stages (non-molting = 3.48 ± 1.36 km, molting = 3.36 ± 1.17 km, manipulated = 3.64 ± 1.96 km).

Effect of Artificial Manipulation

Our experimental manipulation involved removal of one to three primaries, in addition to the primaries missing as part of natural moult (see *Methods*). Wing gap index scores after artificial manipulation showed differences among species corresponding to their natural moult rate, manipulated reed warblers had larger wing gaps than manipulated swallows, bulbuls, or sparrows (swallows = 10.11 ± 2.5, bulbuls = 13.5 ± 2.35, sparrows = 12.56 ± 3.5, reed-warblers = 17.8 ± 1.1). Bulbuls and sparrows whose flight feathers had been removed by manipulation ($12 < \text{wing gap} < 20$) moved shorter distances than naturally molting birds (bulbuls: 68% less, 43 m; sparrows: 16.7% less, 256 m). These observations are in line with the direct effects of severely reduced flight capacity and allocating energy reserves to feather regrowth rather than movement, and an indirect effect of risk-avoidance during a vulnerable period.

Frequency of Patch Switching

We found that in addition to affecting the distance moved between residence patches, the wing gap resulting from natural moult or manipulation also affected the frequency of patch switching in bulbuls and sparrows, but not in reed-warblers (Fig. 3.2). Naturally molting bulbuls moved more often between residence patches than non-molting and artifically manipulated birds (GAM estimate $F = 7.45$, $p < 0.001$; see also *Supplementary Information* Table 3.2). However, naturally

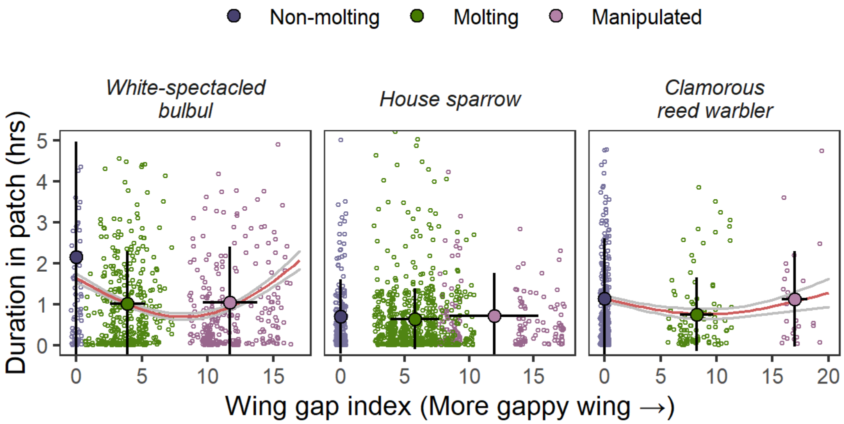

Figure 3.3: Naturally molting bulbuls and reed-warblers, but not sparrows, use residence patches for shorter durations than non-molting and artificially manipulated birds. Bulbuls and reed-warblers use contiguous areas for shorter durations when molting, than either when not molting or when some of their flight feathers have been removed by artificial manipulation. However, sparrows did not show an effect of wing condition on their use of residence patches. The visibility of a patch to low-flying predators reduced the duration for which it was used, but patch vegetation productivity (NDVI) had no effect.

molting sparrows switched between residence patches as often as non-molting birds, but artificially manipulated sparrows switched patches less frequently than molting birds (GAM estimate F = 3.515, p = 0.024; Fig. 3.2). Reed-warblers did not show a change in patch-switching frequency in relation to wing gap size (GAM estimate F = 1.04, p = 0.31).

Moult-related Wing Gap size and Patch Occupancy

We examined whether the time that bird spent in residence patches was affected by their wing gap size, with the expectation — following the results for movements between patches — that molting birds would spend less time in patches than non-molting and manipulated birds (see *Supplementary Information* for model specification). This was indeed the case for both bulbuls and reed-warblers, for which the mean patch duration for molting birds was only about half of that for non-molting and manipulated birds (Fig. 3.3; GAM estimates: bulbuls, F = 18.86, $p < 0.001$; reed warblers, F = 12.854, $p < 0.001$). However, we found that sparrows had similar patch durations across different wing gap sizes (GAM estimate F = 0.023, p = 0.878; *Supplementary Information* Table 3.3).

We expected two environmental attributes — vegetation productivity (NDVI), and visibility to predators — to also affect patch durations. To quantify patch visibility, we calculated the visibility index across our study area (Olsoy et al.

2015; Aben et al. 2018; 2021). The visibility index represents whether a location can be observed from surrounding areas, for example by a commonly occurring predator, the Eurasian Sparrowhawk (*Accipiter nisus*; see *Methods*). Areas with taller vegetation such as orchards, and built-up areas such as settlements have lower visibility indices and are more sheltered (see *Supplementary Information*), as predators' lines of sight are obstructed by intervening objects (Olsoy et al. 2015). We found that NDVI did not appear to influence patch duration (GAM parametric estimate = 0.056, p = 0.86). However, patch durations increased with reduced patch visibility (GAM parametric estimate = -0.70, p = 0.004).

Birds Occupy Sheltered Areas across Moult Rates

Finding that patch visibility influenced patch durations, we examined whether birds' moult-related wing gaps directly influenced their use of sheltered areas (except swallows, which are aerial foragers). First, fitting a GAM with species-specific smooths for bulbuls, sparrows, and reed-warblers (see *Methods*), we found that only reed-warblers had slightly more sheltered patches with larger wing gaps (GAM estimate $F = 9.30$, p = 0.002; Fig. 3.4; visibility: non-molting = 0.33 ± 0.17, molting = 0.31 ± 0.19, manipulated = 0.21 ± 0.06), potentially because their rapid moult rate severely reduces flight capacity and makes increased shelter necessary. This suggests that bulbuls and sparrows, with intermediate moult rates, occupy sheltered areas of similar (low) visibility regardless of the size of their wing gap (visibility: bulbuls = 0.39 ± 0.18; sparrows = 0.47 ± 0.19; see *Supplementary Information* Table 3.4).

We went one step further, and used a step-selection approach to sample patches to which individuals could have moved, and estimated birds' relative preference for visibility and NDVI when making movement decisions (see *Methods*) (Avgar et al. 2016; Aben et al. 2021). Fitting separate step-selection functions for each species and each broad moult group (non-molting, molting, and manipulated), we found that across moult group, all three species preferred low-visibility sheltered sites over higher visibility ones (Fig. 3.4; *Supplementary Information* Table S5). Furthermore, NDVI did not signficantly affect birds' movement decisions at the patch scale (see *Supplementary Information* Table S1). This is consistent with the idea that birds of our study species mostly avoid open agricultural fields, where they might be exposed to potential predators, even though fields are highly productive.

Interpreting the Effect of Wing Moult on Bird Movement

Our study is among the first to quantify how the compromised wing surface associated with moult directly affects movement and habitat selection in wild birds.

Our high-throughput tracking system enabled tracking small birds at temporal (several times per minute) and spatial resolutions (a few metres) far surpassing current technologies for tracking such small birds (< 50g) — mainly through radio triangulation and geolocators, that have low temporal (a few fixes per hour or day, respectively) and spatial resolution (error margins up to 200 km) (Bridge et al. 2013). Focusing on resident birds outside their breeding season, rather than migratory or breeding ones, enables at least some control on confounding factors associated with seasonal physiological changes, and the confounding effect of migration- or breeding-related energy and time requirements (Alerstam and Lindström 1990; Wikelski et al. 2003; Horvitz et al. 2014). Our study also extends the geographic range of the field to an understudied region, and to two less-studied species.

Both rapidly molting clamorous reed-warblers, and slow-molting barn swallows, did not adjust their large-scale movements to their wing condition. Reed-warblers move very short distances (< 25m) in low-visibility areas, and can afford rapid, resource-intensive feather growth (Lindström et al. 1993; Newton 2009; Kiat and Sapir 2017), as this does not compromise their ability to move scansorially through their dense reedbed habitat, which also offers shelter from visual predators. At the other extreme, barn swallows that forage exclusively while flying have evolved a very slow moult rate (Kiat et al. 2016), which likely forestalls significant direct aerodynamic effects of feather loss on flight capacity. Our work shows how birds' evolved moult strategies — which are themselves influenced by movement strategies (Kiat et al. 2016) — are interlinked with the direct, short-term effects of moult on movement.

We also found that birds with intermediate moult rates — white-spectacled bulbuls and house sparrows — adapt their movement strategies to their wing morphology. Surprisingly, these species moved more when naturally molting than non-molting. Birds can compensate for lower wing power output by growing their pectoral muscles, and this may allow them to maintain flight capacity during the moult, enabling increased movement to find resources for feather growth (Chai 1997; Swaddle and Witter 1997). Unsurprisingly, increased movements between putative foraging patches, and an increased frequency of such movements, together translate into a shorter occupancy duration in each patch. While this movement strategy conforms with optimal foraging theory — rapid abandonment of patches to maximise prey intake (Charnov 1976) — it does not appear that vegetation productivity influences patch use.

When increased movement for high quality resources (Charnov 1976) cannot compensate for the costs of inefficient flight and feather growth, moving less overall to conserve energy may be the optimal strategy until new flight feathers develop. This latter strategy should be expected when the wing gap size is in-

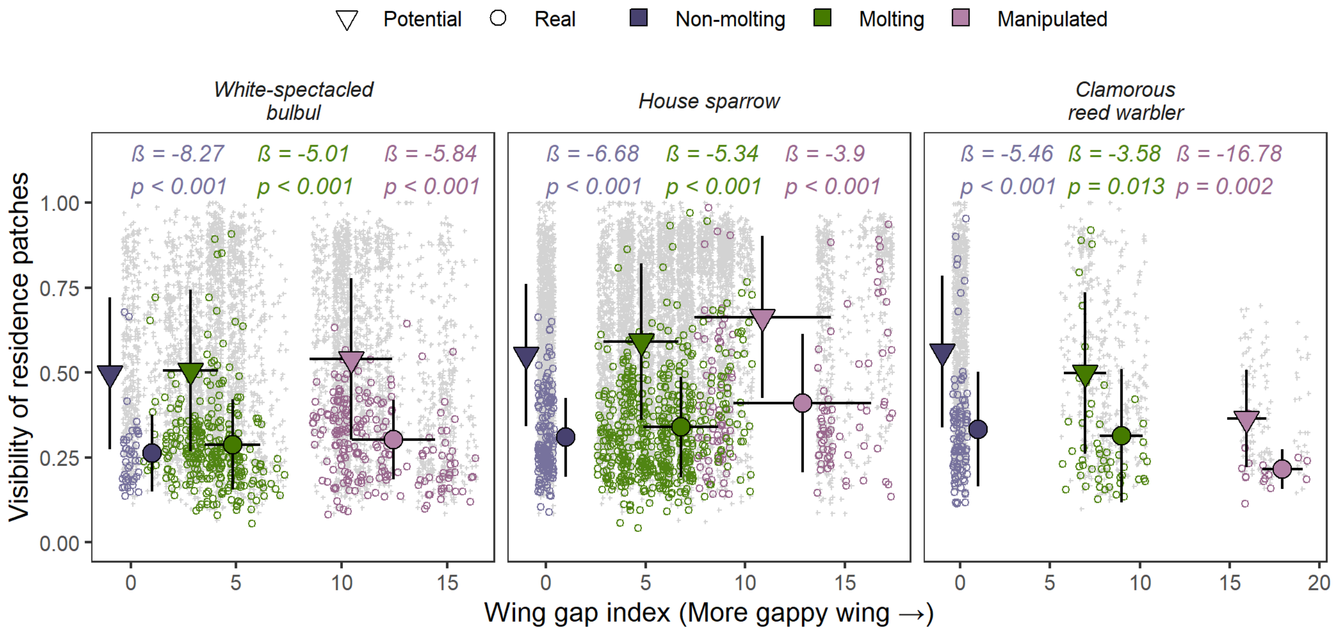

Figure 3.4: Bulbuls, sparrows, and reed-warblers prefer sheltered habitats across wing condition. Across the three species, a GAM indicated that moult-related wing gap index was a poor predictor of the visibility of areas actually occupied by individuals (‘real’ residence patches; small colored circles). A step-selection analysis at patch level, comparing real residence patches to sampled potential residence patches (grey crosses), showed strong selection for patches with low visibility index scores for all wing conditions, indicated by negative estimated selection coefficients (β = natural logarithm of relative selection strength). All β values were statistically significant (see *Supplementary Information*). Filled circles and triangles, and error bars around them, show the mean visibility index of real and potential patches for each moult treatment (indicated by color).

creased beyond the extent of natural moult, as found in our study. The shorter between-patch movements of artificially manipulated sparrows and bulbuls with especially large wing gaps (wing gap index > 12), compared with natural moult, thus fit within this hypothesis. Importantly, our relatively non-invasive method only increases the wing's feather gap size while avoiding wing injury, suggesting that the reduction in flight is actually due to considerations of flight efficiency, rather than trauma.

We have for the first time applied the idea of the cumulative viewshed to directly assess the availability of shelter from visual predators, along birds' real and potential movement paths (Olsoy et al. 2015). Birds, like other animals, are capable of taking the spatial perspective of other individuals (Emery 2000; Krams 2001; Watve et al. 2002; Davidson and Clayton 2016), i.e., whether a location would be visible to another observer, such as a predator (Watve et al. 2002; Olsoy et al. 2015). Previous work has focused on demonstrating spatial perspective taking — and resulting habitat selection — at small spatial scales of a few metres, and typically with a direct predator cue (Krams 2001; Watve et al. 2002). Our work is the first to combine the spatial perspective-taking concept with the emerging framework of animal viewshed ecology at landscape scales (Aben et al. 2018; 2021). Our findings suggest that birds can estimate the visibility (and hence riskiness) of an area from multiple perspectives, and that they can do so at relatively large, landscape scales (many dozens of metres). Our results also show how the modelling of animal movement decisions should incorporate individuals' estimates of what *other animals* can see (Hampton 1994; Emery 2000). Visibility analysis provides a simple, mechanistic way to incorporate animals' potential assessments of landscape risk into habitat selection models. This could help move away from purely correlative studies of animal habitat selection, which usually rely on predictors with very broad applicability (Pettorelli et al. 2011).

All three species studied strongly preferred sheltered, low-visibility habitats over more open sites, even when the available sites had similar vegetation productivity. Predators are unlikely to always be in the vicinity of a specific location, or indeed to always be visible. This instead points to an avoidance of open agricultural areas where predation risk is highest, showing the immediate, small-scale effects of a 'fearscape' (Olsoy et al. 2015) on animal movement. This pre-emptive caution may explain why wing condition, which should be expected to determine vulnerability to predation, did not lead to more sheltered residence patches in two of three relevant species. Furthermore, our findings suggest that avoidance of high-visibility areas may be an overlooked, yet potentially broadly applicable mechanism by which agricultural 'green deserts' exclude avian biodiversity. An unwillingness to break cover from sheltered areas, and move through high-visibility habitat, may explain how individual movement decisions can scale up to restrict animal space use, from short home-range moves to longer dispersal events (Schlägel et al. 2020). Overall, our work provides a template for combining simple experimental methods with technological advances in tracking technology, and with a mechanistic approach to landscape ecology, in animal movement research.

* * *

Supplementary Information for Chapter 3

Individuals' Wing Gap Sizes across the Study Period

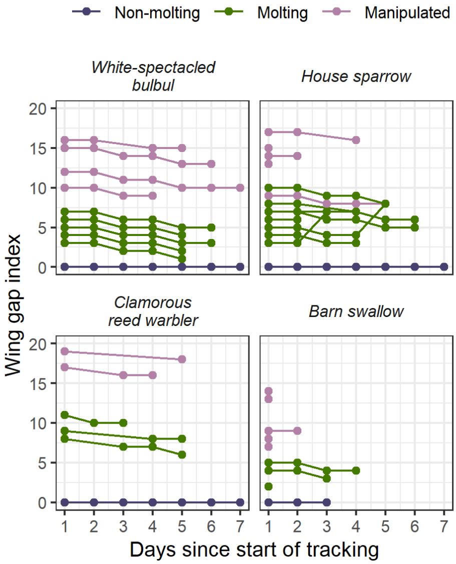

Figure 3.5: Forecast daily change in wing gap index, per individual. The size of the molt-related wing gap decreases slowly and constantly as feathers regrow, but the wing gap size may also increase in gradual jumps as a feather is shed during molt. We calculated the mean daily progress in the molt score, based on a sample of individuals of each species documented twice during the molt process. For each bird included in the study, we calculated the expected daily change in molt-related wing gap size based on the measurement we made at the time of tagging (day 1 in each panel).

Vegetation, Visibility, and Land Use across the Study Area

Land cover

We manually constructed spatial polygons of the land-cover types in our study area, based on aerial imagery and field experience (see Fig. 3.6A). We categorised the study area into five main land-cover classes: settlements and built-up areas, open or agricultural areas, naturally occurring reedbeds, areas with trees (including orchards), and water (including canals and streams).

Vegetation Productivity

We obtained a standard measure of vegetation productivity, the normalised difference vegetation index (NDVI), which is widely used in animal ecology (Pettorelli et al. 2011). We did this by accessing the European Space Agency Copernicus mission's Sentinel 2 imagery from the multi-spectral instrument, at a resolution of 10m. We accessed data from the Level-1C collection, which covered the study area during the period in which we were interested (June – October, 2016), rather than using the somewhat better Level-2A data, which covers the study area only from 2017 onwards. We calculated NDVI using the standard formula $\text{NDVI} = (\text{NIR} - \text{Red})/(\text{NIR} + \text{Red})$, where *NIR* is the near infra-red band, and *Red* is the red band. We used Sentinel band 8 (near infra-red; 835.1 nm or 833 nm) and band 4 (red; 664.5 nm or 665 nm) to calculate NDVI, with minor differences in the band wavelengths due to small differences between the two Sentinel-2 satellites, S2A and S2B. We performed the full pipeline of NDVI calculation on Google Earth Engine (Gorelick et al. 2017), using the Python API (http://code.google.com/p/earthengine-api/) and the *geemap* library (Wu 2020). NDVI across our study area varied between small negative values (indicating water), 0 (usually indicating bare ground), and large positive values up to 0.7 (indicating strong vegetation growth; see Fig. 3.6B). The largest NDVI values were associated with some agricultural fields, as well as with orchards with growing trees, and with natural reedbeds (compare see Fig. 3.6A – B; see correlation below).

Visibility Index

We obtained a canopy height model (CHM) of the majority of our study area from the Survey of Israel at 50cm resolution. We could not access CHM data for some peripheral areas as this is a border region. In contrast to the more conventional elevational model, CHMs can pick up fine-scale variation in the heights of objects above the ground surface. This makes CHMs suitable for investigating animals' interactions with their three-dimensional environment, with substantial spatial detail. CHMs are especially useful in exploring how animal movement decisions are linked to animals' lines of sight (Aben et al. 2018; 2021). We used the Visibility Index plugin v1.2 (https://github.com/zoran-cuckovic/QGIS-visibility-analysis) for QGIS v3.x (i.e., 3.0 or higher) to calculate the visibility index across the CHM. We downsampled the CHM to 1m resolution to speed up computation without losing much detail. We used an observer height of 1.5 m above the canopy surface; this is the height above either the actual tree canopy, or over any other surface present in our landscape (water, open fields, settlements etc.). We used an observer perception distance of 50 m, and calculated the proportion of 16 surrounding angles from which any cell of the CHM could be observed (option *Incoming Views*). This yielded a layer with as many cells as the CHM, and with the same (1 m) resolution, with values of the visibility between 0 and 1.

In biological terms, the visibility index is an estimate of how exposed any location is to a low-flying aerial predator, up to 50 m away. We modelled these values based on the hunting flights of a common bird-preying raptor, the Eurasian sparrowhawk (*Accipiter nisus* Krams 2001; Seress et al. 2011; Krams et al. 2020). We also considered the visibility index of our study site from the point of view of a typically high-flying raptor, the common kestrel (*Falco tinnunculus*), and repeated the visibility index calculations for an observer height of 15m (Fig. 3.6D). Kestrels hovering above the landscape surface are conspicuous to prey species whose avoidance mechanisms are primarily visual, such as small birds which rely on spotting predators early and taking cover (Krams 2001; Krams et al. 2020). Thus the strategy of bird-preying raptors such as sparrowhawks is to fly low over the landscape surface (canopy or ground), and to attempt to surprise birds while they have broken cover (Krams 2001; Seress et al. 2011; Krams et al. 2020). Accounting for these natural history and behavioural aspects of birds' predator-prey interactions, we chose the 1.5m visibility index layer for our analyses.

The visibility index of locations in our study area was strongly tied to land-cover, as expected (Fig. 3.6C; compare Fig. 3.6A). Agricultural areas have visibility index values ≈1.0, and are unlikely to offer much shelter from aerial predators. Orchards and areas of natural vegetation such as reedbeds are much more sheltered, with visibility index values < 0.2. Built-up areas such as settlements, surprisingly, have lower visibility scores than open agricultural fields, as human-made structures are relatively tall and effectively obstruct the lines of sight of predators (Fig. 3.6C; compare Fig. 3.6A).

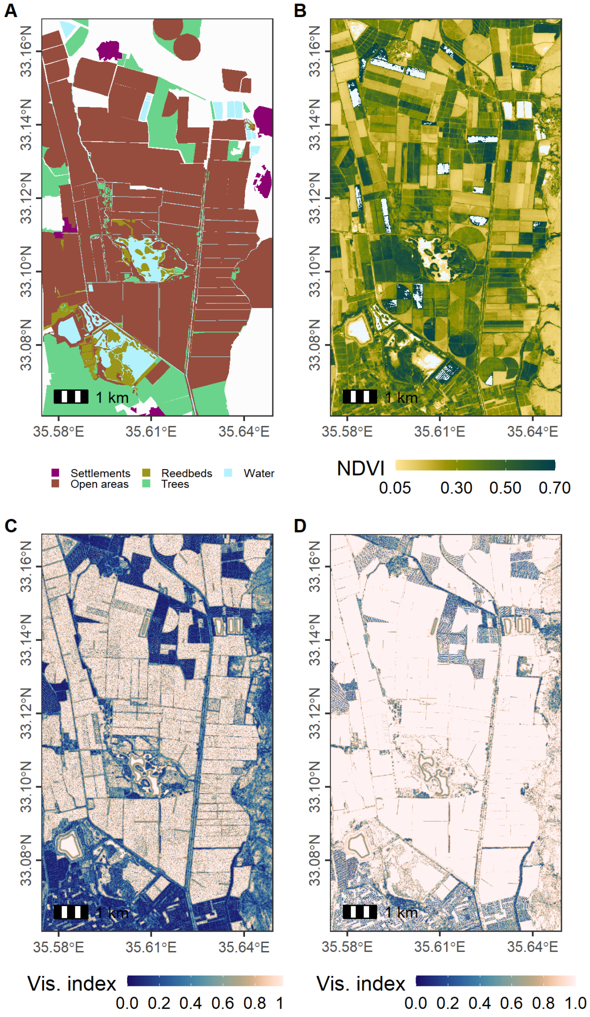

Figure 3.6: Vegetation productivity, exposure to potential predators, and land-cover across the Hula Valley, Israel. **(A)** Our study site in the Hula Valley in northern Israel is an agricultural-natural habitat matrix. **(B)** There is substantial fine-scale variation in vegetation cover and productivity (here, the normalised difference vegetation index: NDVI), even within areas of similar land-cover. Areas shown in white are water bodies. **(C)** Despite substantial areas being covered by growing vegetation, the majority of the study area is relatively exposed to a low-flying aerial predator (such as Eurasian sparrowhawk *Accipiter nisus*, with a visibility index score ≈1.0. Sheltered areas, with lower visibility index scores (< 0.4), form fine-scale refugia within the agricultural landscape. However, areas covered by fruit tree orchards are very sheltered from low-flying predators, with visibility index scores < 0.2. **(D)** The visibility of an area is strongly dependent on the height of the observer, and nearly the entire study area is heavily exposed to a high-flying aerial predator such as the common kestrel (*Falco tinnunculus*), hovering at 15m above the surface. However, this also makes high-flying predators conspicuous to visually oriented prey such as small birds. To counter this, bird-preying raptors such as sparrowhawks typically fly at low heights to surprise small birds emerging from cover.

Relationship between Vegetation Productivity and Visibility

Fine-scale variation in vegetation structure, and especially in plant height, creates three-dimensional habitat complexity, which translates into the sheltering effect of vegetated habitats. This suggests that vegetation indices such as NDVI could be used to examine the availability of shelter. We tested this hypothesis by examining the relationship between NDVI and the visibility index using a generalised additive model (GAM). We extracted the NDVI, visibility index, and land-cover type for 10,000 equally spaced locations across our study area, and excluded areas which were covered by water. We fit a GAM with the formula:

$$visibility\ index \sim s(NDVI, by = landcover) + s(landcover, bs = \text{"}re\text{"})$$

This fit a separate smooth visibility-NDVI curve for each land-cover class, and also modelled land-cover as a random effect (Wood 2017).

We found that the relation between NDVI and visibility index was statistically significant, but the shape of the relationship was strongly influenced by land-cover (Fig. 3.7; GAM degrees of freedom [DOF] = 2.99, estimate F = 1,004.02, $p < 0.001$; $R^2 = 0.596$). In areas covered by trees, NDVI values > 0.2 were uniformly associated with low visibility (< 0.25), and thus, potentially more shelter from aerial predators (GAM DOF = 5.117, estimate F = 28.0, $p < 0.001$). In natural reedbeds, we found a nearly linear relationship, with visibility declining with increasing NDVI (GAM DOF = 2.227, estimate F = 27.13, $p < 0.001$). Surprisingly, in settlements and built-up areas, visibility was consistently < 0.5, despite relatively low NDVI values overall < 0.5 (GAM DOF = 1.0, estimate F = 14.85, $p < 0.001$). This is likely because tall structures such as houses block lines of sight quite effectively. Agricultural fields and open areas had predictably high visibility values (> 0.7) regardless of their NDVI values (GAM DOF = 6.827, estimate F = 26.41, $p < 0.001$). Overall, in landscapes with mixed vegetation types, or with substantial topological complexity, NDVI does not have a simple relationship with the availability of shelter (GAM DOFs > 1.0). Selection for NDVI in animal movement studies should thus be interpreted as selection for shelter only with some caution. It is more accurate to obtain and use canopy height models to calculate visibility indices and so to get an estimate of shelter with a basis in the mechanisms of visual cognition. Where this is challenging, such as at larger spatial scales, accounting for land-cover in habitat selection models may be one alternative.

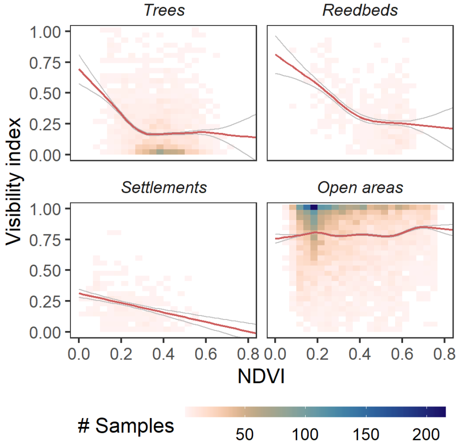

Figure 3.7: Generalised additive model fits showing the relationship between NDVI and the visibility index. Visibility index shown here was calculated with an observer height of 1.5m, which is representative of the hunting flight of bird-preying raptors (see Fig. S2C).

Modelling the Effect of Wing Gap Size on Large-scale Movements

We modelled the effect of wing gap size, given by the wing gap index, on large-scale movements using GAMs. We examined data from four non-migratory birds common to our study area in northern Israel: barn swallows (*Hirundo rustica*), white-spectacled bulbuls (*Pycnonotus xanthopygos*), house sparrows (*Passer domesticus*), and clamorous reed warblers (*Acrocephalus stentoreus*). For bulbuls, sparrows, and reed warblers, we fit one GAM with species-specific curves to relate the average hourly distance moved between areas of prolonged residence ("residence patches" Gupte et al. 2022*b*), and the individual wing gap index We used the GAM formula:

$$\begin{aligned} &distance\ between\ patches\ per\ hour \sim s(wing\ gap\ index, by = species, k = 3) \\ &\qquad\qquad + s(species, bs = "re") \end{aligned}$$

This fit a GAM with wing gap index as a smoothed term with three knots allowed, and species as a random effect (Wood 2017). Model coefficients are in Table 3.1.

To determine whether the molt-related wing gap's size also affected the frequency with which birds moved from one putative foraging patch to another, we

	Coefficients
Intercept	136.89 (60.97)*
WGI - bulbul	1.90 (1.99)*
WGI - sparrow	1.92 (1.99)***
WGI - warbler	1.00 (1.00)
Species	1.96 (2.00)***
AIC	2590.40
BIC	2619.82
Log Likelihood	−1286.41
Deviance	2573521.55
Deviance explained	0.52
Dispersion	12726.89
R^2	0.50
GCV score	13217.10
Num. obs.	210
Num. smooth terms	4

$^{***}p < 0.001$; $^{**}p < 0.01$; $^{*}p < 0.05$

Table 3.1: Generalised additive model coefficients for distance between residence patches.

	Coefficients
Intercept	0.76 (0.13)***
WGI - bulbul	1.93 (2.00)**
WGI - sparrow	1.36 (1.59)*
WGI - warbler	1.00 (1.00)
Species	1.92 (2.00)***
AIC	175.48
BIC	202.97
Log Likelihood	−79.52
Deviance	26.22
Deviance explained	0.29
Dispersion	0.13
R^2	0.27
GCV score	0.13
Num. obs.	210
Num. smooth terms	4

$^{***}p < 0.001$; $^{**}p < 0.01$; $^{*}p < 0.05$

Table 3.2: Generalised additive model coefficients for residence patch switches.

fit a GAM to the number of patch switches (essentially, the number of patches) per hour of daytime tracking, using the formula:

$$\begin{aligned}\textit{number of patches visited per hour} &\sim s(\textit{wing gap index}, \textit{by} = \textit{species}, k = 3)\\ &+ s(\textit{species}, \textit{bs} = \text{``}\textit{re}\text{''})\end{aligned}$$

Model coefficients are in Table 3.2. For swallows, we fit a GAM with distance travelled per hour of tracking as the response, and the individual wing gap index as the smooth predictor. This fit a GAM with wing gap index as a smoothed term with three knots allowed:

$$\textit{distance per hour} \sim s(\textit{wing gap index}, k = 3)$$

These results are reported in the main text.

Modelling the Effect of Wing Gap Size on Patch Occupancy

We examined whether birds' molt-related wing gap size affected the duration that they spent in each residence patch. Following from the results of the models described above (see main text Figs. 1 – 2), we expected that molting birds would spend a shorter duration in each patch, as this is the only way to achieve both farther distances between patches, as well as more frequent patches, given a constant flight speed. We fit a GAM to the duration (in hours) of each residence patch as:

$$\begin{aligned} patch\ duration \sim\ & s(wing\ gap\ index, by = species, k = 3) \\ & + visibility\ index + ndvi \\ & + s(species, bs = \text{"}re\text{"}) \end{aligned}$$

Here, we also included the visibility index and NDVI as parametric fixed effects. Model coefficients are in Table 3.3.

Modelling the Effect of Wing Gap Size on Visibility of Residence Patches

We fit GAMs with species-specific smooths to examine the effect of wing gap size on the availability of shelter in individual birds' residence patches. We included NDVI as a smoothed term to account for the effect of vegetation productivity, using the formula:

$$\begin{aligned} visibility \sim\ & s(winggapindex, by = species, k = 3) \\ & + s(NDVI, k = 5) + s(species, bs = \text{"}re\text{"}) \end{aligned}$$

Here, the wing gap index is allowed 3 knots, while NDVI is allowed five knots for a potentially more complex relationship. We did not find a significant effect of wing gap index on species' use of more sheltered patches. The one exception was clamorous reed warblers, in which the visibility of residence patches decreased linearly with increasing wing gap index (GAM DOF = 1.0 [a linear fit], F = 16.354, $p < 0.001$). Full model coefficients are reported in Table 3.4. NDVI had a significant, non-linear relationship with visibility, as expected from our analysis of the visibility-NDVI relationship above (GAM DOF = 3.885, F = 172.493, $p < 0.001$). Model results are version controlled at *github.com/pratikunterwegs/holeybirds* in the file "data/results/mod_summary_rrv_visibility.txt"

	Coefficients
Intercept	$1.15\ (0.20)^{***}$
Visibility index	$-0.80\ (0.21)^{***}$
NDVI	$0.09\ (0.27)$
WGI - bulbul	$1.98\ (2.00)^{***}$
WGI - sparrow	$1.00\ (1.00)$
WGI - warbler	$1.82\ (1.96)^{*}$
Species	$1.84\ (2.00)^{***}$
AIC	6919.17
BIC	6979.39
Log Likelihood	-3448.94
Deviance	3230.34
Deviance explained	0.06
Dispersion	1.53
R^2	0.06
GCV score	1.54
Num. obs.	2115
Num. smooth terms	4

$^{***}p < 0.001$; $^{**}p < 0.01$; $^{*}p < 0.05$

Table 3.3: Generalised additive model coefficients for residence patch duration.

	Coefficients
Intercept	0.33 (0.02)***
NDVI	1.00 (1.00)**
WGI - bulbul	1.00 (1.00)
WGI - sparrow	1.76 (1.94)
WGI - warbler	3.90 (3.99)***
Species	1.88 (2.00)***
AIC	-2108.51
BIC	-2046.84
Log Likelihood	1065.79
Deviance	22.94
Deviance explained	0.35
Dispersion	0.01
R^2	0.34
GCV score	0.02
Num. obs.	1550
Num. smooth terms	5

$^{***}p < 0.001$; $^{**}p < 0.01$; $^{*}p < 0.05$

Table 3.4: Generalised additive model coefficients for residence patch visibility.

Examining the Effects of Visibility and Vegetation Productivity on Habitat Selection

Finding a correlation between vegetation growth in the form of NDVI, and visibility, we adopted a step-selection approach (Fieberg et al. 2010; Signer et al. 2019; Fieberg et al. 2021) to disentangle the effects of these two factors on the movements of molting birds. We performed this analysis on the movements of bulbuls, sparrows, and reed warblers between their residence patches. We excluded swallows because we had not constructed residence patches for these birds, and because we could not resolve their flight altitude, making it difficult to determine whether they were using shelter.

We drew 9 alternative patch movements for every real patch movement, that is from patch N to patch $N + 1$, and sampled 15 locations distributed around the alternative moves. We drew the locations of the 9 alternative movements by drawing first a distance from a gamma distribution fitted to each individual's daily movements between patches, and second, an angle drawn from a Von Mises distribution fitted to the individual's turning angles during large-scale movements between patches (see main text Fig. 1). For each of these alternative moves, we drew 15 locations from a normal distribution centred on the coordinates of the move, with a standard deviation of 20 m. In this way, we constructed 'alternative residence patches', which we could compare with the patches that birds actually used. At each of the 135 alternative locations (15 locations × 9 patches) we obtained the NDVI and visibility index.

We compared the NDVI and visibility of the 15 points in each potential patch, with the NDVI and visibility of a flexible number of real positions of patches actually used by individuals, by fitting a conditional logistic regression to the patch status (real or alternative). On average, across species and molt status, there were 28.1 real positions (SD = 25.3) compared against 251 potential positions (SD = 228). In this way, we were able to determine how birds selected for vegetation productivity and shelter when moving. Since most birds' residence patches are in high-NDVI low-visibility areas (see main text Fig. 4), but are surrounded by high-NDVI, high-visibility areas, this allowed us to disentangle the provisioning effects of vegetation from its sheltering effects.

We fit separate regressions for each molt status for each of the three species, using the formula:

$$case\_ \sim visibility + NDVI + strata(step\ identity)$$

We chose the “approximate” fitting method to reduce computational time. Model coefficients are presented in Table 3.5; negative coefficients indicate selection against visibility, and for shelter.

	White-spectacled bulbul			House sparrow			Clamorous reed warbler		
	Non-moulting	Molting	Manipulated	Non-moulting	Molting	Manipulated	Non-moulting	Molting	Manipulated
Visibility index	-8.27^{***}	-5.01^{***}	-5.84^{***}	-5.34^{***}	-6.68^{***}	-3.90^{***}	-3.58^{*}	-5.46^{***}	-16.78^{**}
	(1.70)	(0.51)	(0.56)	(0.29)	(0.67)	(0.41)	(1.44)	(0.81)	(5.39)
NDVI	−0.45	0.99	−1.47	-0.69^{*}	0.42	−0.04	1.22	−0.00	−3.04
	(1.57)	(0.67)	(0.84)	(0.35)	(0.82)	(0.70)	(2.33)	(1.20)	(6.77)
AIC	279.66	3014.80	1874.35	5333.12	1190.49	1173.51	421.54	977.53	90.57
R^2	0.12	0.08	0.09	0.10	0.12	0.08	0.06	0.09	0.13
Max. R^2	0.55	0.67	0.63	0.68	0.58	0.61	0.57	0.65	0.50
Num. events	42	300	209	522	164	140	54	103	16
Num. obs.	415	2983	2085	5209	1614	1373	538	1022	160
Missings	0	0	0	209	1	42	0	0	0

$^{***}p < 0.001$; $^{**}p < 0.01$; $^{*}p < 0.05$

Table 3.5: Log relative selection strengths (RSS; also denoted by β) for patch visibility and NDVI.

Part II

MECHANISTIC MODELS OF THE EVOLUTION OF ANIMAL MOVEMENT

Animal movement is neither random nor optimal, but the outcome of individuals making movement decisions based on local information. The strategies underlying these decisions are, like everything in biology, shaped by animals' evolutionary contexts. Yet evolution is rarely considered in animal movement models, possibly because it is considered to be too slow to be relevant to outcomes on human timescales.

In the second part of this thesis, I probe the evolutionary causes and consequences of animal movement using mechanistic, individual-based simulation models.

Interlude B

A Primer to Mechanistic, Individual-based Models as Conceptual Tools in Evolutionary Ecology

Pratik R. Gupte

Here, I present a prototype of the models I outlined in the Introduction, in order to show how my approach differs from approaches used thus far. I show that considering movement as the outcome of evolved preferences for locally available cues leads to very different ecological outcomes when compared to mainstream frameworks such as random walks and optimal local movement. These differences can be important when such models are used as baselines against which to compare patterns observed from empirical animal tracking data, or to make predictions for how key ecological processes — such as the transmission of pathogens or culture — occur in animal populations (Cantor et al. 2021). Here I focus on movement strategies following Bastille-Rousseau and Wittemyer (2019), which are among the behavioural strategies of individuals, and which may also facilitate or constrain which other behavioural strategies individuals can employ (Nathan et al. 2008; Spiegel et al. 2017).

I compare ecological outcomes of four movement scenarios of a model with the same ecological processes. In my model, 200 individuals inhabit a landscape of 30 square units, which also contains 450 discrete food items (see Fig. B-1). Food items are patchily distributed to form distinct clusters (N = 30, 15 items per cluster). For the sake of simplicity, individuals choose only a movement direction, and have the same movement distance of 1 distance unit (like a king in chess; see Fig. B-1). Individuals can perceive food items (F) and other individuals at locations 1 distance unit away. When individuals perceive a food item, they pick it up and handle it for 5 time-steps until they can gain its energetic benefit (Ruxton et al. 1992; Gupte et al. 2021; Gupte et al. 2022*a*); I call such individuals 'handlers' (H). While individuals are handling an item, they are immobilised. Individuals compete with each other exploitatively and an item once picked up by an individual is unavailable to its neighbours; these individuals continue searching for food, and I call them 'non-handlers' (N). Items regenerate at the same location after a fixed number of timesteps, which I call the regeneration time (T_R; default = 100), and while an item is regenerating, it cannot be sensed by nearby individuals. Individuals have a lifetime of 400 timesteps, over which they forage and move over the landscape. The model's four scenarios differ in their implementation of individual movement.

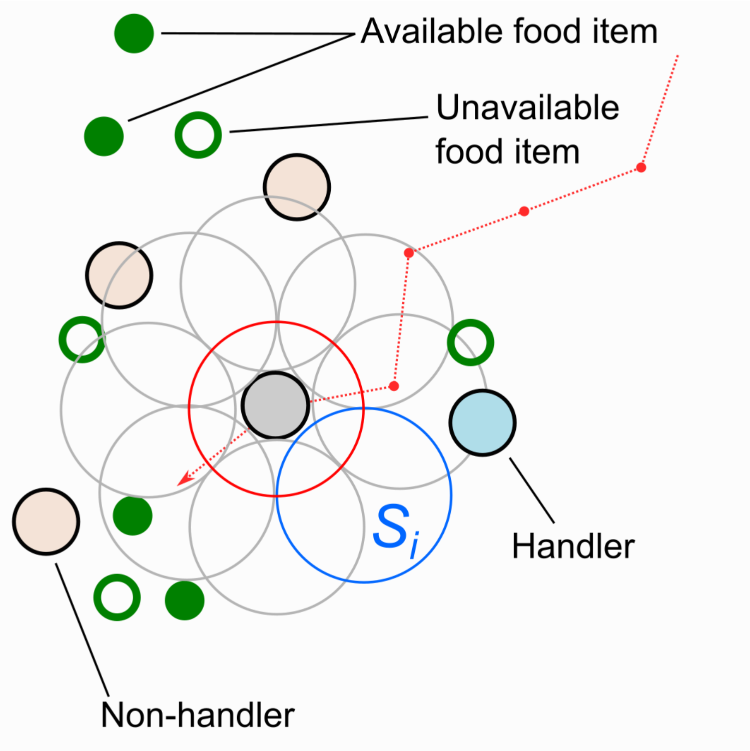

Figure B-1: Schematic for a conceptual model of individual foraging movement as a series of discrete steps in continuous space, with movement steps selected based on individual preferences for environmental cues. In this model, individuals search for patchily distributed food items (**green circles**), which may be immediately available (**filled green circles**; *F*), or may be available only in the future (**open green circles**). Individuals can sense only available items, and not unavailable ones. However, as food items are clustered, available items are a good indirect indicator of where resource clusters are, and where items may become available in the future. Individuals can also sense other foraging individuals, and can sense whether they have successfully found, and are handling, a food item (handlers; **blue circles**), or whether they are unsuccessful foragers still searching for food (non-handlers; **filled pink circles**; *N*). To decide where to move, individuals sample their environment for these three cues (*F, H, N*) at their current location (**red circle**), and at a number of locations around themselves (**large open grey circles**; here, 8 locations). When the sensory range is relatively large there is some small overlap in samples. Individuals take their next step by assigning each potential direction a *suitability*, $S = s_F F + s_H H + s_N N + \epsilon$, where the coefficients s_F, s_H, s_N are individual weights for environmental cues ('cue preferences'), and ϵ is a small error term that helps break ties between locations. The individual moves in the direction of highest suitability the cue weights fully determine the movement of an individual. Then say that the cue weights can be implemented as heritable and, hence, evolvable properties.

Scenarios in the Model

In *scenario 1*, individuals perform a random walk, and have a uniform probability of either remaining in their current location, or moving in a direction chosen from among eight locations within 1 distance unit (see Fig. B-2A); here, movement is independent of local cues. In *scenario 2*, individuals move in a way that is considered locally optimal in foraging ecology (Stephens and Krebs 2019; Scherer et al. 2020). Each individual assesses local cues at its current location, and eight surrounding locations — the number of available food items (F), and the number of potential competitors ($N + H$) — and moves to the location with the highest expected intake, which is given by $(F/(N + H + 1)) + \epsilon$; ϵ is a small error term. I initially contrast these two scenarios to show how adding suitability-based decision making to individual movement can affect the outcomes of movement individual-based models.

Locally optimal movement models are often labelled mechanistic as they include environmental cues in decision making (e.g. Scherer et al. 2020), yet the expected payoff of a location is strongly influenced by the functional response of intake in relation to competitors. Such implementations make the implicit evolutionary assumption that all individuals individuals can ‘sense’ the fitness revenue per location and then move in the direction of fitness increase. I showcase a more mechanistic way in which individuals can determine their optimal step when making foraging movements, which is to have distinct preferences for local cues (food items and potential competitors). These preferences are similar to the coefficients of habitat- and step-selection functions (Manly 2002; Fortin et al. 2005; Thurfjell et al. 2014).

In my model’s *scenario 3*, individuals assesses local cues — the number of available food items (F), and the number of potential competitors ($N + H$) — at eight locations around themselves, and move to the location with the highest assessed suitability: $S = s_F F + s_C(N + H) + \epsilon$. Here, s_F and s_C are inherited *movement preferences* for food items and potential competitors respectively, and can take any positive or negative numeric values; ϵ is a small error term. It is the relative contribution of s_F and s_C that determines individuals’ *movement strategy* (similar to the behavioural hypervolume of Bastille-Rousseau and Wittemyer 2019). I initialised the populations to have a broad range of movement strategies, so that it contained individuals with different combinations of preferences and avoidances of either food items or competitors. This assumption matters, as it speeds up initial evolution by orders of magnitude. This method is useful for obtaining a first ‘quick’ overview of the evolutionary outcome, but it is advisable to check whether the same outcome is achieved when starting with a monomorphic population with zero cue weights.

In my evolutionary approach, I am more interested in cue weights (and strategies) that have evolved subject to natural selection. Since individuals inherit their cue weights from their parents, and successful parents produce more offspring (lifetime intake is the proxy for 'fitness'), successful movement strategies are transmitted to more offspring and will thus spread in the population (an expectation from the replicator equation: Hofbauer and Sigmund 1988). To examine which movement strategies evolved, I added an evolutionary component to the model: over 100 generations, individuals reproduce, passing on their preferences (s_F, s_C) to their offspring. The preference values undergo random, independent mutations with a probability $p = 0.01$, and with a mutation step size drawn from a Cauchy distribution with a scale of 0.01. Consequently, most mutations are small, but larger mutations do occasionally occur.

For simplicity, I assume fixed population size, discrete, non-overlapping generations, asexual reproduction, and haploid individuals. I implemented large-scale natal dispersal, such that individuals are typically initialised ('born') within a standard deviation of 10 units of their parents (see Travis et al. 1999 for a consideration of how dispersal itself evolves). This makes scenario 3 relatively similar to the random initialisation of individual positions in scenarios 1 and 2. These modelling choices must be explicitly implemented in simulation models' code, bringing the assumptions of classical models — treated as received wisdom and hence ignored — to the fore.

A key feature of individual-based simulation models is their ability to incorporate great amounts of ecological detail (DeAngelis and Diaz 2019). With a simple extension to scenario 3, I show how to add biologically relevant details to models, and how these details can affect model outcomes. Foraging can be a form of public information, serving as an indirect cue of the presence of resources, and furthermore, helping distinguish between individuals that are *immediate* competitors (here, non-handlers), and those which are only future potential competitors (Dall et al. 2005; Beauchamp 2008; 2013; Giraldeau and Caraco 2018: here, handlers). Thus in my *scenario 4*, I allow individuals to sense the handling status of nearby potential competitors, and to have separate heritable preferences for handlers (sH) and non-handlers (sN). Individuals assess the suitability of locations as $S = s_F F + s_H H + s_N N + \epsilon$; ϵ is a small error term. I implemented the same evolutionary and dispersal assumptions as in scenario 3.

Comparing Scenario Outcomes

As expected, optimally moving scenario 2 individuals had a higher per-capita intake than randomly moving scenario 1 individuals (Fig. B-2). Individuals with higher intake should be expected to move less, as my model — in line with foraging ecology theory (Charnov 1976) — explicitly considers a tradeoff between movement and intake. Specifically, the tradeoff is that when an individual is handling, it cannot move towards areas of higher future expected intake, and if an individual moves into locations where there are no food items, it loses out on intake. Individuals following a locally optimal strategy moved *more* than random walkers (Fig. B-2), a clear confirmation of the expectation that such a strategy is more efficient than random walking (i.e., more food for less movement). Nonetheless, individuals in both scenarios had very similar numbers of spatial associations with other individuals (Fig. B-2, Fig. B-3). Overall, this comparison demonstrates the importance of active decision making in animal movement, and suggests why animals have evolved sophisticated sensory apparatuses to gather information from their environment (Avgar et al. 2013; Mann 2021; Swain et al. 2021; Berger et al. 2022). Such evolution is likely to be strongly dependent on fine-scale ecological conditions, primarily the *availability* of information in the environment, as well as the energetic cost of evolving and maintaining sensory capabilities (Swain et al. 2021).

I found that all 20 replicates of scenario 3 models showed that populations converged to a similar movement strategy within only a few (100) generations. This strategy was to primarily prefer moving towards food items, while having a small preference or avoidance of potential competitors. The ‘evolved’ scenario 3 individuals had better ecological performance than their ancestral populations (which I consider the first generation, G = 1), taking in more food items on average, and moving less. Indeed, these populations outperformed both the random walk and locally optimal movement implementations as well. Adapting their movement strategies to the landscape also affected the social structure of scenario 3 populations — there were fewer isolated individuals, more spatial clustering, and consequently, individuals encountered more unique conspecifics on average (higher mean degree; Fig. B-3).

Individuals evolved after 100 generations in scenario 4 had mostly evolved a movement strategy that I describe as ‘handler tracking’, i.e., having a preference for successful neighbours handling a food item ($sH > 0$), but avoiding unsuccessful neighbours that were still searching for a food item ($sN < 0$; Gupte et al. 2021; Gupte et al. 2022*a*). Importantly this strategy allows individuals to use indirect social information (Dall et al. 2005; Spiegel and Crofoot 2016), in the form of the positions of successful neighbours, to find resource clusters — even when these clusters are not immediately perceptible (due to earlier depletion).

Consequently, scenario 4 individuals outperform all three previous scenarios’ individuals by having a higher mean per-capita intake (Fig. B-2; in some cases, substantially higher). This naturally leads to the conclusion that the resource landscape in scenario 4 is more depleted than in the three previous scenarios. While not shown here, scenario 4 individuals after 100 generations of selection,

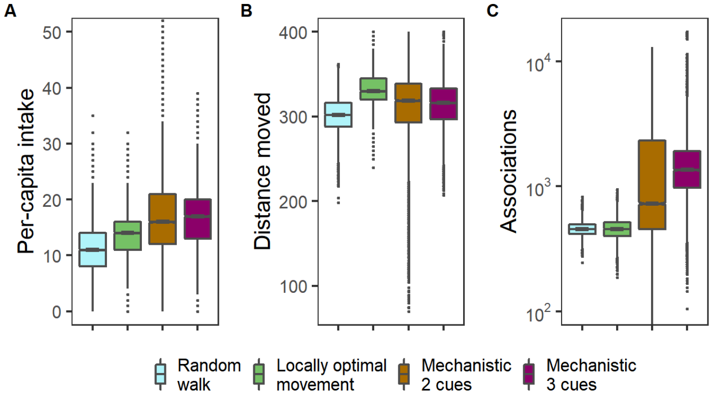

Figure B-2: Population ecological outcomes resulting from four types of movement strategy. (A) In *scenario 1*, individuals moving randomly across the landscape had expectedly lower per-capita intake than individuals moving in a locally optimal way (*scenario 2*). When individuals selected their movement step based on heritable movement preferences for food items and conspecific competitors (*scenario 3, 'mechanistic 2 cues'*), after only 100 generations of natural selection for adaptive movement preferences, scenario 3 populations had a higher intake than ostensibly locally 'optimal' movement. Allowing individuals to differentiate between current and future competitors (non-handlers and handlers, respectively; *scenario 4, 'mechanistic 3 cues'*), improved individuals' intake by a small amount, suggesting that adding information sources likely has diminishing returns, and that relatively simple step-selection movement strategies may suffice on even complex, fluctuating resource landscapes. **(B)** Surprisingly, locally optimal movers also moved more than random walkers, with no apparent trade-off between movement and intake. Individuals in scenario 3 moved less than those in scenario 2 (locally optimal), but still more than random walkers. Individuals in scenario 4 moved about the same as those in scenario 3, suggesting that being able to perceive neighbours' foraging status does indeed lead to more efficient movement strategies (i.e., more intake for similar movement). **(C)** Movement implementations strongly influenced individuals' associations (based on proximity), with step-selection based movement leading to many times more associations than random or locally optimal movement. Surprisingly, individuals in scenario 4 had many more associations than in scenario 3; this shows an unexpected difference that could have substantial consequences for the outcomes of social processes such as the transmission of animal culture or infectious pathogens.

also outperform scenario 4 populations that have not undergone selection (i.e., their ancestors), demonstrating the difference that adding evolutionary dynamics makes even to a mechanistic, habitat selection model.

Scenario 4 individuals' evolved use of social information on the potential locations of resource clusters also leads them to have more spatial associations with conspecifics — indeed, up to three times as many as in the random walk and locally optimal movement models (Fig. B-2). These associations likely occur at or near resource clusters, leading to substantial spatial-social clustering in the final generation of scenario 4 populations (Fig. B-3); and scenario 4 individuals across replicates associated with more individuals than in scenarios 1, 2 and 3. Spatial-social structure in animal populations can have important consequences for a wide range of processes and phenomena in animal ecology, including the transmission of animal culture as well as the spread of infectious pathogens (Romano et al. 2020; Cantor et al. 2021; Romano et al. 2021). The class of models I advocate are thus well suited to investigating questions around the emergent structure of animal societies (see Chapter 5 for more on this).

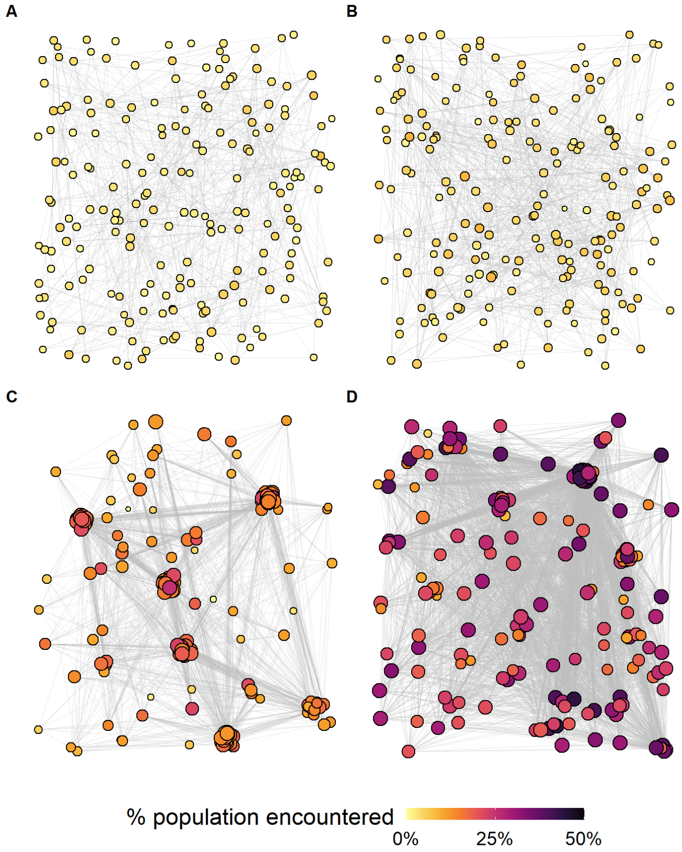

Figure B-3: Different movement strategies lead to substantially different patterns of spatial-social associations. Individuals moving randomly (**A**: scenario 1), or in locally optimal ways (**B**: scenario 2) have sparse social networks, with individuals spread out over the simulated resource landscape. Most individuals have a low degree, i.e., few unique social partners. **(C)** In contrast, individuals making step-selection based movement decisions based on two cues (food and competitors; scenario 3) have much more spatially clustered networks, with a substantially higher mean degree (more unique social partners). Over 100 generations, scenario 3 individuals are selected for their preference for food items, and the resulting populations form networks that are also clustered, but with strong connectivity between clusters, and more unique partners overall. **(D)** A similar dynamic is seen in scenario 4, where most individuals still avoid immediate competitors (non-handlers), leading to more dispersed populations than scenario 3, though with strong links between nodes.

Visualising and Interpreting Evolved Variation

In scenarios 3 and 4, individuals' movement preferences (their weights for local environmental cues) may take any numeric value. It is the combination of these weights that altogether forms each individual's movement strategies; this approach has been referred to as the 'behavioural hypervolume' approach when applied to step-selection coefficients estimated from real animal tracking data (Bastille-Rousseau and Wittemyer 2019). One challenge in encoding behavioural strategies in this way is interpreting the evolved variation in strategies, if any. A key step in doing so is exploratory visualisation — the evolved movement preferences can be plotted in relation to each other to check for any obvious clusters.

Here, I would caution that conceptual individual-based models (and step-selection functions fitted to empirical data) may have to deal with a large number of model parameters (Mueller et al. 2011), or function coefficients (Bastille-Rousseau and Wittemyer 2019). This makes clustering and interpreting these individual-level attributes a challenge, requiring complex classification approaches (Bastille-Rousseau and Wittemyer 2019). This challenge is a powerful incentive to keep conceptual models' step-selection calculations as simple as possible.

In contrast, in my conceptual models, cue weights can be readily plotted in three dimensional space (with scenario 3 requiring only two dimensions for s_F and s_C). Here, I show how the three-weight individuals of scenario 4 (with s_F, s_H, and s_N) can be represented in a convenient figure: with s_F and s_H as the X and Y axes respectively, and the weight for non-handlers s_N represented by a diverging colour scale (Fig. B-4).

The interpretation of this figure, which also helps with similar figures in chapters 4 and 6 is as follows. Each point on the figure represents a single individual. Each individual is plotted in a three dimensional space (colour representing position in the third dimension); this is Bastille-Rousseau and Wittemyer (2019)'s behavioural hypervolume. Each individual's position is calculated by scaling each of its cue preferences (say, s_i) by the sum of the absolute cue preferences: scaled $s_i = s_i / (\Sigma |s_n|)$. This means that regardless of the number of cue preferences (in this case, three), all axes are bounded by [-1, +1]. The regions individuals can take in the two primary axes is bounded by the dashed lines.

Individuals that lie towards the extremes (-1 or +1) of any axis should be interpreted as making their movement decisions primarily based on that particular cue. For example, in Fig. B-4, many individuals have values of s_F close to +1.0, indicating that they 'assign' food item cues the highest, and indeed nearly all the weight when making movement decisions. Another perspective on this is that for such individuals, the combination of cue values and the individuals' weight for them (e.g. $s_N \times N$) is often less than ϵ, i.e., their sensitivity to the cue is on the order of their perception error — not of great importance. This same interpretation applies to individuals' position on the colour scale; extreme values indicate a strong preference or avoidance of the relevant cue (here, s_N).

Interestingly, plotting individuals' evolved movement strategies in this way reveals that there is a substantial amount of variation among individuals. Indeed, individuals appear to occupy a spectrum between prioritising only food item cues (high s_F) and only handler cues (high s_H). More rarely, some individuals' position indicates that they have a strong avoidance of non-handlers. In this model, this suggests that a broad range of movement strategies can and does coexist, neatly demonstrating that behavioural variation can arise spontaneously from simple mechanistic assumptions in this class of models. Similar figures in chapters 4 show how strong correlations can arise between movement strategies as shown here, and other behavioural strategies.

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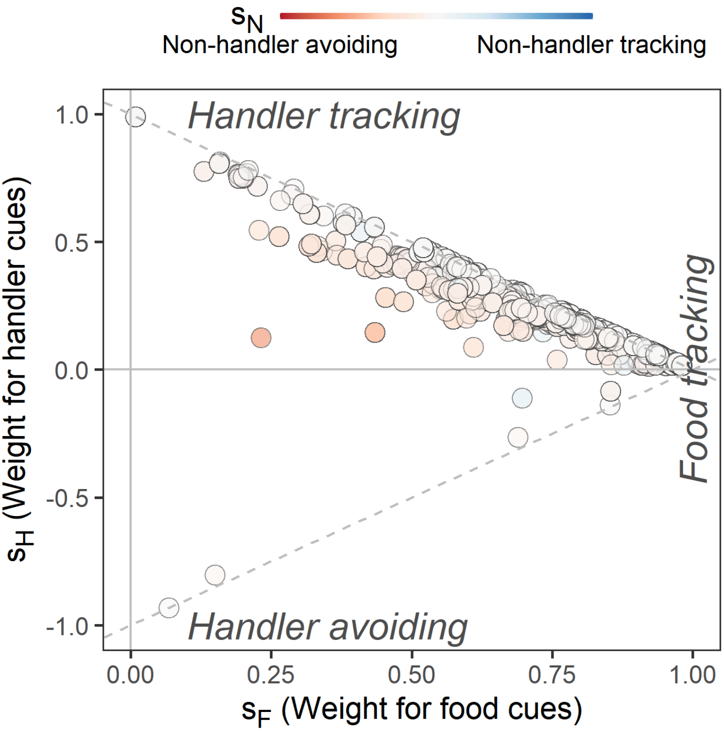

Figure B-4: Evolved variation in step-selection movement strategies revealed by simple visualisation of evolved cue weights in scenario 4. Plotting the scaled values of the heritable movement preferences (weights for local environmental cues) in a trait space bounded by [-1, +1] can reveal evolved individual variation in movement strategies. Here, most individuals lie along a behavioural spectrum: on one end ($s_F \approx +1.0$), some individuals' movement decisions are mostly influenced by differences (if any) among food item counts at the potential destinations. On the other end ($s_H \approx +1.0$), some individuals prioritise moving towards locations where there are many handlers. These patterns emerge spontaneously as results of natural selection from the simple mechanisms encoded by the model, without being forced by the modeller to represent any specific phenomenon. Yet they can be interpreted as showing the evolution and maintenance of individual variation, and especially of a broad mixture of producer-scrounger foraging strategies (Beauchamp 2008).

Chapter 4

The Joint Evolution of Animal Movement and Competition Strategies

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...[T]he highest function of ecology is the understanding of consequences.
— from Dune, by Frank Herbert.

Abstract

Competition typically takes place in a spatial context, but eco-evolutionary models rarely address the joint evolution of movement and competition strategies. Here we investigate a spatially explicit forager-kleptoparasite model where consumers can either forage on a heterogeneous resource landscape, or steal resource items from conspecifics (kleptoparasitism). We consider three scenarios: (1) foragers without kleptoparasites; (2) consumers specializing as foragers or as kleptoparasites; and (3) consumers that can switch between foraging and kleptoparasitism depending on local conditions. We model movement strategies as individual-specific combinations of preferences for environmental cues, similar to step-selection coefficients. Using mechanistic, individual-based simulations, we study the joint evolution of movement and competition strategies, and we investigate the implications for the distribution of consumers over this landscape. Movement and competition strategies evolve rapidly and consistently across scenarios, with marked differences among scenarios, leading to differences in resource exploitation patterns. In scenario 1, foragers evolve considerable individual variation in movement strategies, while in scenario 2, movement strategy shows a swift divergence between foragers and kleptoparasites. When individuals' competition strategy is conditional on local cues, movement strategies facilitate kleptoparasitism, and individual consistency in competition strategy also emerges. Across scenarios, the distribution of consumers differs substantially from 'ideal free' predictions. This is related to the intrinsic difficulty of moving effectively on a depleted resource landscape with few reliable movement cues. Our study emphasises the advantages of a mechanistic approach when studying competition in a spatial context, and suggests how evolutionary modelling can be integrated with current work in animal movement ecology.

Introduction

INTRASPECIFIC competition is an important driver of population dynamics and the spatial distribution of organisms (Krebs and Davies 1978), and has two main types, ‘exploitation’ and ‘interference’. In exploitation competition, individuals compete indirectly by depleting a common resource, while in interference competition, individuals compete directly by interacting with each other (Birch 1957; Case and Gilpin 1974; Keddy 2001). A special case of interference competition which is widespread among animal taxa is ‘kleptoparasitism’, in which an individual steals a resource from its owner (Iyengar 2008). Since competition has an obvious spatial context, animals should account for the locations of competitors when deciding where to move (Nathan et al. 2008). This is expected to have downstream effects on animal distributions across spatial scales, from resource patches (Fretwell and Lucas 1970), to species distributions (Duckworth and Badyaev 2007; Schlägel et al. 2020). Animal movement strategies are thus likely to be adaptive responses to landscapes of competition, with competitive strategies themselves being evolved responses to animal distributions. Empirical studies of this joint evolution are nearly impossible at large spatio-temporal scales. This makes models linking individual movement and competition strategies with population distributions necessary.

Contemporary individual-to-population models of animal space-use (reviewed in DeAngelis and Diaz 2019) and competition, however, are only sufficient to represent very simple movement and prey-choice decisions. For example, models including the ideal free distribution (IFD; Fretwell and Lucas 1970), information-sharing models (Giraldeau and Beauchamp 1999; Folmer et al. 2012), and producer-scrounger models (Barnard and Sibly 1981; Vickery et al. 1991; Beauchamp 2008), often treat foraging competition in highly simplified ways. Most IFD models consider resource depletion unimportant or negligible (continuous input models, see Tregenza 1995; Van Der Meer and Ens 1997), make simplifying assumptions about interference competition, or even model an *ad hoc* benefit of grouping (e.g. Amano et al. 2006). Meanwhile, producer-scrounger models primarily examine the benefits of choosing either a producer or scrounger strategy given local conditions, such as conspecific density (Vickery et al. 1991), or the order of arrival on a patch (Beauchamp 2008). Overall, these models simplify the mechanisms by which competition decisions are made, and downplay spatial structure (see also Holmgren 1995; Spencer and Broom 2018; Garay et al. 2020).

On the contrary, spatial structure is key to foraging (competition) decisions (Beauchamp 2008). How animals are assumed to integrate the costs (and potential benefits) of competition into their movement decisions has important consequences for theoretical expectations of population distributions (Van Der

Meer and Ens 1997; Hamilton 2002; Beauchamp 2008). In addition to short-term, ecological effects, competition also likely has evolutionary consequences for individual *movement strategies*, setting up feedback loops between ecology and evolution. Modelling competition and movement decisions jointly is thus a major challenge. Some models take an entirely ecological view, assuming that individuals move or compete ideally, or according to fixed strategies (Vickery et al. 1991; Holmgren 1995; Tregenza 1995; Amano et al. 2006), but see (Hamilton 2002). Models that include evolutionary dynamics in movement (De Jager et al. 2011; 2020) and foraging competition strategies (Beauchamp 2008; Tania et al. 2012) are more plausible, but they too make arbitrary assumptions about the functional importance of environmental cues to individual decisions.

Mechanistic, individual-based models are well suited to capturing the complexities of spatial structure, animal decision-making, and evolutionary dynamics (Guttal and Couzin 2010; Kuijper et al. 2012; Getz et al. 2015; 2016; White et al. 2018*b*; Long and Weissing 2020; Netz et al. 2021*b*); for conceptual underpinnings see Huston et al. (1988), Mueller et al. (2011), and DeAngelis and Diaz (2019). Individual-based models can incorporate the often significant variation in movement and competition preferences found in populations, allowing individuals to make different decisions given similar cues (Laskowski and Bell 2013). Individual-based models also force researchers to be explicit about their modelling assumptions, such as *how exactly* competition affects fitness. Similarly, rather than taking a purely ecological approach and assuming individual differences (e.g. in movement rules: White et al. 2018*b*), allowing movement strategies to evolve in a competitive landscape can reveal whether individual variation emerges in plausible ecological scenarios (as in Getz et al. 2015). This allows the functional importance of environmental cues for movement (see e.g. Scherer et al. 2020) and competition decisions in evolutionary models to be joint outcomes of selection, and lets different competition strategies to be associated with different movement strategies (Getz et al. 2015).

Here, we present a spatially-explicit, mechanistic, individual-based model of intraspecific foraging competition, where movement and competition strategies jointly evolve on a resource landscape with discrete, depletable food items that need to be processed ('handled') before consumption. In our model, foragers make movement decisions using inherited, evolvable preferences for local ecological cues, such as resource and competitor densities; the combination of preferences for each cue forms individuals' movement strategy (similar to relative step-selection: Fortin et al. 2005; Avgar et al. 2016). Lifetime resource consumption is our proxy for fitness; more successful individuals produce more offspring, transmitting their movement and foraging strategies to future generations (with small mutations). We consider three scenarios: in the first scenario, we examine only exploitation competition. In the second scenario, we introduce kleptoparasitic interference as an inherited strategy, fixed through an individual's life. In the third scenario, we model kleptoparasitism as a behavioural strategy conditioned on local environmental and social cues; the mechanism underlying this foraging choice is also inherited.

Our model allows us to examine the evolution of individual movement strategies, population-level resource intake, and the spatial structure of the resource landscape. The model enables us to take ecological snapshots of consumer-resource dynamics (animal distributions, resource depletion, and competition) proceeding at evolutionary time-scales. Studying these snapshots allows us to check whether, when, and to what extent the spatial distribution of competitors resulting from the co-evolution of competition and movement strategies corresponds to standard IFD predictions. We investigate *(1)* which movement strategies evolve in our three competition scenarios, *(2)* whether movement strategies differ within and between competition strategies in our scenarios, and *(3)* whether the emergent spatial distributions of consumers corresponds to 'ideal free' expectations.

The Kleptomove Model of Movement and Competition

Individual-based models have to explicitly specify numerous assumptions (e.g. spatial structure, individual interactions, event timescales), but this helps expose assumptions that are often hidden below the surface in analytical models. We kept our model assumptions as simple and generic as possible, striving for general, conceptual insights. To keep the model realistic, we based it on the foraging behavior of shorebirds such as oystercatchers (*Haematopus* spp.), which are extensively studied in the context of foraging competition, both empirically (e.g. Vahl et al. 2005*a*,*b*; 2007; Rutten et al. 2010*a*,*b*), and using individual-based models (reviewed in Stillman and Goss□Custard 2010).

Our environment is a fine grid of cells, and each grid cell can hold multiple individuals. Resources are discrete, as is our conception of time within and between generations. Our population, with a fixed number of individuals (N = 10,000), moves on a landscape of 512^2 grid cells (approx. 1 individual per 26 cells), with wrapped boundaries (i.e., a torus); individuals passing beyond the bounds at one end re-appear on the opposite side. The model has two time scales, first, an ecological time scale of T timesteps comprising one generation (default T = 400), during which individuals move, make foraging decisions, and handle prey-items they find or steal. Individuals are immobile while handling food items, creating the conditions for kleptoparasitism (Brockmann and Barnard 1979; Ruxton et al. 1992). At the end of each generation, individuals reproduce, transmitting their movement and foraging strategies to their offspring, whose number is proportional to individual intake at the ecological time scale. Our model has 1,000 generations, and this comprises the evolutionary timescale.

Resource Landscape

We considered our discrete resources, called ‘prey-items’ to represent mussels, a common prey of many shorebirds, whose abundances are largely driven by external gradients. We assigned each cell a constant probability of generating a new prey-item per timestep, which we refer to as the cell-specific growth rate r. We modelled clustering in landscape productivity by having the distribution of r across the grid take the form of 1,024 resource peaks, placed at regular distances of 16 grid cells from the peaks around them; r declines from the centre of each peak (called r_{max}) to its periphery (see Fig. 4.1A). Thus the central cell generates prey-items five times more frequently than peripheral cell: at $r_{max} = 0.01$, central cells generate one item per 100 timesteps (four items/generation), while the peripheral cells generate one item only every 500 timesteps (< one item/generation). All landscape cells have a uniform carrying capacity K of 5 prey-items. While a cell is at carrying capacity its r is 0. Cells are initialised with prey-items proportional to their r (see e.g. Fig. 4.1A).

Foragers perceive a cue indicating the number of prey-items P in a cell, but fail to detect each item with a probability q, and are thus successful in finding a prey-item with a probability $1 - q^P$. Individuals on a cell forage in a randomised sequence, and the probability of finding a prey-item ($1 - q^P$) is updated as individuals find prey, reducing P. Foragers that find a prey-item must handle it for a fixed handling time T_H (default = 5 timesteps), before consuming it (Ruxton et al. 1992). Natural examples include the time required for an oystercatcher to break through a mussel shell, or a raptor to subdue prey; overall, the handling action is obvious, and the prey is not fully under the control of the finder (Brockmann and Barnard 1979). Foragers that do not find a prey-item are considered idle in that timestep, and are counted as ‘non-handlers’. Similarly, handlers that finish processing their prey in timestep t can only forage again in timestep $t + 1$, i.e., they are idle in the timestep t.

All individuals move simultaneously at the end of each timestep t, and then implement their foraging or kleptoparasitic behaviour to acquire prey. However, handlers do not make any movements until they have fully handled and consumed their prey. We model movement as comprised of small, discrete steps between adjacent cells. Across scenarios, individuals make movement decisions using evolved cue preferences. Individuals select a destination cell, after assessing potential destinations based on available cues, similar to approaches used previously (Getz et al. 2015; 2016; White et al. 2018*b*; Scherer et al. 2020; Netz et al. 2021*b*).

To move, individuals scan the nine cells of their Moore neighbourhood for three environmental cues, *(1)* an indication of the number of discrete prey-items P, *(2)* the number of individuals handling prey H (‘handlers’), and *(3)* the number of individuals not handling prey N (‘non-handlers’). Individuals rank the potential destinations (including their current cell) by their suitability S, where $S = s_P P + s_H H + s_N N$, and move to the most suitable cell in timestep $t + 1$. The individual preferences for each cue, s_P, s_H, and s_N, have numeric values, are considered to be evolvable traits that can be transmitted between generations, and undergo independent mutation. Since individuals are constrained to perceiving and moving short distances, they may not always sense their best long-term move.

It is the combination of cue preferences, and especially their value relative to each other, that determines individual movement decisions (similar to relative selection coefficients, Fortin et al. 2005; Avgar et al. 2016; White et al. 2018*b*). For example, an extreme value of s_P relative to the other preferences would mean that an individual’s movement decisions are guided primarily by differences in the local density of prey-items. We call an individual’s combination of inherited preferences its *movement strategy* (see e.g. Fig. 4.1E).

Competition Strategies

In scenario 1, we simulate only exploitative competition; individuals (henceforth called ‘foragers’) move about on the landscape and probabilistically find, handle, and consume prey-items. Foragers can be either in a ‘searching’ or a ‘handling’ state (Holmgren 1995).

In scenario 2, the competition strategy is genetically determined and transmitted from parents to offspring: exploitative competition (by foragers), or kleptoparasitic interference (by kleptoparasites). Kleptoparasites cannot extract prey-items directly from the landscape, and only steal from handlers (see Holmgren 1995). Kleptoparasites are always successful in stealing from handlers, and such successful surprise attacks are commonly observed among birds (Brockmann and Barnard 1979). When multiple kleptoparasites target the same handler, only one (randomly selected) is considered successful — thus kleptoparasites compete exploitatively among themselves. Kleptoparasites displace the handler that they robbed of prey up to 5 cells away from their location. Having acquired prey, kleptoparasites become handlers, but need only handle prey for $T_H - t_h$ timesteps, where t_h is the time that the prey has already been handled by its previous owner. Once a kleptoparasite becomes a handler, it can also be targeted by other kleptoparasites. Unsuccessful kleptoparasites are considered idle, and are counted as non-handlers. Movement strategies evolve independently of the competition strategy, as in scenario 1; however, the optimal movement strategy for foragers need not be the same as that for kleptoparasites.

In scenario 3, each individual can either act as a forager, or as a kleptoparasite, depending on its assessment of local conditions. Similar to how movement decisions are made based on local cues, individuals process cell-specific environmental cues in timestep t to determine their competition strategy in the next timestep as

$$\text{strategy} = \begin{cases} \text{forager}, & \text{if } w_P P + w_H H + w_N N \geq w_0 \\ \text{kleptoparasite}, & \text{otherwise} \end{cases} \tag{4.1}$$

where the cue preferences w_P, w_H and w_N, and the threshold value w_0, are numeric values, and heritable between generations (with small, rare, independent mutations). The combination of the cue preferences for competition decisions forms each individual's *competition strategy*. Individuals' competition strategies may lead to specialisation as foragers or kleptoparasites (as in scenario 2), or to plastic behaviour conditioned on local cues. The competition dynamics are the same as in scenario 2.

Reproduction and Inheritance

Our model considers a population of fixed size (10,000 individuals) with discrete, non-overlapping generations. For simplicity, we assume that individuals are haploid and reproduction is asexual. In scenarios 1 and 2, individuals only inherit and transmit their cue preferences (s_P, s_H, s_N) which determine movement decisions. In scenario 3, individuals also inherit cue preferences for competition decisions (w_P, w_H, w_N, w_0), and transmit them to offspring. The movement and competition cue preferences all mutate independently in scenario 3. Each individual's number of offspring is proportional to the individual's total lifetime intake of resources; hence, resource intake is used as a proxy for fitness. A weighted lottery (with weights proportional to lifetime resource intake) selects a parent for each offspring in the subsequent generation (see e.g. Tania et al. 2012; Netz et al. 2021*b*). Across scenarios, the cue preferences for movement decisions are subject to rare, independent mutations ($\mu = 0.001$). The mutational step size (either positive or negative) is drawn from a Cauchy distribution with a scale of 0.01 centred on zero, allowing for a small number of very large mutations while most mutations are small. In scenario 2, foragers may infrequently mutate into a kleptoparasite (or *vice versa*; $\mu = 0.001$). In scenario 3, the competition cue preferences also mutate as described above. Each offspring is initialised at random locations on the landscape, leading individuals to experience conditions potentially different from those of their parent. We chose this option because it allows us to focus on adaptive movement strategies, whereas limited dispersal confounds movement and local adaptation.

Simulation Output and Analysis

We ran all three scenarios at a default r_{max} of 0.01, which we present in the Results, and also across a range of r_{max} values between 0.001 and 0.05 (see Fig. 4.6 and Supplementary Material Figs. 7 – 9). We initialised the cue preferences with values drawn from a Cauchy distribution with a scale of 0.01 centred on zero; this allows a very small amount of variation in the population (see e.g. Fig. 4.1E), and is equivalent to a single generation of mutation from all preferences initialised at zero (see Reproduction and Inheritance above). Normalising each individual's cue preferences by the sum of the absolute values of all preferences $s_I = s_I / (|s_P| + |s_H| + |s_N|)$, for $s_I \in s_P, s_H, s_N$, makes it possible to visualise individuals on a three-dimensional trait space of relative preferences bounded by (-1.0: *strongly avoid*, +1.0: *strongly prefer*). With remarkably consistent outcomes across replicates in each scenario, and as each simulation run produced massive datasets, we show the outcomes of three replicates here. More data can be generated and analysed using the code linked below.

Across scenarios, in each generation, we counted the number of times foragers were searching for prey, kleptoparasites were searching for handlers, and the number of timesteps that individuals of either strategy were handling a prey-item. We refer to the ratio of these values as the population's 'activity budget'. We examined how the population activity budget developed over evolutionary time, and whether a stable equilibrium was reached. Furthermore, we counted the population's mean per-capita intake per generation as a measure of population productivity.

To understand the evolution of individual movement and competition strategies, we exported the cue preferences of each individual in every generation of the simulation. We scaled each cue preference by the sum of the absolute values of the preferences, allowing us to plot individuals in a standardised three-dimensional trait space of relative cue preferences (with colour as an axis on a two-dimensional plot). Individuals' position in this space allowed us to easily visualise and compare variation in movement strategies within and between competition strategies and across scenarios.

Scenario 3 competition strategies are determined by four values (3 preferences and threshold value), and competition decisions are outcomes of the interactions of these preferences with individuals' movement decisions and ecological conditions. This makes strategies *per se* difficult to visualise. We first scaled the competition cue preferences and the threshold value as we did the movement cue preferences. To illustrate variation in the competition strategies evolved, we presented each individual in representative generations (G = 10, 30, 100, 300, 950) with combinations of two key cues, handler and prey density (each 0 – 5; 36 combinations overall). We summarised the proportion of individuals that would attempt to steal at each combination of cue values (see Eqn. 1; Fig. 4.4F).

We exported snapshots of the entire simulation landscape at the mid-point of each generation (t = 200). Each snapshot contained data on *(1)* the number of prey-items, *(2)* the number of handling individuals, and the number of individuals using either a *(3)* searching forager strategy or *(4)* kleptoparasitic strategy, on each cell. We used a subset of the total landscape (60^2 of 512^2 cells) for further analyses to speed up computation. We determined the availability of direct resource cues for movement in each cell by calculating the cell-specific item gradient for each landscape snapshot, as the difference in prey counts between each cell and its neighbouring cells. For each generation, we calculated the proportion of cells from which it was possible to sense differences in prey-items, i.e., a neighbouring cell with either more or fewer items.

A basic prediction of the IFD and the related matching rule is that the number of individuals on occupied patches should be proportional to patch productivity (Fretwell and Lucas 1970; Parker 1978; Houston 2008). Patch productivity is challenging to measure in real world systems, but is among our model's building blocks, and we examined the correlation between the number of individuals (excluding handlers) and the cell-specific productivity r, expecting large positive values.

Outcomes from the Kleptomove Model

Scenario 1: No Kleptoparasitism

In scenario 1, foragers deplete prey-items faster than they are replenished, drastically reducing the overall number of prey within 50 generations (Fig. 4.1A). The population activity budget is split between searching and handling (Fig. 4.1B); while handling and the mean per-capita intake are both initially low, they peak within ten generations (Fig. 4.1C), as individuals easily acquire prey-items from the fully stocked landscape in the first few generations. With dwindling prey-items, fewer searching foragers find prey, and handling as a share of the activity budget declines to a stable ~ 45% within 50 generations, and mean per-capita intake also stabilises (Fig. 4.1C). Across generations, the correlation between the number of foragers and cell productivity is only slightly positive (Fig. 4.1D). This is in contrast with the perfect correspondence between resource input rate and

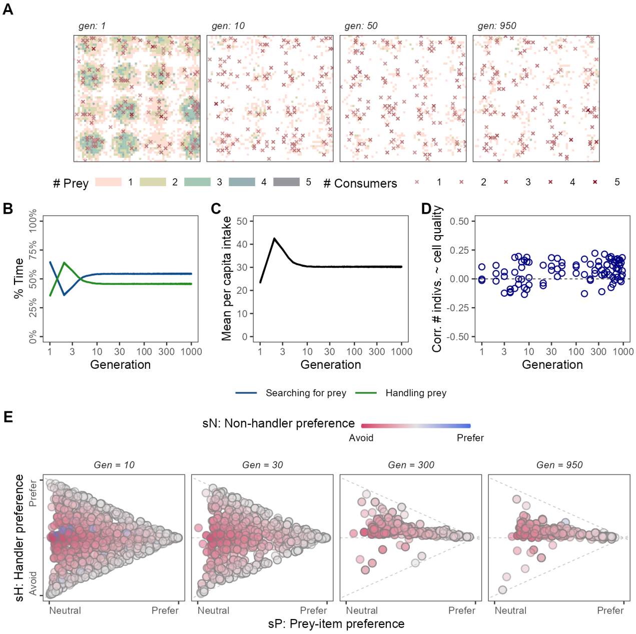

Figure 4.1: Eco-evolutionary implications of pure exploitation competition in scenario 1. (A) A population comprised solely of foragers seeking prey on a resource landscape swiftly depletes initially abundant prey-items within 10 generations (of 1,000 simulated). Foragers maintain this prey-item scarcity throughout the remaining generations of the simulation, despite regular resource regeneration (see G = 950). **(B)** Within 20 generations of evolution, the population reaches an equilibrium in the relative proportion of time spent on searching for prey and handling prey, and in **(C)** mean per-capita intake. **(D)** The number of foragers per cell is only weakly correlated with cell productivity r, contrary to the input matching rule of Ideal Free Distribution theory. **(E)** A wide range of movement strategies co-exist on the landscape over hundreds of generations. Individuals may focus on moving up gradients of prey-items (sP ≈ 1.0: *prefer*), moving towards successful foragers (handlers), or moving away from unsuccessful foragers which are potential competitors (sN ≈ red). Panels **A, E** show a single replicate, panels **B, C, D** and **D** show three replicate simulations with log-scaled X-axes (lines overlap almost perfectly); all panels are for r_{max} = 0.01; panel **E** shows 2,500 individuals.

forager density (the ‘input matching rule’), which is a defining property of the IFD (Parker 1978; Houston 2008). Contrary to standard IFD assumptions, foragers cannot directly sense the local cell productivity r; instead they can only use the (small) number of prey-items available in a cell as a cue for local productivity. A wide range of movement strategies co-exist on the landscape (see all generations in Supplementary Material Fig. 2, 6). Some individuals mostly move up gradients of prey-items (Fig. 4.1E; $s_P \approx 1.0$), some move primarily towards successful foragers (handlers), while others move away from unsuccessful foragers which are potential competitors (more red s_N).

Scenario 2: Co-existence of Foragers and Kleptoparasites

In scenario 2, with fixed foraging and kleptoparasitism allowed, the spatial distribution of prey-items at equilibrium is very different from scenario 1. Consumers graze down resource peaks until few prey-items remain on the landscape; however, within 50 generations the resource landscape recovers with prey abundances higher than in the earliest generations (Fig. 4.2A). This is because of the emergence of kleptoparasites (Fig. 4.2B): in early generations, kleptoparasites are rare, and the activity budget, the mean per-capita intake, and the distribution of consumers over the landscape, are similar to scenario 1. As resources are depleted and kleptoparasite-handler encounters become more common than forager-prey encounters, kleptoparasitism becomes the majority strategy (a stable ~70% of the population; see Fig. 4.2B), and searching for handlers to rob becomes the commonest activity. However, the high frequency of this activity and the low frequency of handling, indicate that few kleptoparasites are successful at robbing handlers.

With few foragers, few prey-items are extracted from the landscape, which recovers beyond its initial prey abundance within 50 generations (Fig. 4.2A). As fewer prey-items are extracted overall, mean per-capita intake also declines from an initial peak (Fig. 4.2C). Despite the strong spatial structure of the resource landscape within 50 generations, the correlation between consumers (of either strategy) and cell productivity remains weak or zero across generations (Fig. 4.2D). This may be partially explained by the ecology of kleptoparasitism: foragers are regularly displaced by kleptoparasites, and kleptoparasites must themselves move to find handlers.

There is a sharp evolutionary divergence of movement strategies between foragers and kleptoparasites. While both foragers and kleptoparasites evolve to prefer prey and avoid non-handlers, their response to handlers is very different (Fig. 4.3; see also Supplementary Material Fig. 3, 5). Kleptoparasites very rapidly evolve a strong preference for moving towards handlers, which are their primary resource (Fig. 4.3). In the absence of kleptoparasites, foragers would also evolve a similar preference (Fig. 4.1E), but, with kleptoparasites common in the population, foragers converge upon a handler-avoiding strategy (Fig. 4.3). This completes the explanation for why consumers do not match landscape productivity: foragers evolve strategies to avoid high productivity areas (which are more likely to have many handlers), while kleptoparasites evolve strategies to find handlers (which need not be on high productivity cells).

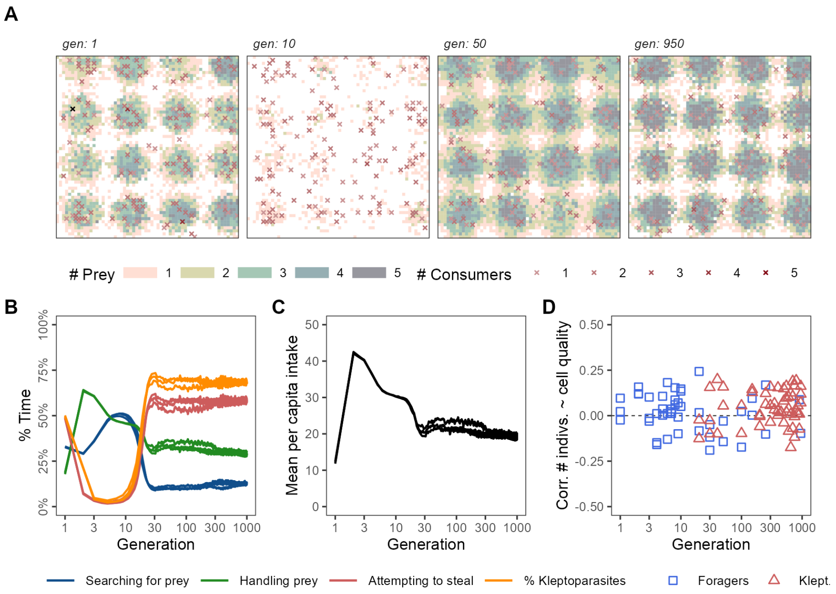

Figure 4.2: Eco-evolutionary implications of the coexistence of foragers and kleptoparasites following fixed competition strategies in scenario 2. (A) Populations with both foragers and kleptoparasites drastically deplete the initially well-stocked resource landscape by generation 10; however, prey densities recover strongly by generation 50, even beyond the densities in generation 1. **(B)** A surprisingly stable equilibrium between the forager and kleptoparasite strategies is reached within 30 generations, with the relative frequency of kleptoparasites (orange line) first dropping to very low levels but later recovering to reach a high level (~ 70%) in all three replicates. Consequently, at equilibrium, only about 10% of individuals are foragers searching for prey, 50% are kleptoparasites attempting to steal from handlers, and 40% are handlers processing prey-items (either foragers or kleptoparasites). **(C)** When kleptoparasites are rare, the population intake rate exhibits the same pattern as in scenario 1, dropping to a lower level with the emergence of kleptoparasites. Naturally, there is an increase in the proportion of time spent on stealing attempts (red line – **B**), and a corresponding decrease in prey seeking (by searching foragers; blue line – **B**), and handling (green line – **C**). **(D)** Neither foragers nor kleptoparasites follow the input matching rule, and the correlation of their abundance with cell productivity r is zero at equilibrium. Panel **A** shows a single replicate, while **B, C, D** and **D** show three replicates with log-scaled X-axes; all panels are for $r_{max} = 0.01$.

Scenario 3: Condition-dependent Kleptoparasitism

When individuals are allowed to choose their competition strategy (foraging or kleptoparasitism) based on local environmental cues, the distribution of prey-items is substantially different from the two previous scenarios (Fig. 4.4A). Initially, individuals deplete the resource landscape of prey-items within ten generations. By generation 50, the resource landscape recovers some of the spatial structure of early generations, but prey-item abundances do not match the recovery seen in scenario 2. This is because unlike scenario 2, individuals search for

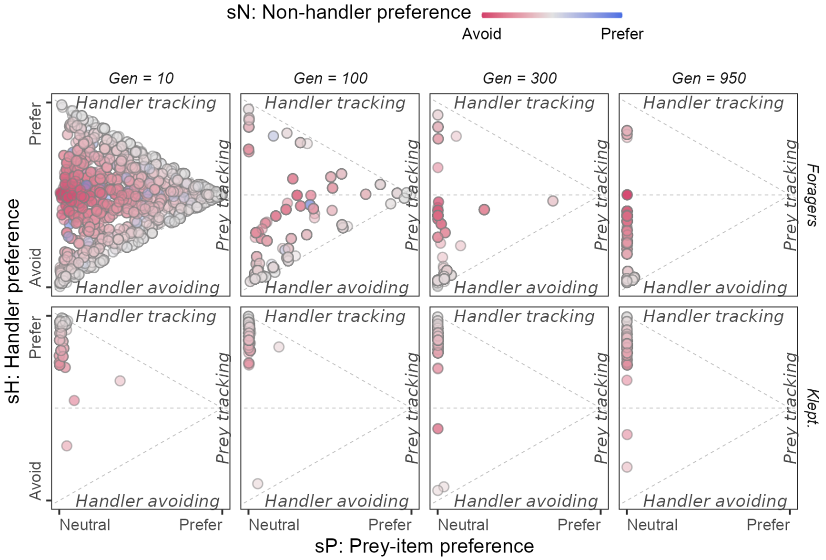

Figure 4.3: Rapid divergence of movement strategies between foragers and kleptoparasites in scenario 2. In scenario 2, kleptoparasites rapidly diverge (within 10 generations) from foragers in their movement strategy, clustering around sH = 1.0: a handler-tracking strategy. This strategy is stably maintained throughout the simulation (G = 100, 300, 950). Foragers retain substantial diversity in movement strategies for many generations (see G = 100), but unlike scenario 1, tend to be repelled (relative sH < 0), as well as attracted to handlers (relative sH > 0). Over time, foragers adopt a strategy that helps them avoid all other individuals (G = 300, 950). A few individuals sporadically adopt a movement strategy associated with the opposite competition strategy; this is most likely due to mutations in the competition strategy, rather than a new movement morph within either foragers or kleptoparasites. At the evolutionary equilibrium then, social information (either sH or sN) is the strongest component of all individuals' movement strategies. All panels show 2,500 individuals (25% of total) from the same simulation replicate (r_{max} = 0.01), and earlier generations are ancestors of later generations.

prey more often and steal less (at or below 25%; compare Figs. 4.4B and 4.2B), preventing a full recovery of the resource landscape. Consequently, mean per-capita intake stabilises (after an initial spike, as in scenarios 1 and 2) within ten generations to a level similar to scenario 1 (Fig. 4.4C). While not as strong as predicted by IFD theory, the correlations between consumer abundance and cell productivity are weakly positive (Fig. 4.4D).

The weak input matching is likely because all individuals prefer to move up gradients of prey density, and towards handlers, which are more likely to be found on resource peaks (Fig. 4.4E; see also Supplementary Material Fig. 4, 7). Using conditional foraging strategies, individuals are able to switch between resource types (prey and handlers) depending on which is more profitable (Emlen 1966) ('opportunistic kleptoparasitism'; Fig. 4.4F; see Supplementary Material Fig. 6). All individuals would choose to steal when handlers are present, even when prey items are more common. Indeed, about 40% of individuals would choose to steal even when prey are abundant and there are no handlers at all, showing the prevalence of a ‘fixed kleptoparasite’ clade similar to scenario 2. In a further parallel with scenario 2, about 70% of individuals have an intrinsic bias towards kleptoparasitism, i.e., they would by default attempt to steal when there are no cues to inform their decision (Fig. 4.4F: $P = 0$, $H = 0$).

Movement Strategies on Depleted Landscapes

Orienting movement towards resources (Nathan et al. 2008: *where to move*) can be a challenge in a system with low densities of discrete prey-items, because the local prey *density* may provide very limited information about local *productivity*. In our model, prey-depletion leads parts of the resource landscape to become ‘clueless regions’ (Perkins 1992), where foragers cannot make directed movements based on prey-item abundances alone, as all neighbouring item abundances are identical (see white areas in Fig. 4.5A; A1: scenario 1, A2: scenario 2, A3: scenario 3). At the beginning of all three scenarios, about 75% of landscape cells have a different number of prey-items from the cells around them; these are primarily cells with an intermediate r, which have more prey than peripheral cells of resource peaks, but fewer prey than the central cells. This proportion rapidly declines to a much lower value within 10 generations in all three scenarios.

The ‘cluelessness’ of the landscapes develops differently across scenarios on evolutionary timescales (Fig. 4.5B). In scenario 1, the proportion of cells with a different number of items in the neighbourhood is initially very high (Fig. 4.5A1). This proportion rapidly declines to ~25% within 10 generations, as foragers deplete most prey-items, making most of the landscape a clueless region. In this context, foragers evolve to move towards handlers, with > 75% of individuals showing a preference for handlers within 100 generations (Fig. 4.5B1). Forager preference for handlers may be explained as the sensing of a long-term cue of local productivity. Since handlers are immobilised on the cell where they find a prey-item, handler density is an indirect indicator of cell r, and due to spatial autocorrelation, also of the r of bordering cells.

Scenario 2 landscapes develop similarly to scenario 1 in early generations (Fig. 4.5A2). However, within 50 generations, most cells bear items as extraction is reduced, with differences among cells according to their r (see also Fig. 4.2A). Thus > 75% of cells have a different number of items from neighbouring cells (Fig. 4.5A2 – panel *gen: 50*, 5B2). Unlike scenario 1, the rapid increase in handler preference is driven by kleptoparasites becoming the majority strategy (see above). Scenario 3 is similar to scenario 2, except that only about half of all cells have a different number of prey-items from neighbouring cells (Fig. 4.5A3, 5B3). Here, the rapid evolution of a handler preference in movement decisions cannot be

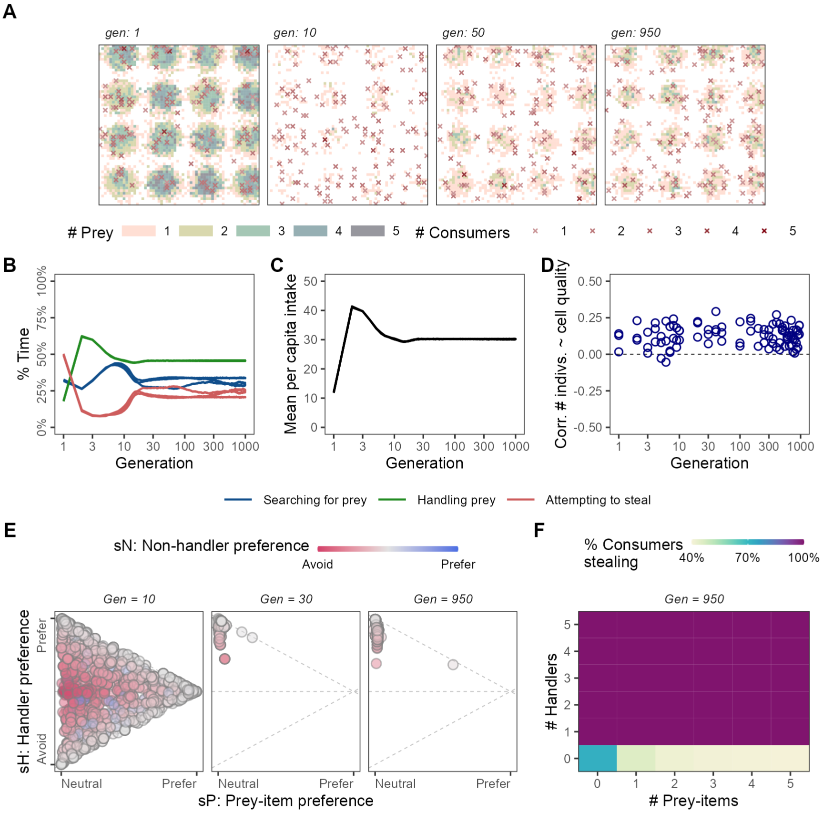

Figure 4.4: Eco-evolutionary implications of conditional foraging strategies in scenario 3. (A) The initially well-stocked resource landscape is rapidly depleted within 10 generations, yet within 50 generations, prey abundances recover on many cells, though not to the extent of scenario 2. The local density of individuals on occupied cells is shown as coloured crosses. **(B)** By generation 30, the proportion of time spent searching (blue line), handling (green line), and stealing prey (red line) reach an equilibrium that differs somewhat across replicates, but **(C)** the total intake of the population reaches the same equilibrium value in all three replicates. **(D)** The correlation between the local density of individuals on a cell, and its productivity r is stronger than in scenario 2. **(E)** From an initially high diversity of movement strategies, there is a rapid convergence (within 30 generations) of all individuals to strongly prefer moving towards successful foragers, or handlers, nearly to the exclusion of all other movement cues. This handler-tracking strategy once established is maintained (Gen = 300, 950). **(F)** Population competition strategies are more varied. While most individuals will choose to forage as prey density increases, about 40% of individuals attempt to steal even when prey is abundant and handlers are scarce. All individuals will steal when handlers are available. Panels **A, E** show a single replicate, while **B, C** and **D** show three replicates, **F** shows the mean across replicates; all panels are for r_{max} = 0.01.

assigned a clear cause, since handlers are both a potential direct resource as well as indirect cues to the location of productive cells.

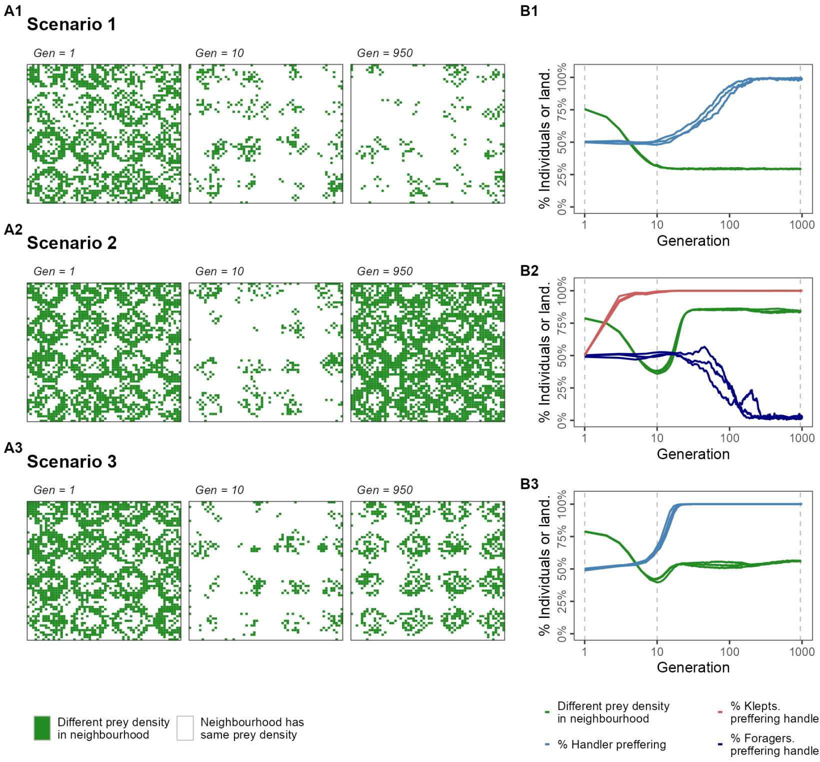

Figure 4.5: Uninformative prey densities and the evolution of social information as an alternative movement cue. (A1, A2, A3) On cells coloured green, local prey densities are informative for movement, as the central and neighbouring cells have different prey densities. While differences in local prey densities provide informative cues for 'adaptive' movement in early generations, this is much less true once the resource landscape is depleted of prey-items (depending on the scenario). **(B1, B2, B3)** The proportion of cells where differences in local prey densities provide informative movement cues (green line), and the proportion of individuals preferring to move towards handlers (blue line), whose presence may be used as an alternative cue for movement towards higher-productivity areas of the landscape. In **(B2)** representing scenario 2, this proportion is shown separately for foragers (blue line) and kleptoparasites (red line). While panels in **(A)** show a single representative replicate for r_{max} = 0.01, panels in **(B)** show three replicates.

Effect of Landscape Productivity

The prey-item regrowth rate that characterises the peaks of the resource landscape (r_{max}) is a measure of the productivity of the resource landscape overall. Having thus far focused on scenarios with $r_{max} = 0.01$ (corresponding to a peak production of 4 food times per consumer lifetime), we find that, not unexpectedly, the value of r_{max} has a marked effect on evolved population activity budgets, mean per capita intake, and even evolved strategies. The frequency of foraging reduces with r_{max} in scenarios 1 and 3; this is caused by more frequent acquisition of prey-items (as regrowth keeps pace with depletion), which results in a greater frequency of handling rather than foraging.

In scenario 2 however, the frequency of handling is relatively unaffected by increasing r_{max} (Fig. 4.6A). The difference between scenarios 2 and 3 has to do with the change in the frequency of kleptoparasitism (Fig. 4.6B). In scenario 2, kleptoparasitism forms > 75% of all activities at low r_{max}, and is much more common than in scenario 3 populations at the same regrowth rate. However, at relatively high r_{max} (0.03), the fixed kleptoparasitic strategy goes extinct. This is because at high r_{max}, forager-prey encounters are more common than kleptoparasite-handler encounters, in both early (< 10) and later generations (> 50). Consequently, kleptoparasites have relatively much lower fitness than foragers, and do not proliferate. Thus at high r_{max}, a scenario 2 population is nearly identical to a scenario 1 population; while some kleptoparasites may be seen in later generations, these occur most likely due to ephemeral mutations in the forager strategy.

In scenario 3, kleptoparasitism persists at low frequencies even at the highest regrowth rates (Fig. 4.6B); thus some foragers lose time in extracting items which are then stolen from them. Consequently, while populations in all three scenarios achieve very similar mean per-capita intakes at low r_{max}, at intermediate regrowth rates (0.01, 0.02), conditionally kleptoparasitic populations achieve a higher mean per-capita intake than populations using fixed strategies. Only at high r_{max}, when fixed strategy populations effectively convert to purely forager populations, do they achieve a higher intake than conditional strategy populations (Fig. 4.6C).

Contextualising the Outcomes of the Kleptomove Model

Our spatially-explicit individual-based model implements the ecology and evolution of movement and foraging decisions, as well as resource dynamics, in biologically plausible ways, and offers a new perspective on the distribution of animals in relation to their resources under different scenarios of competition. First, individuals moving with a limited perception range and competing only by exploitation, evolve movement strategies for both direct and indirect resource cues (prey-items and handlers, respectively). Regardless, on a resource landscape with discrete prey-items, large areas may become devoid of any movement cues, leading to a mismatch between individual distribution, prey-item distribution, and landscape productivity. Second, interference competition in the form of kleptoparasitism rapidly establishes itself on landscapes where stealing is more time-efficient than searching for prey, even when such interference is a fixed strategy and kleptoparasites cannot forage for prey. This rapid increase in kleptoparasitism as a strategy is accompanied by the divergent evolution of movement

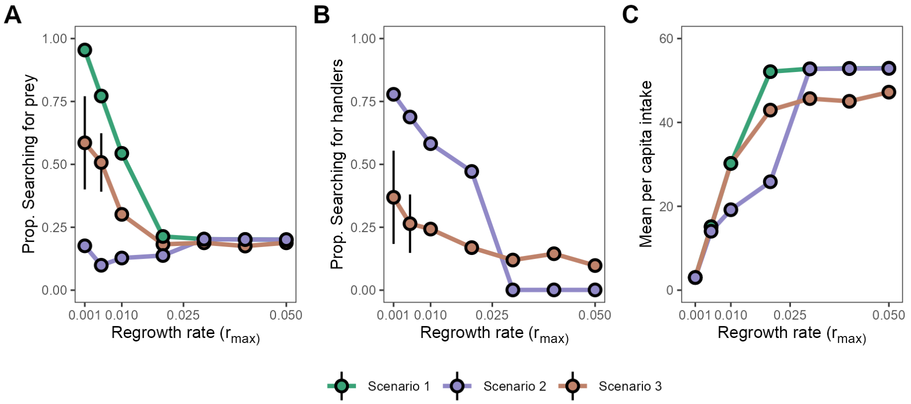

Figure 4.6: Landscape productivity strongly affects scenario outcomes. (A) The proportion of time spent searching for food decreases with increasing r_{max} in scenarios 1 and 3 but remains relatively stable within scenarios. This is partly due to a higher proportion of time spent handling at higher prey densities. **(B)** The proportion of time spent searching for handlers (in order to steal prey from them) also decreases with increasing r_{max}. In scenario 2, kleptoparasites go extinct for r_{max} values above 0.025. **(C)** At low productivity, the average intake is similar in all three scenarios. For higher r_{max} values the average intake rate is lowest in scenario 2, until r_{max} is larger than 0.025 and kleptoparasites go extinct (leading to the same kind of population as in scenario 1). At high r_{max}, the average intake rate in populations with conditional kleptoparasites (scenario 3) is substantially lower than in populations without kleptoparasitism. All panels show conditions at G = 1,000; error ranges where present show standard deviation around values; some error ranges are too small to be visible.

strategies that favour moving towards handlers, which are the primary resource of the kleptoparasites. In this sense, obligate kleptoparasites may be thought of as forming a higher trophic level, with handlers as their prey. Third, when foraging strategy is allowed to be conditional on local cues, *(1)* the population's mean per capita intake is significantly higher than that of a population with fixed strategies, and *(2)* unlike fixed strategy populations, kleptoparasitism as a strategy does not go extinct on high-productivity landscapes. However, across scenarios, individuals are broadly unable to match the productivity of the resource landscape, contrary to the predictions of IFD based models, which predict input matching for some (Parker and Sutherland 1986; Holmgren 1995; Hamilton 2002), or all of the competitive types (Korona 1989).

Comparison with Existing Models

Existing models of competition and movement impose fixed movement rules on individuals to mimic either ideal or non-ideal individuals (Vickery et al. 1991; Amano et al. 2006; Cressman and Křivan 2006; Beauchamp 2008; Stillman and Goss□Custard 2010; White et al. 2018*b*). When individual competitive strategies are included in models, they represent differences in competitive ability (e.g. Parker and Sutherland 1986; Holmgren 1995; Hamilton 2002), or a probabilistic switch between producing and scrounging (Beauchamp 2008). In contrast, our model allows individuals' movement (and competition) decisions to be adaptive responses to local environmental cues. Similar to Getz et al. (2015; 2016) and White et al. (2018*b*), our individuals choose from among the available movement options after weighing the local environmental cues, similar to step selection functions (Fortin et al. 2005; Avgar et al. 2016; White et al. 2018*b*). Local environmental cues are constantly changing, as we model discrete, depletable prey-items, contrasting with many IFD models (Tregenza 1995; Amano et al. 2006). This allows for a more plausible, fine-scale consideration of exploitation competition, which is often neglected, and allows the cues sensed by individuals to strongly structure the distribution of competitors (see below).

Adaptive responses must have an explicit evolutionary context, and consider multiple generations of the population. We follow Beauchamp (2008) and Getz et al. (2015) in allowing the cue preferences that decide movement, and variation therein, to be the outcomes of natural selection. However, instead of using 'evolutionary algorithms' (Beauchamp 2008; Getz et al. 2015; 2016) to 'optimise' individual movement rules, we consider a more plausible evolutionary process: *(1)* Instead of allowing the fittest 50% of the population to replicate, the number of offspring are proportional to individual fitness. *(2)* The cue preferences are subject to mutations independently, rather than subjecting all preferences of an individual to simultaneous mutation. *(3)* Finally, we avoided 'simulated annealing', which adapts the mutation rate or the mutational step sizes to the rate of evolutionary change. Instead we drew mutation sizes from a Cauchy distribution, so that most mutations are very small, but large-effect mutations do rarely occur throughout the simulation. Similarly, rather than determining competition strategy probabilistically or ideally (Vickery et al. 1991; Beauchamp 2008; Tania et al. 2012), our individuals' competition decisions are also shaped by selection (in scenarios 2 and 3).

Evolution of Movement Strategies Using Social Information

In scenario 1, depletion of discrete prey can leave many areas empty of prey-items: in such areas, movement informed by a resource gradient is impossible, and individuals may move randomly (Perkins 1992). This lack of direct resource cues for locally optimal movement might be among the mechanisms by which unsuitable 'matrix' habitats modify animal movement on heterogeneous landscapes (Kuefler et al. 2010). When individuals do not sense resource gradients, the presence of more successful conspecifics may indicate a suitable foraging spot (local enhancement; Giraldeau and Beauchamp 1999; Beauchamp 2008;

Cortés-Avizanda et al. 2014). The presence of unsuccessful individuals, meanwhile, may signal potential costs from exploitation or interference competition. This selects for movement strategies incorporating the presence and condition of competitors into individual movement decisions, or *social movement strategies* (see e.g. Guttal and Couzin 2010). Consequently, consumer aggregation — often explained by invoking external costs such as predation (Krause and Ruxton 2002; Folmer et al. 2012) — could also be the outcome of movement strategies that have evolved to trade competition costs for valuable social information on the underlying spatial structure (here, r) of uninformative landscapes (Folmer et al. 2010; Cortés-Avizanda et al. 2014).

Individual Variation in Movement Strategies

Our movement strategies, comprising preferences for local ecological cues, may lead individuals to move in ways that are potentially unique to each individual. These strategies may not maximise their intake over short timescales (a few timesteps), but their coexistance implies equivalent fitness overall. This makes them consistent with prevalent ideas about consistent individual differences in behaviour, or 'animal personalities' (Wolf and Weissing 2012; Laskowski and Bell 2013; Spiegel et al. 2017; Shaw 2020). In scenario 1, the persistence of multiple movement strategies across generations indicates that they have equivalent fitness (see Getz et al. 2015), and that there are multiple ways to navigate a heterogeneous environment (Wolf and Weissing 2010; Shaw 2020). Such differences may help reduce competition as individuals make subtly different movement decisions when presented with the same cues (Wolf and Weissing 2012; Laskowski and Bell 2013). Interestingly, scenario 3 has the least individual variation in movement rules, presumably because plasticity in competition strategy reduces the need for such diversification (Pfennig et al. 2010).

Scenario 2 cautions that *(1)* Individual variation may only be evident when accounting for the main driver of movement decisions (s_H or s_N; see Supplementary Material Fig. 8 for scenario 3 as well). *(2)* Spatial context determines whether individual differences in movement strategy lead to functional variation in movement outcomes. Subtle variation in relative prey density preferences (s_P) could be revealed if individuals were measured in isolation, and could lead to differences in movement paths (given a continuous gradient in prey cues). However, in natural settings with substantial collective behaviour, different social movement strategies (correlated with foraging competition strategy) would be the primary driver of movement. Overall, then, *(a)* measuring movement behaviour in settings that correspond to animals' evolutionary context, and *(b)* accounting for movement-competition strategy correlations, are both key when studying how individual differences translate to functional consequences.

Competition Strategies and the Ideal Free Distribution

IFD models predict that individual movement should result in consumer distributions tracking the profitability of resource patches (Fretwell and Lucas 1970; Parker 1978), with dominant competitive types (including kleptoparasites) monopolising the best patches (Parker and Sutherland 1986; Holmgren 1995; Hamilton 2002), though Korona (1989) predicts otherwise. In scenarios 2 and 3, kleptoparasitic individuals unsurprisingly and rapidly evolve to track handlers (a direct resource), while avoiding non-handlers (potential competitors). However, these evolved rules do not lead kleptoparasites to occupy the best cells as predicted by Parker and Sutherland 1986, Holmgren 1995, and Hamilton 2002. Across our scenarios (including scenario 1), local population density is only weakly correlated with cell productivity, and is not stronger than if individuals were moving randomly (see Supplementary Material Fig. 1). In scenario 2, this departure from predictions is driven by the contrasting movement rules of foragers, which evolve to *avoid* handlers as well as non-handlers, both of which might be kleptoparasites (cryptic interference; seen in interference-sensitive shorebirds Bijleveld et al. 2012). Thus, foragers likely avoid resource peaks, which are more likely to have handlers (due to the higher probability of forager-prey encounters Parker and Sutherland 1986; Holmgren 1995; Hamilton 2002). Fixed kleptoparasites cannot extract prey themselves, and must move off resource peaks to track and rob handlers (similar to Parker and Sutherland 1986), breaking the link between individual density and productivity. This shows the pitfalls of simplistically linking current ecological conditions with population distributions without considering competitive strategies or evolutionary history.

Constraints on Competition Strategies

Foraging strategies involving specialisation on a resource type are expected to be constrained by the availability of that resource. Thus kleptoparasitism, seen as a prey-choice problem, should be constrained by the density of targets (Ens et al. 1990). In scenarios 2 and 3, more kleptoparasitism should be expected with increasing r_{max}, as prey and consequently, handlers, are expected to be more abundant. Instead, kleptoparasitism declines with increasing r_{max}, in line with Emlen (1966), who predicted that the commoner food type (prey) rather than the more efficiently exploited one (handlers) should be preferred. This prey choice problem, playing out at evolutionary scales, leads kleptoparasites in scenario 2 to go extinct when prey are very common at high r_{max}. At stable population densities, the persistence of fixed kleptoparasitism depends on their intake *relative to foragers*. Modelling discrete prey-items and individuals in a spatial context, then, leads to the finding that obligate kleptoparasitism is only a viable strategy when forager-prey encounters are less common than kleptoparasite-handler encounters. Reducing the relative profitability of kleptoparasitism in other ways — such as imposing a cost on kleptoparasitic attacks for the initiator, or reducing the probability of success (currently, 1.0) — would also lead to a reduced incidence of kleptoparasitism, and eventual extinction even on less productive landscapes. In scenario 3, about 40% of individuals choose to attempt to steal even when prey are available and handlers are not. This suggests a more realistic proportion of consistently kleptoparasitic individuals among populations with flexible foraging strategies. Many seabirds, which forage for prey when they are super-abundant, but also readily harass other birds for prey, are a good example (Brockmann and Barnard 1979). Finally, comparing across regrowth rates shows why possibly cryptic behavioral complexity should be considered in predictions of the long-term effect of environmental change on populations. While both scenario 1 and 2 populations appear identical at high r_{max}, even a small decrease in environmental productivity could lead to an abrupt drop in per-capita intake — and potentially, strongly reduced growth or survival — for fixed strategy populations due to unexpected, emergent kleptoparasitism.

Comparison with Conceptual Models

Classical models of animal movement and foraging largely consider homogeneous populations and environmental conditions, and movements that are made either optimally or at random. While these models provide powerful insights, individual-based models such as ours have the advantage that they can accommodate individual variation, local environmental conditions, and the mechanisms of movement and decision-making. Individual-based modeling has the obvious drawback that numerous specific assumptions have to be made, which might not all be founded on empirical evidence, and might seem to limit the generality of the conclusions. Nevertheless, as long as these models are not mistaken for attempts at faithful representations of real systems, their exploration provides valuable perspectives on the conceptual models that have dominated theory in the past. After all, traditional models also include numerous assumptions (the spatio-temporal structure, the timing of events, the distribution and inheritance of traits) that are usually not stated and therefore less visible. For the future, we envisage pluralistic approaches, where both types of model are applied to the same research question. Only comparing the outcomes of diverse models will reveal which conclusions and insights are robust, and which reflect peculiarities of the model structure. Only such model comparison can tell us whether and when simple models produce general insights, where simple models fail, and when mechanisms can explain initially counterintuitive observations, such as the attraction to competitors that we observed in our study.

Roles for Individual-Based Models in Animal Movement Ecology

Linking individual-based models with empirical data is difficult, and is still rarely used (see works tailored to management: Stillman and Goss□Custard 2010; Diaz et al. 2021). Animal tracking technology is only on the cusp of allowing us to track entire populations (though small ones), and classifying their behaviour at the fine temporal scales of animal decision-making Nathan et al. in press. *Science*; see e.g. Lieber et al. 2021; Sankey et al. 2021. Classifying dyadic and collective behaviour from animal tracking is especially challenging (Sankey et al. 2021; Vissat et al. 2021); this makes the detection of rapid competitive interactions in large populations unlikely. Instead, experimental approaches may reveal movement strategies that reduce competitive interactions (Vahl et al. 2005*a*,*b*; Rutten et al. 2010*a*; Bijleveld et al. 2012). However, consistent behaviour in cue-poor captive environments does not always translate to consistency in natural settings with abundant resource cues (Carter et al. 2013*a*).

Animal movement ecology takes an explicitly individual-based approach, centred around individual decisions (Nathan et al. 2008). This makes individual-based models a good choice when seeking general insights into the evolutionary ecology of animal movement strategies (see e.g. Getz et al. 2015), whose ultimate causes are otherwise difficult to study empirically. Modelling mechanistic movement decisions has substantial consequences for ecological outcomes (e.g. Mueller et al. 2011; White et al. 2018*b*; Scherer et al. 2020), yet few individual-based models in animal movement are mechanistic (see review in: DeAngelis and Diaz 2019), and even fewer models include evolutionary dynamics (but see Getz et al. 2015; 2016; Netz et al. 2021*b*). Yet explicitly modelling both ecological interactions and evolutionary dynamics, as we do here, can reveal surprising outcomes ranging from innovative predator-prey strategies (Netz et al. 2021*b*) to sympatric speciation (Getz et al. 2016).

The use of resource- and step-selection functions in mechanistic modelling (see White et al. 2018*b*) gives empirical movement ecologists a familiar starting point in individual-based modelling. Simulating an animal's potential space-use, conditional on environmental data (similar to our cues), and using selection coefficients estimated from tracking data (our cue preferences), is already accepted in movement ecology, and follows our grid-based approach (Avgar et al. 2016; Signer et al. 2019; Avgar et al. 2020; Fieberg et al. 2021). It is relatively easy to implement movement decisions in continuous space, by sampling cues at discrete locations and *(1)* choosing among them, or *(2)* translating these cues into a movement distance and turning angle. The second approach would require more complex functions with more coefficients (preferences), such as neural networks (Mueller et al. 2011), and this could make it difficult to interpret the evolved movement strategies. Models could implement survival and reproduction (the key ingredients of natural selection), as well as other demographic processes, and reproduction and inheritance can be incorporated in a more realistic manner.

We call for a substantial increase in mechanistic, evolutionary, individual-based modelling in animal movement ecology. Adding realistic ecological and evolutionary dynamics on top of current empirical work is key to transforming movement ecology into a more applied, predictive discipline. For example, by allowing habitat selection coefficients from animal-tracking studies to undergo even short-term selection on projected landscapes from climate modelling, such models could help explore population changes in movement strategies. This approach would require very accurate estimation of the fitness outcomes of movement — no easy task. Consequently, individual-based models are not (yet) intended to be 'fit' to empirical movement data. Rather, they can provide valuable perspective on existing population-level models, and could be used to define the envelope of possibilities for how movement strategies could evolve in dynamic environments.

* * *

Supplementary Information for Chapter 4

Evolutionary Ecology of Random Movement

We ran our model on a fourth scenario: random movement. In this scenario, the landscape is set up as in our first three scenarios (see Figure panel A). The prey-item handling dynamics are the same as well, and if individuals, which can choose their competition strategy depending on environmental conditions (as in scenario 3), ever encounter a handler and choose to steal from it, they can do so. Individuals have heritable, evolving preferences for environmental cues, as in all our previous scenarios. The major change in this scenario is that individuals cannot actually perceive any environmental cues, and are essentially then, moving to random locations in their neighbourhood. This scenario serves as a useful null model for what one should expect when directed movement is not possible, or has no bearing on fitness.

1. In contrast to scenario 1, the resource landscape regenerates much more strongly, suggesting that despite the paucity of movement cues in scenario 1, foragers are still capable of finding their way to isolated prey-items, and consuming them (panel **A**).
2. This scenario reveals that directed movement is, understandably, absolutely key to kleptoparasitism. When individuals cannot move towards handlers, the low density of foragers on the landscape, only some of which will be handling an item at any one time, means that encountering a handler is essentially impossible. As expected then, the number of stealing attempts drops to zero within only three generations, and all individuals thereon are foragers (panel **B**).
3. Despite being unable to move towards resources, the population's mean intake is comparable to scenarios 1 and 3, and actually higher than in scenario 2. This highlights the cost that fixed-strategy kleptoparasitism imposes at a population wide level (panel **C**).
4. The near-zero correlation between consumer abundance and resource productivity is unsurprising (panel **D**). Nonetheless, it shows that regardless

of whether individuals are moving with (relatively) sophisticated movement strategies, or at random, they are very far from following the ideal free distribution's input matching rule. This also confirms the true cost of resource landscape depletion in scenario 1: the loss of prey-item gradients with which to orient movement leaves individuals navigating a clueless landscape, on which they simply cannot find the way to areas of high productivity.

5. Finally, the evolution of movement strategies, when they are not actually under selection, supports our findings of strong selection on movement in the first three scenarios (panel **E**).

Effect of Local Dispersal

In order to focus on adaptive movement strategies, we chose to implement large dispersal distances in our default simulation setup, which we refer to as 'global' natal dispersal. Under global dispersal, offspring are homogeneously distributed over the entire landscape (dispersal radius = 512). Our results are not changed in any way when dispersal is much more strongly localised, which we refer to as simply 'local' natal dispersal. In this implementation, the natal dispersal distance is comparable in magnitude as the distance between resource peaks. If offspring dispersal is more local, the spatial population dynamics may become more intricate, and kin competition or local adaptation may become influential. We therefore ran the simulations presented in the main text also under local dispersal (dispersal radius = 2).

In summary, scenarios 1 and 3 yield similar results under local as under global dispersal, while scenario 2 shows some interesting dynamics typical of reaction-diffusion systems. In scenario 1 (see Fig. S13), the resource landscape plots A, the activity budget and intake plots B and C, as well as the evolved movement strategies E exactly match the simulation results shown in Figure 1 of the main text. Only the correlations between number of foragers and cell productivity are higher under local dispersal than under global dispersal (panel D). This is a straightforward consequence of local dispersal, where individuals occurring on more productive cells have a higher intake rate and therefore produce more offspring than individuals on less productive cells. Thus, under local dispersal many agents already start out on more productive cells. This does not seem to impact movement strategies. The same is true for scenario 3 (Fig. S14): After the initial depletion of the landscape, kleptoparasitic behavior spreads, and the landscape is somewhat replenished again. Also here, the landscape snapshots, the activity budget, as well as the intake plot and the evolved movement strategies match the global dispersal case. The difference in competition strategy (panel F)

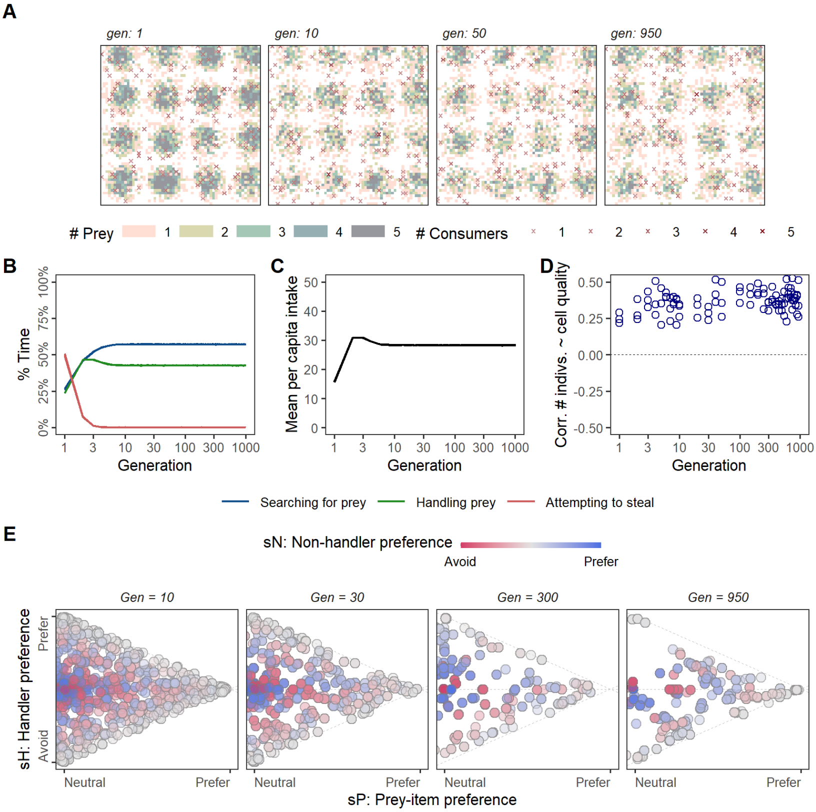

Figure 4.7: The evolutionary ecology of random movement serves as a useful baseline against which to compare other scenarios. **(A)** Individuals deplete the landscape (r_{max} = 0.01) at random, allowing it to regenerate more than scenario 1, yet less than scenario 2. **(B)** Kleptoparasitism as a strategy very rapidly goes extinct, as individuals cannot move towards handlers, and encountering a handler at random is very unlikely. **(C)** Surprisingly, moving at random yields a similar mean per-capita intake as in scenarios 1 and 3, and actually better than scenario 2. **(D)** Random movement leads, unsurprisingly, to no correlation with landscape productivity. **(E)** When movement strategies are not under selection, individuals occupy a large area of the potential strategy space, including negative values of s_P (which is not shown here).

corresponds to the observed bistability (compare *Main Text* Fig. 6). Again, the correlation between number of foragers and cell productivity is higher under local dispersal than under global dispersal, in the latter averaging in late generations around 0.1, and in the former around 0.2.

Scenario 2 is the only one where we observed a marked difference between local and global dispersal (see Fig. S15). As soon as kleptoparasites occur, they spread and become locally abundant, driving foragers to local extinction. The kleptoparasites themselves then wither away due to a lack of foragers to steal from, after which foragers may colonize the area once again. This spatial instability repeats itself over wide parts of the landscape, driven by the extinction, recolonization and diffusion of foragers and kleptoparasites. Kleptoparasites and foragers here effectively form a reaction-diffusion system. Snapshots of this dynamic pattern can be seen in Fig. S15A. As a consequence, the proportions of kleptoparasites and foragers, as well as the total per capita intake of the population fluctuate widely (panels B and C). The correlations between individual densities and cell quality lie around zero and are therefore not much different from the results observed under global dispersal (*Main Text* Fig. 2D). An interesting contrast with global dispersal is to be found in the movement strategies. While kleptoparasites have similar preferences under global and local dispersal, foragers have much stronger item preferences under local dispersal. Due to the pattern of extinction and recolonization under local dispersal, there are parts of the landscape not only rich in food items, but also free from kleptoparasites, and thus a strong preference for items becomes beneficial.

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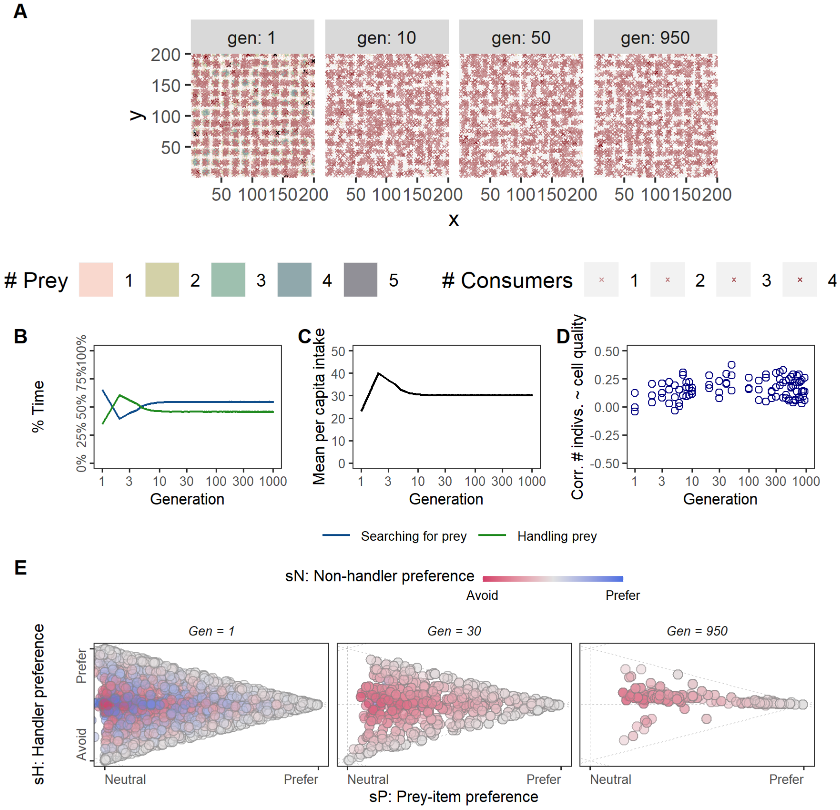

Figure 4.8: The effect of strongly localised dispersal in scenario 1. **(A)** Foragers swiftly deplete the resource landscape and maintain item scarcity throughout the rest of the simulation, just like under global dispersal. Items and agents are distributed in proportion to cell productivity, *r*. The population quickly reaches an equilibrium in its **(B)** activity budget and **(C)** mean per-capita intake, that is identical to global dispersal. **(D)** The number of foragers per cell is more positively correlated with cell productivity under strongly localised ('local') dispersal, compared with global dispersal. **(E)** The same wide range of movement strategies observed under global dispersal exists under local dispersal as well.

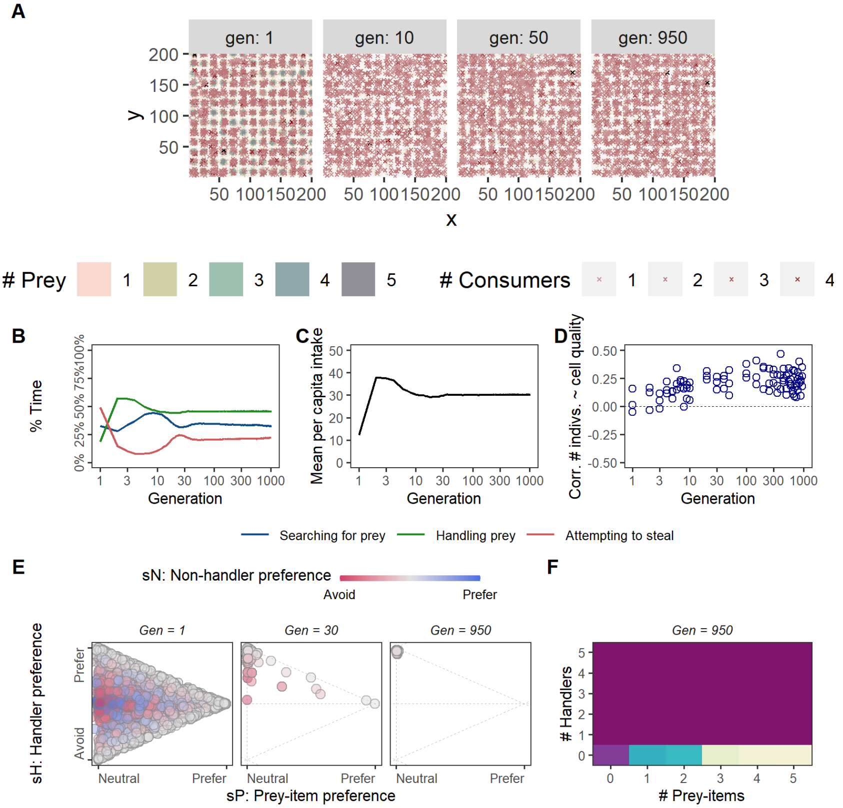

Figure 4.9: The effect of strongly localised dispersal in scenario 3. (A) Individuals swiftly deplete the resource landscape, but prey abundances recover with the rise of kleptoparasitism, as is observed under global dispersal. Items and agents are distributed in proportion to cell productivity, *r*. **(B)** By generation 30, the proportion of time spent searching (blue line), handling (green line), and stealing prey (red line) reach values in the range of the ones observed under global dispersal. **(C)** The mean per-capita intake drops after the initial peak, and then recovers slightly, identically to global dispersal. **(D)** The number of foragers per cell is more positively correlated with cell productivity under local than under global dispersal. **(E)** Movement strategies concentrate around a strong preference for handlers, and **(F)** individuals tend to steal even when there are no handlers and less than 3 prey items available. This falls into the range of variation observed between replicates under global dispersal.

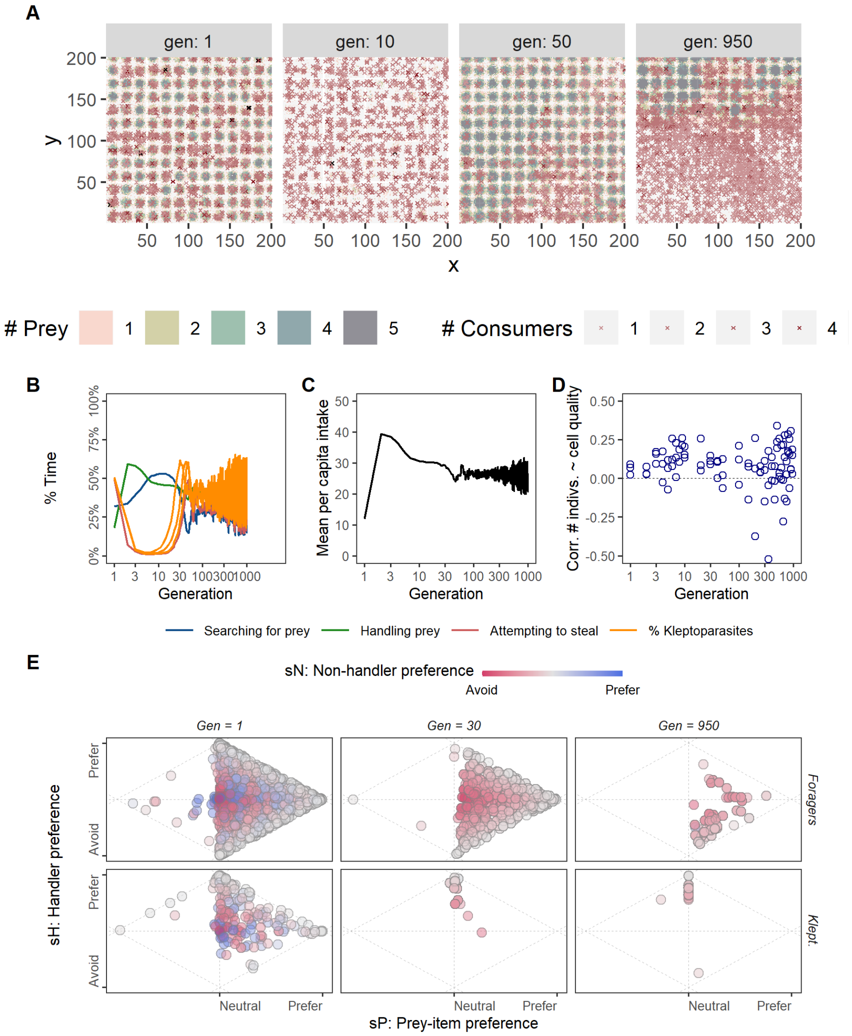

Figure 4.10: The effect of strongly localised dispersal in scenario 2. **(A)** Foragers initially deplete prey items, but with the rise of kleptoparasitism, the resource landscape becomes very heterogeneous, with some areas densely populated and scarce in prey items, and others without consumers and fully stocked with items. This pattern is produced by the local dynamics of kleptoparasites and foragers: Kleptoparasites become more common where foragers are common, until the latter go locally extinct. Thereupon also the kleptoparasites vanish, and prey items replenish until foragers are reintroduced via diffusion. **(B)** Proportions of kleptoparasitses and foragers, as well as **(C)** mean per-capita intake fluctuate greatly. **(D)** Cell quality and number of individuals are uncorrelated as the spatial dynamics between kleptoparasites and foragers dominate over any interaction between cell quality and number of individuals. **(E)** Kleptoparasites evolve the same preferences under local dispersal as under global dispersal, but foragers have a much stronger preference for prey-items, caused by the abundance of deserted, fully-stocked parts of the landscape.

Interlude C

Details Matter When Modelling the Effects of Animal Personality on the Spatial Distribution of Foragers

Christoph F.G. Netz[1], Aparajitha Ramesh[1], Jakob Gismann[1], **Pratik R. Gupte**, and Franz J. Weissing[1]

Δ This text is adapted from Netz et al. (2022*b*), now published in *Proceedings of the Royal Society B: Biological Sciences* as “Details Matter When Modelling the Effects of Animal Personality on the Spatial Distribution of Foragers.”

By means of a simulation study, DiNuzzo and Griffen[1] investigate whether individual variation in a personality trait can explain “undermatching”, an often-observed deviation from the ideal free distribution (IFD). Here we raise five points of concern about this study, regarding *(i)* the interpretation of the results in terms of personality variation; *(ii)* deficiencies in the technical implementation of the model, leading to wrong conclusions; *(iii)* the effects of population size on deviations from the IFD; *(iv)* the measure used for quantifying deviations from the IFD; and *(v)* the analysis of the mud crab data. Finally, we give an outlook over the evolutionary ramifications of the relation between animal personality and the IFD.

Personality Variation and the IFD

The individuals in DiNuzzo and Griffen’s model tend to maximize their intake rate. At each point in time, they are perfectly informed about the distribution of resources (which remains constant) and the distribution of foragers (which can change due to movement). Individuals differ in “activity”, that is the rate at which they recognize that their current intake rate is suboptimal; once they observe a discrepancy, they move instantaneously to the habitat patch yielding a maximal intake rate. In this model, each individual has to move at most once: if all individuals have moved (or stayed at their initial position, as this already yielded a maximal intake rate), the IFD is reached. It is therefore obvious that less active individuals that, by definition, take on average more time steps for making a movement decision, retard the approach of the population to the IFD. Hence,

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[1] DiNuzzo, E. R. and Griffen, B. D. (2020), “The Effects of Animal Personality on the Ideal Free Distribution,” *Proceedings of the Royal Society B: Biological Sciences*, 287/1934: 20201095.

it is also obvious that the "time to reach IFD" increases with an increase of the proportion of inactive individuals. In other words, it is not personality variation per se that retards the approach to the IFD, but rather the presence of inefficient movers.

Problems with the technical implementation of the model

Above we argued that it is obvious that the "time to reach IFD" increases with the proportion of inactive individuals. In view of this, it is surprising that DiNuzzo and Griffen report a hump-shaped relationship in one of their simulation scenarios (their Figure 4E) and even a monotonic decline of the time to reach IFD with the proportion of inactive individuals in case of a type II functional response (their Supplementary Figure S1, reproduced here in Figure C-1A). We think both results are artefacts. The pattern in Figure S1 is caused by a comparison between intake rates calculated with different formulas. As a consequence, individuals can "believe" that they are already in a habitat maximizing their intake rate, while really they are not. In addition, an incorrect formula of a ratio-dependent functional response type 2 is used (following Abrams and Ginzburg 2000)[2]. A detailed explanation of these mistakes can be found in our Supplementary Information. If these mistakes are corrected, the time to reach IFD shows the expected declining trend with the proportion of inactive individuals (fig. 1B), rather than the increasing trend reported in Figure S1. Hence, a saturating type II functional response leads to a similar relationship between the proportion of active consumers and time-to-IFD as an unlimited linear (type I) functional response. Special explanations for discrepancies between type I and type II models (the "domino effect" explanation in Supplementary Information 1.4 of DiNuzzo and Griffen 2020) are not needed and are actually misleading.

We can further show by a simple mathematical argument that the correspondence between the two model variants considered by DiNuzzo and Griffen should be even stronger: the special version of the type II functional response used by DiNuzzo and Griffen (following Abrams and Ginzburg 2000) should lead to exactly the same time-to-IFD and the same consumer distribution over patches as their type I functional response. We were therefore surprised our Figure C-1B does not exactly match Figure 3 in (DiNuzzo and Griffen 2020): it generally takes 100 time steps longer to reach the IFD. Rerunning the scenario underlying Figure 3 in (DiNuzzo and Griffen 2020) with DiNuzzo and Griffen's published NetLogo code, we obtained an exact replicate of our Figure C-1B. We conclude that DiNuzzo and Griffen must have used a different version of their simulation program to produce their Figure 3.

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[2] Abrams, P. A. and Ginzburg, L. R. (2000), "The Nature of Predation: Prey Dependent, Ratio Dependent or Neither?" *Trends in Ecology & Evolution*, 15/8: 337–41.

In addition, the simulation program in (DiNuzzo and Griffen 2020) produces a substantial bias in reported time to reach the IFD. Each simulation run stops once movement has ceased for 50 time steps, assuming that this is a clear indication that the IFD has been reached. The problem is that movement can cease for longer time periods even in situations where the population is still far from an IFD (Figure C-2A). This easily happens in populations with a large proportion of highly inactive individuals: the lack of movement of these individuals may just reflect the reluctance of these individuals to move (rather than having reached a habitat with maximal intake rate, where movement is no longer necessary).

Figure C-2 shows two replications of Figure 4E in DiNuzzo and Griffen (2020), one with the published NetLogo code (Fig. 2B) and a second with an improved version (see Supplementary Information) where DiNuzzo and Griffen's stopping criterion is replaced by a check whether the IFD has indeed been reached (Fig. 2C). It is obvious that the stopping criterion has a large effect on the simulation outcome. Notice that neither outcome shows the puzzling "hump" in Figure 4E in (DiNuzzo and Griffen 2020). As we produced Figure C-2B with DiNuzzo and Griffen's published NetLogo code, we have to conclude again that a different version of their simulation program was used to derive their Figure 4E. A more detailed account of the technical issues reported above (and some additional issues) and corrected versions of the NetLogo program can be found in the Supplementary Information.

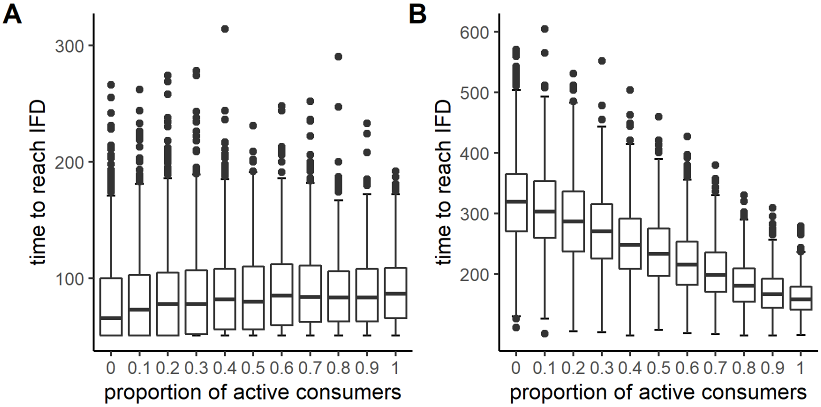

Figure C-1: Replication of DiNuzzo and Griffen's Figure S1 **(A)** using their original NetLogo code and **(B)** using a corrected version of their code. Both panels show the time to reach the Ideal Free Distribution (IFD) for various proportions of "active" (80% activity) and "inactive" (20% activity) consumers with a type 2 functional response in 1,000 replicate simulations. According to DiNuzzo and Griffen's *NetLogo* code, the time- to-IFD increases with the proportion of active consumers. A corrected version of the code yields the expected pattern of decreasing waiting times with increasing proportions of active consumers.

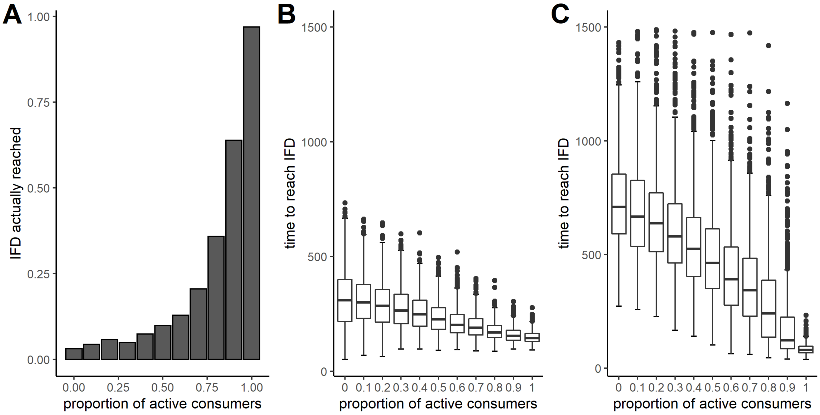

Figure C-2: Systematic bias in outcomes due to premature termination of simulations. The *NetLogo* code underlying the simulations in DiNuzzo and Griffen's work assumes that the IFD is reached after 50 time steps of inactivity. **(A)** Proportion of simulations that have actually reached the IFD after 50 time steps in inactivity in the scenario underlying Figure 4E in DiNuzzo and Griffen (2020). **(B)** Replication of Figure 4E, using DiNuzzo and Griffen's *NetLogo* code. **(C)** The same set of simulations for an improved version of the *NetLogo* code, where a simulation now stops when the IFD is actually reached. In all simulations, "active" consumers have an activity level of 90% while "inactive" consumers have an activity level of 10%.

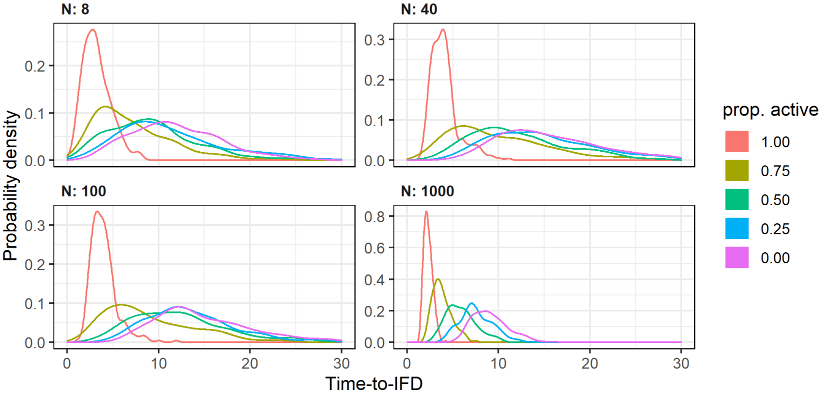

Figure C-3: Probability distributions of the time until the ideal free distribution is reached, based on 1,000 replicate simulations per setting. In a system with 49 habitat patches, the panels show for four population sizes N how the time to reach IFD depends on the proportion of "active" (movement rate 0.8) and "inactive" (movement rate 0.2) individuals.

Effects of population size

DiNuzzo and Griffen investigated the effect of population size on the time to reach the IFD. However, the time scale of their model implementation is quite different from a 'natural' time scale. In their simulation program, individuals make decisions sequentially, and only one individual can make a decision in each time step. As in a larger population more individuals have to take decisions, this automatically increases the time to reach a certain target. Moreover, the time to reach the IFD is inflated by the fact that active individuals are restricted in their movement because they have to "wait" for the inactive individuals. For these reasons, it is more natural to use a continuous time scale, where individuals take movement decisions independently of each other, at a rate that is proportional to their activity level. This can be done in a straightforward manner, by translating the discrete-time model of DiNuzzo and Griffen into an otherwise equivalent event-based model (making use of the Gillespie algorithm[3] — a description and implementation of such a model can be found in Netz et al. (2021*a*)[4]). Figure C-3 shows how in the event-based version of the model the time to reach the IFD depends on the population size N and the proportion of active individuals. For each population size, the time to reach the IFD is, as expected, positively related to the proportion of inactive individuals. However, the event-based version of the model does not support DiNuzzo and Griffen's conclusion that the time to reach the IFD increases with population size. This only occurs for very low population densities (N = 8 and N = 40 in Figure C-3), and even in these cases the effect is small.

At higher population sizes, the time to reach the IFD decreases with population size: as shown in Figure C-3, the IFD is reached much faster in a population with N = 1000 individuals than in any of the smaller populations. This can be explained as follows. In case of the low population sizes considered by DiNuzzo and Griffen, the initial density of individuals is very low (typically only one individual per patch). In such a case, an individual can only improve its intake rate by moving to a more profitable patch. In case of a large population size (and a higher initial density per patch), there is an additional option: if an individual on a patch decides to leave in order to improve its intake rate elsewhere, all remaining individuals on that patch profit as their intake rate increases due to alleviated within-patch competition[5]. This effect is not addressed by the study of DiNuzzo and Griffen, although the authors state: "in most natural systems, there are many more consumers than patches."

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[3] Gillespie, D. T. (1976), "A General Method for Numerically Simulating the Stochastic Time Evolution of Coupled Chemical Reactions," *Journal of Computational Physics*, 22/4: 403–34.

[4] Netz, C. F. G. et al. (2021*a*), *Christophnetz/Time-to-IFD_simulator: Comment to DiNuzzo and Griffen 2020 - Supplementary Material* (version v1.0.0) (Zenodo).

[5] Wolf, M. et al. (2008), "Evolutionary Emergence of Responsive and Unresponsive Personalities," *Proceedings of the National Academy of Sciences*.

Quantifying the approach to the IFD

DiNuzzo and Griffen conducted their study in order to investigate whether personality differences can explain “undermatching”, the commonly observed phenomenon that high-resource patches tend to be underexploited while low-resource patches are overexploited. Yet, they devote only one figure (their Figure C-2) to this phenomenon. In general, they quantify deviations from the IFD by measuring the time to reach the IFD. This measure has at least three disadvantages. First, “time-to-IFD” is determined by the last individual that moves to a patch with an optimal intake rate. In other words, a single individual with very low activity can have a very large effect on time-to-IFD. Second, “time-to-IFD” depends on the initial conditions; it takes longer to reach the IFD if the initial distribution of individuals over patches differs a lot from the IFD. Third, “time-to-IFD” is only a sensible measure when the IFD is actually reached. This, however, will only be the case in highly standardized simulation models with a fixed resource distribution. As stated by DiNuzzo and Griffen: “In most systems, the IFD is a moving target owing to temporal environmental variation and directional change (i.e. habitat degradation).” In Section 1.5 of their Supplementary Information, DiNuzzo and Griffen show some simulation results for a scenario with temporally varying patch quality. Surprisingly, “time-to-IFD” is also used for this scenario (their Supplementary Figure S2), where it is difficult for us to understand how the IFD can ever be reached in case of rapid environmental change. How can movement cease for 50 time steps (the criterion for reaching the IFD) if the distribution of patch qualities changes completely every 10 or 20 time steps? Under such changing conditions, we would advocate using a more robust, population-level measure for deviations from the IFD, such as the variance in intake rates across patches.

Analysis of the mud crab system

We are puzzled by the fact that DiNuzzo and Griffen revert to a simple calculation of ratios in their analysis of the refuge use data on the mud crab *Panopeus herbstii*[6] instead of taking advantage of their individual-based model. The model becomes necessary because such a simple calculation does not suffice, as it ignores the distribution of personality in the population. Hence, Figure 5 illustrates the influence of personality on the IFD only in the sense that no single crab is “ideal” in immediately leaving its refuge and moving to the patch with highest profitability, but not the implications of the distribution of activity levels in the population. Additionally, the data comes from a special (predation cue) treatment, not from standard conditions; and the crabs differ substantially in size

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[6] Toscano, B. J. et al. (2014), “Effect of Predation Threat on Repeatability of Individual Crab Behavior Revealed by Mark-Recapture,” *Behavioral Ecology and Sociobiology*, 68/3: 519–27.

(actually body size is used as a proxy for activity level) and accordingly also in their resource needs and competitive abilities.

Outlook

We have the impression that DiNuzzo and Griffen view "personalities" mainly as (maladaptive) deviations from optimal or efficient behaviour. In contrast, many studies show that personality variation is often shaped by adaptive evolution[7]. For example, Wolf and colleagues demonstrate that "inactivity" (called "unresponsiveness") may be viewed as an efficient strategy in achieving a high foraging success and approaching an ideal free distribution. An adaptive perspective on personality variation leads to novel eco-evolutionary questions regarding the interplay of individual behavioural variation and the spatial distribution of foragers.

Future research is needed to reconcile the IFD with the eco-evolutionary causes and consequences of personality for at least two reasons: First, the IFD model presupposes that the resource intake rate is a proxy for fitness[8]. But how, then, can different personality types persist at stable proportions, when inactive individuals consistently achieve a lower intake rate than their more active conspecifics? Second, a personality perspective may change what spatial distribution is optimal. In animals, differences in activity are usually associated with (adaptive) differences in energy metabolism[9]. When foraging individuals differ in energetic expenditure, they should not only take maximizing the intake rate as their sole guiding principle[10]. In other words, individuals differing in activity should use different decision rules, and the optimal behaviour of a polymorphic population may, even at equilibrium, deviate considerably from the IFD of a monomorphic population.

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[7] Wolf, M. and Weissing, F. J. (2012), "Animal Personalities: Consequences for Ecology and Evolution," *Trends in Ecology & Evolution*, 27/8: 452–61.

[8] Tregenza, T. (1995), "Building on the Ideal Free Distribution," in *Advances in Ecological Research*, xxvi (Elsevier), 253–307.

[9] Careau, V. et al. (2008), "Energy Metabolism and Animal Personality," *Oikos*, 117/5: 641–53.

[10] Campos-Candela, A. et al. (2019), "A Mechanistic Theory of Personality-Dependent Movement Behaviour Based on Dynamic Energy Budgets," *Ecology Letters*, 22/2: 213–32.

Supplementary Information for Interlude C

The supplementary material for this interlude may be found online as Supporting Information published along with the manuscript, Netz et al. (2022*b*), "Details Matter When Modelling the Effects of Animal Personality on the Spatial Distribution of Foragers," at: https://royalsocietypublishing.org/doi/10.1098/rspb.2021.0903.

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Chapter 5

Rapid Evolution of Movement Strategies Following Novel Pathogen Introduction

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...[E]volution codifies happenstance into strategy.

– from Spillover, by David Quammen.

Abstract

Animal social interactions are the outcomes of evolved strategies that integrate the costs and benefits of being sociable. We study a scenario in which a fitness-reducing infectious pathogen is introduced into a population which has initially evolved movement strategies in its absence. Within only a few generations, pathogen introduction provokes a rapid evolutionary shift in animals' social movement strategies, and the importance of social cues in movement decisions increases. Individuals undertake a dynamic social distancing approach, trading more movement (and less intake) for lower infection risk. Pathogen-adapted populations disperse more widely over the landscape, and thus have less clustered social networks than their pre-introduction, pathogen-naive ancestors. Running epidemiological simulations on these emergent social networks, we show that diseases do indeed spread more slowly through pathogen-adapted animal societies. Finally, the mix of post-introduction strategies is strongly influenced by a combination of landscape productivity, the usefulness of social information, and disease cost. Our model suggests that the introduction of an infectious pathogen into a population can trigger a rapid eco-evolutionary cascade, rapidly changing animals' social movement strategies, which alters movement decisions and encounters between individuals. In turn, this changes emergent social structures, and our model informs how such change can make populations more resilient to future disease outbreaks. Overall, we offer both a modelling framework and initial predictions for the evolutionary and ecological consequences of wildlife pathogen spillover scenarios.

Introduction

Animal sociality emerges from individual decisions that balance the benefits of associations against the costs of proximity or interactions with neighbours (Tanner and Jackson 2012; Gil et al. 2018; Webber and Vander Wal 2018; Webber et al. 2022). While such associations can inadvertently or deliberately yield useful social information about resource availability (Danchin et al. 2004; Dall et al. 2005; Gil et al. 2018), they also provide opportunities for the transmission of parasites and infectious pathogens among associating individuals (Weinstein et al. 2018; Romano et al. 2020; Albery et al. 2021; Cantor et al. 2021; Romano et al. 2021). Wildlife pathogen outbreaks affect most animal taxa, including mammals (Blehert et al. 2009; Fereidouni et al. 2019; Chandler et al. 2021; Kuchipudi et al. 2022), birds (Wille and Barr 2022), amphibians (Scheele et al. 2019), and social insects (Goulson et al. 2015). Weighing the potential risk of infection from social interactions against the benefits of social movements — where to move in relation to other individuals' positions — is thus a common behavioural context shared by many animal species. Movement strategies incorporating social information — the presence and status of neighbours — can facilitate or reduce spatial associations, and help animals balance the costs and benefits of sociality (Gil et al. 2018; Webber and Vander Wal 2018; Albery et al. 2021; Webber et al. 2022). Animals' social movements link landscape spatial structure, individual distributions, and the emergent structure of animal societies (Kurvers et al. 2014; Gil et al. 2018; Webber et al. 2022). Together, they influence the dynamics of disease outbreaks in animal populations (Keeling et al. 2001; White et al. 2018*a*; Romano et al. 2020; 2021), and such outbreaks may in turn have cascading effects on landscape structure and community ecology (Monk et al. 2022).

On ecological timescales, pathogen outbreaks often reduce social interactions among individuals. This is due to a combination of mortality-induced decreases in population density (e.g. Fereidouni et al. 2019; Monk et al. 2022), and adaptive behavioural responses by which animals reduce encounters between infected and healthy individuals (Stroeymeyt et al. 2018; Weinstein et al. 2018; Pusceddu et al. 2021; Stockmaier et al. 2021). The latter case includes self-isolating when infected, or avoiding potentially infectious individuals (Stroeymeyt et al. 2018; Weinstein et al. 2018; Pusceddu et al. 2021; Stockmaier et al. 2021). However, when pathogens are first introduced into a population, such as during novel cross-species spillover (Chandler et al. 2021; Kuchipudi et al. 2022), fine-tuned avoidance responses are less likely, as individuals may have no prior experience of cues that indicate infection (Weinstein et al. 2018; Stockmaier et al. 2021). Spreading through host-host contacts, pathogens causing chronic infections (Bastos et al. 2000; Vosloo et al. 2009; Jolles et al. 2021) may instead impose fitness costs, thus selecting against host social behaviour, and hence against social connectivity itself (Altizer et al. 2003; Cantor et al. 2021; Poulin and Filion 2021; Romano et al. 2021; Ashby and Farine 2022).

Yet novel pathogen introductions are primarily studied for their immediate demographic (Fey et al. 2015), and potential medical (Levi et al. 2012; Chandler et al. 2021; Kuchipudi et al. 2022; Wille and Barr 2022) and economic implications (Keeling et al. 2001; Goulson et al. 2015; Jolles et al. 2021), with host evolutionary dynamics (and especially changes in sociality) mostly ignored. This is presumably because the evolution of pathogen host traits, and moreover complex behavioural traits such as sociality, is expected to be slow and not immediately relevant. Since important aspects of animal ecology, including the transmission of foraging tactics (Klump et al. 2021) and migration routes (Guttal and Couzin 2010; Jesmer et al. 2018), depend on social interactions, it is necessary to understand the long-term consequences of pathogen introductions for animal societies. Climate change is only expected to make novel pathogen introductions more common (Sanderson and Alexander 2020; Carlson et al. 2022*a*), making such studies more urgent.

Theory suggests that animal sociality evolves to balance the value of social associations against the risk of pathogen transmission (Bonds et al. 2005; Prado et al. 2009; Ashby and Farine 2022). However, analytical models often reduce animal sociality to single parameters, while it actually emerges from individual decisions conditioned on multiple internal and external cues. Social decision-making and movement often also vary among individuals (Tanner and Jackson 2012; Wolf and Weissing 2012; Spiegel et al. 2017; Gartland et al. 2021), but analytical models are unable to include individual differences in sociability. Epidemiological models based on contact networks can incorporate individual variation in social behaviour by linking these differences to positions in a social network (White et al. 2017; Albery et al. 2020; 2021). Yet network models often cannot capture fine-scale feedbacks between individuals' social and spatial positions (Albery et al. 2020; 2021), nor spatial variation in infection risk (Albery et al. 2022), making such models sensitive to both the network formation process, and to sampling biases in empirical data collection (White et al. 2017).

Mechanistic, individual-based simulation models (IBMs) suggest themselves as a natural solution; they can incorporate substantial ecological detail, including explicit spatial settings (DeAngelis and Diaz 2019), and detailed disease transmission (White et al. 2018*a*,*b*; Scherer et al. 2020; Lunn et al. 2021). Individual-based models hitherto haved focused on immediate epidemiological outcomes, such as infection persistence, and do not have an evolutionary component (White et al. 2018*b*; Scherer et al. 2020; Lunn et al. 2021). Incorporating an evolutionary component to movement-disease IBMs could allow predictions on important feedbacks between the ecological outcomes of infectious disease and the consequences for the evolution of host behaviour (Cantor et al. 2021). This could include the emergence of tradeoffs in the costs and benefits of sociability (Gartland et al. 2021), with cascading ecological and social effects (Tanner and Jackson 2012; Spiegel et al. 2017; Monk et al. 2022; Webber et al. 2022). The range of animal taxa at risk from a wide array of pathogens and parasites (Sanderson and Alexander 2020; Carlson et al. 2022*a*) makes it important to conceive of models that can capture the key features of diverse host-pathogen dynamics and offer broad conceptual insights (White et al. 2018*a*,*b*).

We built a model that seeks to capture the essential elements of pathogen (or parasite) transmission among animals foraging on patchily distributed resources — this is a common behavioural context shared by many potential host species (White et al. 2018*a*,*b*). We examined the eco-evolutionary consequences of the introduction of a pathogen into a novel host population (such as during cross-species spillover: Bastos et al. 2000; Blehert et al. 2009; Fereidouni et al. 2019; Scheele et al. 2019; Sanderson and Alexander 2020; Carlson et al. 2022*a*; Kuchipudi et al. 2022; Monk et al. 2022; Wille and Barr 2022). In our evolutionary, spatial, individual-based simulation, we modelled the repeated introduction of an infectious pathogen to populations that had already evolved foraging movement strategies in its absence. Our model could be conceived as an abstract representation of, among others, spillovers of foot-and-mouth disease from buffalo to impala (Bastos et al. 2000; Vosloo et al. 2009), or sarcoptic mange from llamas to vicuñas (Monk et al. 2022), current and historic spread of avian influenza among sea- and wading bird species (Global Consortium for H5N8 and Related Influenza Viruses 2016; Wille and Barr 2022), or SARS-CoV-2 from humans to deer (Chandler et al. 2021; Kuchipudi et al. 2022).

We compared how social information was used in movement strategies evolved before and after pathogen introduction, and the ecological outcomes for individual intake, movement, and associations with other foragers. Using both IBMs and network epidemiological models (Bailey 1975; White et al. 2017; Stroeymeyt et al. 2018; Wilber et al. 2022), we examined whether pathogen-risk adapted populations were more resilient to the spread of infectious disease than their pathogen-risk naive ancestors. We also investigated the effect of landscape productivity and the cost of infection, which are both expected to influence the selection imposed by pathogen transmission (Hutchings et al. 2000; Almberg et al. 2015; Ezenwa et al. 2016). Overall, we provide a theoretical framework broadly applicable to novel host-pathogen introduction scenarios, and demonstrate the importance of including evolutionary dynamics in movement-disease models.

The Pathomove Model of Novel Pathogen Introduction

We implemented an individual-based simulation model to represent foraging animals ('foragers') seeking discrete, immobile, depleteable food items (see *SI Appendix Fig. S1 – S2*) (Spiegel et al. 2017; Gupte et al. 2021). Food items are distributed over a two-dimensional, continuous-space resource landscape with wrapped boundaries (a torus). Our model, similar to previous eco-evolutionary individual based models (Getz et al. 2015; Gupte et al. 2021; Netz et al. 2021*b*), has two distinct timescales: (1) an ecological timescale comprising of T timesteps that make up one generation ($T = 100$ by default), and (2) an evolutionary timescale consisting of 5,000 generations (G). At the ecological timescale, individuals sense local counts of food items and competitors, move according to inherited movement strategies, and forage for food. At the same timescale, individuals that carry an infectious, fitness-reducing pathogen, may, when in close proximity with uninfected individuals, pass on the pathogen with a small probability (see *Pathogen Transmission and Disease Cost*). At the evolutionary timescale, individuals reproduce and transmit their movement strategies (see *Starting Location and Inheritance of Movement Rules*) to the their offspring. The number of offspring is linked both to individuals' success in finding and consuming food items, and to the duration that they were infected by the pathogen at the ecological timescale. The model was implemented in R and C++ using Rcpp (Eddelbuettel 2013; R Core Team 2020) and the *Boost.Geometry* library for spatial computations (*www.boost.org*); model code is at *github.com/pratikunterwegs/pathomove*.

Distribution of Food Items

Our landscape of 60 × 60 units contains 1,800 discrete food items, which are clustered around 60 resource 'kernels', for a resource density of 0.5 items per unit^2 (see *SI Appendix Fig. S1 – S2*). This prevents synchronicity in the availability and regeneration of food items. Each available food item can be sensed and harvested by foraging individuals (see below). Once harvested, another food item is regenerated at the same location after a fixed regeneration time R, which is set at 50 timesteps by default; alternative values of 20 and 100 timesteps represent high and low productivity landscapes respectively. Food item regeneration is delinked from population generations. Thus the actual number of available food items is almost always in flux. In our figures and hereafter, we chose to represent R as the number of times a food item would regenerate within the timesteps in a single generation T (default = 100), resulting in R values of 1, 2, and 5 for regeneration times of 100, 50 (the default), and 20 timesteps. Items that are not harvested remain on the landscape until they are picked up by a forager. Each food item must be processed, or 'handled', by a forager for T_H timesteps (the handling time, default = 5 timesteps) before it can be consumed (Ruxton et al. 1992; Gupte et al. 2021). The handling time dynamic is well known from natural systems in which there is a lag between finding and consuming a food item (Ruxton et al. 1992), and may be caused by the need to extract edible portions from inedible structures, such as mussels from their shells, or seeds from their casings.

Individual Foraging and Movement

Individuals forage in a randomised order, harvesting the first available food item within their movement and sensory range ($d_S = d_M$, a circle with a radius of 1 unit (see *SI Appendix Fig. S1 – S2*). Once harvested, the item is no longer available to other individuals, leading to exploitation competition among nearby foragers. Furthermore, the location of the item also yields no more cues to other foragers that an item will reappear there, reducing direct cues by which foragers can navigate to profitable clusters of food items. Individuals that harvest a food item must handle it for T_H timesteps (default = 5 timesteps), while all individuals not handling a food item are considered idle (Ruxton et al. 1992; Gupte et al. 2021). As handlers are immobilised at the location where they encountered food, they may be good indirect indicators of the location of a resource cluster ('social information') (Danchin et al. 2004; Romano et al. 2020; Gupte et al. 2021). Once individuals finish handling a food item, they return to the non-handling, searching state.

Our model individuals move in small, discrete steps of fixed size (d_M = 1 unit). Each step is chosen based on the individuals' assessment of local environmental cues, and this assessment is made using evolved movement strategies (as in Gupte et al. 2021; Netz et al. 2021*b*). First, individuals scan their current location, and five equally spaced points around their position, at a distance of 1 unit for three cues (d_S, see *SI Appendix Fig. S1 – S2*): the number of food items (F), the number of foragers handling a food item ('handlers': H) and the number of idle foragers not handling a food item ('non-handlers': N). Individuals assign a suitability (see Gupte et al. 2021; Netz et al. 2021*b*) to their current position and each of the five locations, using their inherited preferences for each of the cues: $S = s_F F + s_H H + s_N N + \epsilon$. The preferences s_F, s_F, and s_N for each of the three cues are heritable from parents to offspring, while ϵ is a very small error term drawn for each location, to break ties among locations. The values of each of the cue preferences *relative to each other* determine individuals' movement strategies (Gupte et al. 2021). All individuals move simultaneously to the location to which they have assigned the highest suitability ('step selection') (akin to step-selection; Fortin et al. 2005); this may be their current location, in which case individuals are stationary for that timestep. Since individuals may differ in their inherited preferences for each of the three cues, two individuals at the same location may make quite different movement decisions based on the same local cues. Handlers, however, are considered immobile and do not make any movement decisions.

Pathogen Transmission and Disease Cost

We modelled circumstances that are expected to become increasingly common due to rapid global changes; the population evolves for 3/5th of the simulation (until G = 3,000; of 5,000) in the absence of a pathogen, after which a pathogen is introduced in each generation until the end of the simulation (G = 5,000). Our model captures some essential features of pathogen or parasite transmission among animals (White et al. 2017): the pathogen may transmit from infected host individuals to their susceptible neighbours with a per-timestep probability p of 0.05. This transmission is only possible when the two individuals are within a the transmission distance, d_β. For simplicity, we set d_β to be the movement range (1 unit). Once transmitted, the pathogen is assumed to cause a chronic disease which reduces host energy stores by a fixed amount called δE in every following timestep; δE is set to 0.25 by default (alternative values: 0.1, 0.5). Since novel pathogen introductions can periodically re-occur in natural environments (Bastos et al. 2000; Vosloo et al. 2009; Almberg et al. 2015; Goulson et al. 2015; Jolles et al. 2021; Carlson et al. 2022*a*; Wille and Barr 2022), we set up our model such that the pathogen was introduced to 4% of individuals in each generation (N = 20; 'primary infections'). This is necessary to kick-start the pathogen-movement eco-evolutionary feedback dynamics, and populations may indeed repeatedly acquire novel pathogens (or strains) through external sources, such as infected individuals of other spatially overlapping species (e.g. Bastos et al. 2000; Keeling et al. 2001; Vosloo et al. 2009; Chandler et al. 2021; Carlson et al. 2022*a*; Kuchipudi et al. 2022; Monk et al. 2022; Wille and Barr 2022). For completeness, we also considered scenarios in which novel pathogen introductions only occur sporadically in the generations after the initial event, rather than in every generation (see *SI Appendix*).

Starting Location and Inheritance of Movement Rules

For simplicity, we considered a population of haploid individuals with discrete, non-overlapping generations, and asexual inheritance. At the end of the parental generation, the net lifetime energy of each individual was determined as the difference of the total energy gained through food intake and the energy lost through infection. In the *SI Appendix*, we also consider an alternative implementation in which potential immune resistance against the pathogen requires a certain percentage of individual intake, reducing the value of each food item. The parental population produces an offspring population (of the same size) as follows: to each offspring, a parent is assigned at random by a weighted lottery, with weights proportional to lifetime net energy (an algorithm following the replicator equation) (Hofbauer and Sigmund 1988; Hamblin 2013). This way, the expected number of offspring produced by a parent is proportional to the parent's lifetime success (Hofbauer and Sigmund 1988). The movement decision-making cue preferences s_F, s_H, and s_N are subject to independent random mutations with a probability of 0.01. The mutational step size (either positive or negative) is drawn from a Cauchy distribution with a scale of 0.01 centred on zero. Thus, while the majority of mutations are small, there can be a small number of very large mutations. As in real ecological systems, individuals in the new generation are intialised around the location of their parent (within a standard deviation of 2.0), and thus successful parents give rise to local clusters of offspring (see an alternative implementation in *SI Appendix*).

Model Output

To understand the evolution of movement strategies, and especially how individuals weighed social information, we recorded the population's evolved cue preferences in every second generation, and interpreted them using the 'behavioural hypervolume' approach (Bastille-Rousseau and Wittemyer 2019). We classified individuals based on how they used social information — the presence and status of competing foragers — into four social movement classes: (1) agent avoiding, if $s_H, s_N < 0$, (2) agent tracking, if both $s_H, s_N > 0$, (3) handler tracking, if $s_H > 0, s_N < 0$, and (4) non-handler tracking, if $s_H < 0, s_N > 0$. We calculated the relative importance of social cues — H, N — to each individual's movement strategy as $SI_{imp} = (|s_H| + |s_N|)/(|s_H| + |s_N| + |s_F|)$, with higher values indicating a greater importance of social cues.

Animal movements and foraging distributions provide opportunities for between-individual associations, which usually have a spatial context. Associations which depend on spatial proximity can be captured at the individual- and population-level by proximity-based animal social networks (Whitehead 2008; Farine and Whitehead 2015). Social networks measured from empirical studies have been broadly informative about the structure of animal societies, and the consequences of this structure for animal culture, such as the learning of migration routes or foraging skills (Aplin et al. 2012; 2013; Cantor et al. 2021), and for disease transmission (Stroeymeyt et al. 2018; Albery et al. 2021; Cantor et al. 2021). We created a proximity-based adjacency matrix by counting the number of times each individual was within the sensory and pathogen transmission distance d_β (= d_S, d_M = 1 unit) of another individual (Whitehead 2008; Wilber et al. 2022). We transformed this matrix into an undirected social network weighted by the number of pairwise encounters: in a pairwise encounter, both individuals were considered to have associated with each other (White et al. 2017). The strength of the connection between any pair was the number of times the pair were within d_β of each other over their lifetime. We logged encounters and constructed social networks after every 10% of the total generations (i.e., every 500th generation), and at the end of the simulation. We constructed adjacency matrices using Rcpp (Eddelbuettel 2013), and converted them to networks using the *igraph* (Csardi and Nepusz 2006) and *tidygraph* (Pedersen 2020) libraries for R. We omitted ephemeral pairwise associations with a weight < 5.

We plotted the mix of social information-based movement strategies evolved across generations in each parameter combination. Focusing on our default scenario ($\delta E = 0.25$, R = 2), we visualised the mean per-capita distance moved, mean per-capita intake, and mean per-capita encounters with other foragers. We examined how the three main social movement strategies — agent avoidance, agent tracking, and handler tracking — changed in frequency over generations. We also examined differences among strategies in the movement distance, associations with other agents, and frequency of infection, after they had reached an eco-evolutionary equilibrium following pathogen introduction (G > 3,500). We visualised the proximity based social networks of populations in a representative scenario ($\delta E = 0.25$, R = 2), focusing on the generations just before and after the pathogen introduction events begin (pre-introduction: G = 3,000; post-introduction: G = 3,500). We plotted the numbers of individuals infected in each generation after pathogen introduction to examine whether evolutionary changes in movement strategies actually reduced infection spread. We also ran simple network epidemiological models on the emergent individual networks in generations 3,000 and 3,500 (Bailey 1975; White et al. 2017; Stroeymeyt et al. 2018; Wilber et al. 2022), for robust comparisons of potential pathogen spread in pathogen-naive and pathogen-adapted populations, respectively.

Outcomes from the Pathomove Model

In our model, individuals move and forage on a landscape with patchily distributed food items, and select where next to move in their vicinity, based on inherited preferences for environmental cues — food items, and other individuals (see *SI Appendix Fig. S1*). Food items, once consumed, regenerate at a rate R, and pathogen infection imposes a per-timestep cost δE. We classified individuals' social movement strategies in our model using a simplified 'behavioural hypervolume' approach (Bastille-Rousseau and Wittemyer 2019), based on the sign of their preferences for successful foragers handling a food item ('handlers', preference s_H), and for unsuccessful foragers still searching for food ('non-handlers', preference s_N). In our default scenario, R = 2, food regenerates twice per generation, and

$\delta E = 0.25$, i.e., consuming 1 food item offsets 4 timesteps of infection. Over the 3,000 generations before the introduction of the pathogen, populations reached an eco-evolutionary equilibrium where the commonest social movement strategy was to prefer moving towards both handlers and non-handlers ('agent tracking'; $s_H, s_N > 0$; but see below) (Fig. 5.1A).

Rapid Evolutionary Shift in Social Movement Strategies Following Pathogen Introduction

Introducing an infectious pathogen to 4% (n = 20) of individuals in each generation (after G = 3,000), leads to a remarkably rapid evolutionary shift — within only 25 generations of pathogen introduction — in how social information is incorporated into individuals' movement strategies. There is a marked increase in the frequency of individuals that track successful foragers, but avoid non-handlers ('handler tracking'; $s_H > 0$, but $s_N < 0$) (Fig. 5.1A; $3{,}000 < G < 3{,}025$). Surprisingly, after a brief period (in evolutionary terms) of handler tracking being the most common strategy, a third strategy also becomes more common: avoiding both handlers and non-handlers ('agent avoiding'; $s_H, s_N < 0$). Within 250 generations after pathogen introduction, agent avoiding becomes as common as the handler tracking strategy, and this appears to be a stable equilibrium that is maintained until the end of the simulation (2,000 generations after pathogen introduction; Fig. 5.1A). The *SI Appendix* shows how the occurrence of rapid evolutionary shifts is broadly robust to modelling assumptions; in brief, such shifts occur even when individuals cannot benefit from evolved adaptation to local conditions (Badyaev and Uller 2009), and when the pathogen saps a percentage, rather than an absolute value, from daily intake.

In addition to qualitative changes in social movement strategies, pathogen introduction also leads to social information becoming more important to movement decisions. Prior to pathogen introduction ($G < 3{,}000$), individuals' handler- and non-handler preferences ($|s_H| + |s_N|$; taken together, social information) barely influence their movement strategies (Fig. 5.1B). These are instead guided primarily by the preference for food items (s_F; see *Model and Analysis*; see also *Supplementary Information*). Social movement decisions are joint outcomes of individual preferences for social cues and the cue value: consequently, in clustered populations (see below), even small positive values of s_H and s_N lead to strong emergent sociality. After pathogen introduction, there is a substantial increase in the average importance of individuals' preferences (or aversions) for the presence of other foragers (Fig. 5.1B). However, there is significant variation among individuals in the importance of social information to their movement strategies, with distinct evolved polymorphisms that vary substantially between simulation replicates (Fig. 5.1B).

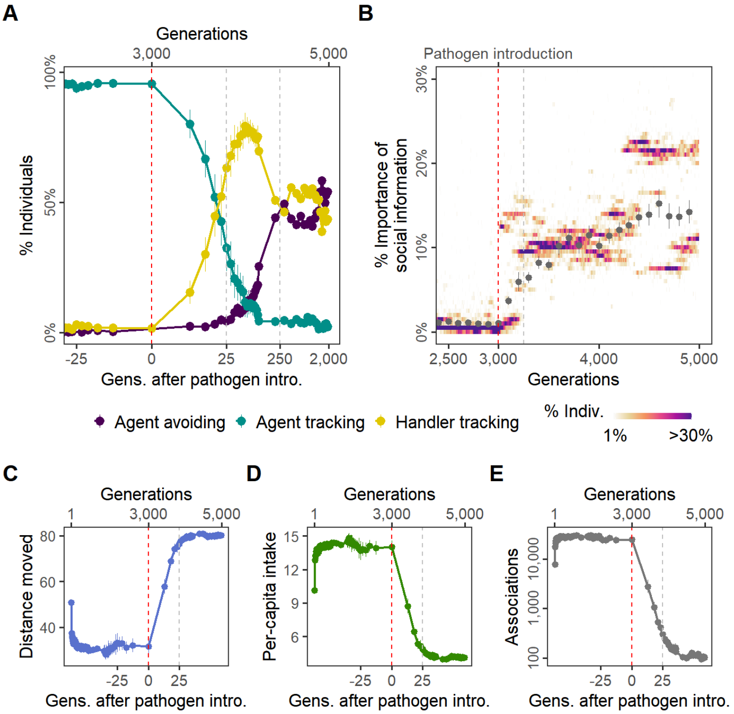

Figure 5.1: Pathogen introduction leads to rapid evolutionary changes in social information use, with cascading effects on population ecological outcomes. (A) Before pathogen introduction in the default scenario (R = 2, $\delta E = 0.25$), populations rapidly evolve a social movement strategy that tracks all other individuals ('agent tracking'; $G \leq 3{,}000$) — however, their overall movement strategy is primarily guided by the presence of food items **(B)**. Pathogen introduction leads to the rapid replacement, within 25 generations, of agent tracking with 'handler tracking' (preference for successful foragers; $3{,}000 < G < 3{,}025$). Within 250 generations, 'agent avoidance' (avoidance of both successful and unsuccessful foragers; $G > 3{,}250$) also becomes common, stably co-existing with the handler tracking strategy in an eco-evolutionary equilibrium. **(B)** After pathogen introduction ($G > 3{,}000$), the importance of social cues (the presence of other individuals; the sum of the absolute, normalised preferences sH, sN) increases substantially on average (grey points). Additionally, there is significant variation in the importance of social cues to individuals (shaded regions), which is not captured by the mean or standard error. At G = 4,500, for example, social information comprises ≈ 10% of some individuals' movement strategies, but some individuals have evolved a stronger weight for social cues (> 20%). The rapid change in social movement strategies following pathogen introduction has cascading effects on ecological outcomes. Individuals, which have evolved strong aversions to at least some kinds of foragers (depending on their strategy), **(C)** move more on average, **(D)** have only 25% of the pre-pathogen average intake, and **(E)** have 100-fold fewer associations with other individuals. All panels show data averaged over 10 replicates, but shaded region in panel B shows only a single replicate for clarity.

Disease-dominated Ecological Cascade Due to Evolutionary Shift in Movement Strategies

The evolutionary shift in social movement strategies causes a drastic change in ecological outcomes (Fig. 5.1C – E; see *SI Appendix Fig. S3* for other scenarios). There is a sharp increase in mean distance moved by individuals; while pre-introduction individuals moved 35% of their lifetimes on average (i.e., 35 timesteps; handling for the remainder), post-introduction, individuals move for 80% of their lifetimes (i.e., 80 timesteps; Fig. 5.1C). The handler tracking and agent avoiding strategies lead individuals to move away from groups of individuals ('dynamic social distancing'; Pusceddu et al. 2021). Individuals being most likely to be found near resource clusters, this leads to movement away from productive areas of the landscape. Consequently, there is a rapid, four-fold drop in mean per-capita intake after pathogen introduction (Fig. 5.1D). The concurrent, near 100-fold drop in encounters between individuals after pathogen introduction (Fig. 5.1E) suggests that most encounters were likely taking place on or near resource clusters. The reductions in intake observed are equivalent to those expected from halving landscape productivity (*SI Appendix Fig. S3*). Our model shows how even a non-fatal pathogen, by influencing the evolution of movement strategies, can have substantial indirect ecological effects — a disease dominated ecological cascade (Monk et al. 2022).

Co-existence of Social Movement Strategies

At eco-evolutionary equilibrium (G > 3,500) the relationship between movement and avoiding associations (and further, infection) is mediated by individual differences in how exactly social information is incorporated into movement strategies. Individuals using the agent avoiding strategy move more than handler tracking ones (Fig. 5.2A), about 85% of their lifetime (default scenario: R = 2; $\delta E = 0.25$). At this limit, every step moved allows them to avoid approximately 2 encounters with other individuals. Handler tracking individuals move much less (~ 60% – 80%), but are able to avoid approximately 20 encounters with other individuals with every extra step. These differences may explain why agent avoiding and handler tracking individuals have similar mean infection rates, at ~ 25% and ~ 33% respectively (Fig. 5.2B). All other strategies, especially the agent tracking strategy common in pre-introduction populations, are barely able to translate increased movement into fewer associations (Fig. 5.2A). These strategies have a wide range of infection rates (Fig. 5.2B), potentially because they are very rare — these likely represent mutants that do not give rise to persistent lineages.

Reorganisation of Spatial-social Structure

Following pathogen introduction, the mixture of individual-level movement strategies elicits a substantial re-organisation of emergent spatial and social structure at the population level. Pre-introduction populations are strongly clustered in space (Fig. 5.3A), due to movement strategies that favour following most other

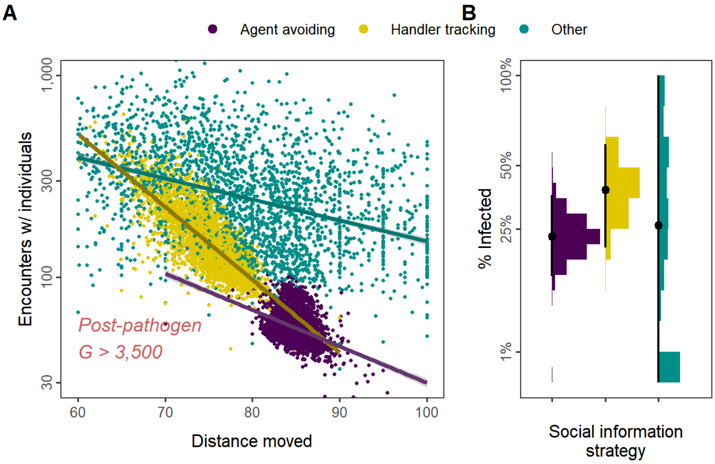

Figure 5.2: Social movement strategies trade movement for associations through dynamic social distancing, leading to differences in infection rates. In post-introduction populations at eco-evolutionary equilibrium (G > 3,500), **(A)** both agent avoiding and handler tracking individuals can reduce encounters with other individuals by moving to avoid other foragers (dynamic social distancing). Handler tracking individuals have many more encounters than agent avoiding individuals, but surprisingly, are better able to reduce encounters through increased movement. Individuals using other strategies (mostly agent tracking) have a wider range of movement distances, but cannot efficiently avoid other foragers by moving more. **(B)** Avoiding all other foragers leads to marginally lower infection rates than tracking successful foragers (and avoiding unsuccessful ones; handler tracking). Surprisingly, rare pre-introduction strategies such as following any nearby individuals (agent tracking) may also have low infection rates, potentially due to their rarity. Panel A shows linear model fits with a log scale Y-axis; panel B shows infection rates; all data represent generation- and replicate-specific means (G > 3,500; R = 2, δE = 0.25).

foragers. This spatial proximity means that most individuals encounter each other at least once, leading to numerous unique partners (the 'degree') for each forager (Fig. 5.3 inset 1: *blue*). In contrast, the spread-out networks in pathogen-risk adapted populations suggest that most foragers move substantially from their initial locations over their lifetime, associating only ephemerally with foragers from all over the landscape (Fig. 5.3B). This reflects movement strategies which lead to near-perpetual movement to avoid associations; a sort of dynamic social distancing seen in real animal societies under risk of pathogen spread (Stroeymeyt et al. 2018; Weinstein et al. 2018; Pusceddu et al. 2021; Stockmaier et al. 2021). This dispersed population structure means that most pathogen-risk adapted foragers encounter fewer than 10% of the population over their lifetime (Fig. 5.3 inset 1: *red*).

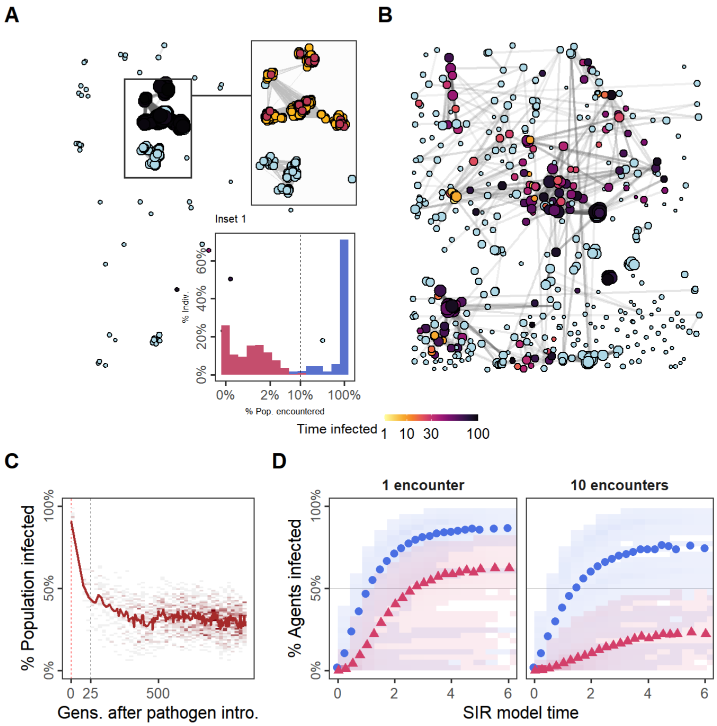

Figure 5.3: Reduced spatial-social clustering and disease transmission in populations adapted to the presence of an infectious pathogen. pathogen-risk naive populations (**A**; G = 3,000) are much more spatially clustered than pathogen-risk adapted populations (**B**; G = 3,500), and are thus rapidly infected (red: primary infections; yellow: secondary infections; blue: never infected). Pre-introduction individuals encounter many more unique neighbours (**inset 1**, blue) than pathogen-risk adapted individuals (**inset 1**; red). Dashed grey line represents 10% of individuals encountered (N = 50). Main panels show social networks from a single replicate of the default scenario (R = 2, δE = 0.25), insets show 10 replicates. Nodes represent individuals positioned at their final location. Connections represent pairwise encounters, and node size represents encounters (larger = more encounters). Darker node colours indicate longer infection (light blue = no infection). **(C)** In the first generations following pathogen introduction, nearly every single individual in the population is infected. However, within 25 generations, tracking the evolutionary shift towards movement strategies that avoid some or all other individuals, only about 50% of individuals are ever infected; this drops to a stable 30% within 500 generations after pathogen introduction. **(D)** The progression of two hypothetical diseases, requiring a single encounter, or 10 encounters for a potential transmission, on emergent social networks. The transmission of both diseases is reduced in populations with disease-adapted movement strategies (pre-introduction: G = 3,000, blue circles; post-introduction: G = 3,500, red triangles). Subfigures in panel D show means of 25 SIR model replicates (transmission rate β = 5.0, recovery rate γ = 1.0), run on emergent social network; both panels represent 10 simulation replicates the default scenario.

Pathogen-risk Adapted Movement Strategies Make Animal Societies More Resilient to the Spread of Disease

Nearly every individual in the generations just after pathogen introduction was infected. However, tracking the evolutionary change in movement strategies, the number of infected individuals fell to just about 50% within 25 generations (Fig. 5.3C). To examine potential pathogen spread in pre-introduction populations, we ran a simple epidemiological model on the social networks emerging from individuals' movements before and after pathogen introduction (pre-introduction: G = 3,000; post-introduction: G = 3,500). We modelled two diseases, *(i)* first, a disease requiring one encounter,and *(ii)* second, a disease requiring ten encounters between individuals for a potential transmission event (transmission rate $\beta = 5.0$, recovery rate $\gamma = 1.0$).

Both the single encounter and multiple encounter diseases would infect 75% – 80% of individuals when spreading through the networks of pre-introduction populations (Fig. 5.3D). Pathogen-risk adapted populations' social networks are more resilient to both the single encounter and multiple encounter disease, compared to their pre-introduction, pathogen-risk naive ancestors, as these social networks are sparser and individuals are more weakly connected (Fig. 5.3D). Less than 60% of post-introduction populations were finally infected by the single encounter disease, compared with > 75% of pre-introduction, pathogen-risk naive ancestors; in pathogen-risk adapted populations, the spread of the multiple encounter disease was even slower (ever infected: ≈ 20%).

Usefulness of Social Information and Infection Cost Influence Evolution of Social Movement Strategies

We further explored the effect of two ecological parameters, landscape productivity ($R \in 1, 2, 5$) and infection cost per timestep ($\delta E \in 0.1, 0.25, 0.5$) on simulation outcomes. Before pathogen introduction, landscape productivity alone determines the value of social information, and thus which social movement strategies evolve (Fig. 5.4). On low-productivity landscapes (R = 1), social information is valuable as direct resource cues are scarce; here, the handler-tracking strategy persists. On high-productivity landscapes ($R \in 2, 5$), social information is less valuable as individuals can directly detect food items more often; here, the agent tracking strategy is most common. Across parameter combinations, the introduction of the infectious pathogen leads to a rapid evolutionary shift in social movement strategies. The benefits of social information, and infection cost jointly determine how pathogen introduction alters the mix of social movement strategies, but populations generally shift away from indiscriminate agent tracking, as that strategy is associated with higher infection risk (see Fig. 5.3A).

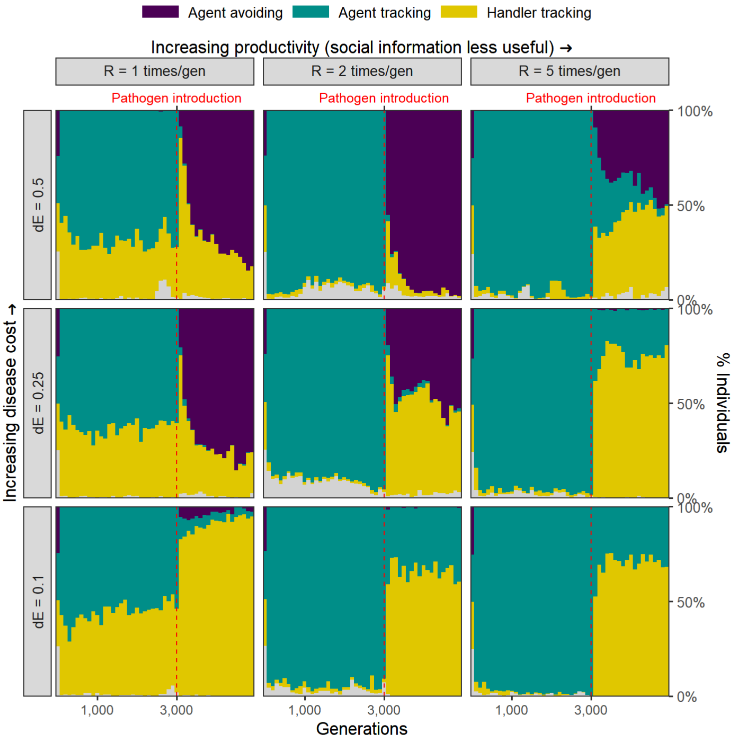

Figure 5.4: The balance of infection cost and the usefulness of social information together shape the rapid evolutionary change in movement strategies triggered by pathogen introduction. Pre-introduction (G = 3,000; dashed line) populations contain a mix of individuals that either track all foragers (agent tracking), or only successful foragers (handler tracking). Handler tracking is more common on low-productivity landscapes (R = 1), where social information is more useful to find patchily distributed resources. After pathogen introduction, handler tracking rapidly becomes the most common strategy when the apparent usefulness of social information is greater than the cost of infection. This occurs both when productivity is low (R = 1) and infection costs are low ($\delta E = 0.1$), but also when productivity is high (R = 5) with intermediate infection costs ($\delta E = 0.25$). When the cost of infection outweighs the apparent usefulness of social information, the agent avoidance (avoiding both successful and unsuccessful foragers) emerges and rapidly becomes a common strategy ($\delta E = 0.5$; $\delta E = 0.25$, R = 1). In scenarios of high landscape productivity combined with low infection costs (e.g. R = 5, $\delta E = 0.1$), the agent tracking strategy persists in a large proportion after pathogen introduction, as these individuals can balance disease costs with intake alone. All panels show mean frequencies over 10 replicate simulations in 100 generation bins; frequencies are stacked. Grey areas show the relatively uncommon 'non-handler' tracking strategy.

When the benefit of social information is equivalent to the cost of infection, the handler tracking strategy is common (R = 1, $\delta E = 0.1$; R = 5, $\delta E = 0.25$). When apparent social information benefits are lower than infection costs (e.g. $\delta E = 0.5$), the agent avoiding strategy is common. The effect of landscape productivity in obviating a sensitivity to social information cues (especially, conspecific status) is also eroded by pathogen introduction. On high-productivity landscapes where individuals were indiscriminately social, ($R \in 2, 5, \delta E = 0.1$), the handler tracking strategy becomes common, as individuals prioritise higher-quality social information (handlers, which indicate a resource cluster). However, high landscape productivity can also compensate for the cost of infection, as evidenced by the agent tracking strategy remaining prevalent: this is only possible if these individuals can consume sufficient resources to overcome disease costs.

Contextualising the Outcomes of the Pathomove Model

Our general model captures important features of infectious pathogen (or parasite) transmission among host animals in a (foraging) context that is relevant to most species. The combination of ecological, evolutionary, and epidemiological dynamics in a spatial setting is unprecedented for movement-disease models, and extends current understanding of animal spatial and social ecology (Kurvers et al. 2014; Webber and Vander Wal 2018; Romano et al. 2020; Albery et al. 2021; Romano et al. 2021; Webber et al. 2022). Presently, most movement-disease models are non-evolutionary (White et al. 2017; 2018*b*; Scherer et al. 2020; Lunn et al. 2021), presumably because evolution is expected to be too slow to impact epidemiological-ecological outcomes (Monk et al. 2022). We demonstrate the pitfalls of this assumption: evolutionary transitions in sociality occur over fewer generations than required for the development of key aspects of animal ecology, such as migration routes (Jesmer et al. 2018; Cantor et al. 2021). We also demonstrate the tension inherent to sociality under the risk of an infectious pathogen, in an explicitly spatial context. Our work shows how qualitatively and quantitatively different social movement strategies — making different trade-offs between social information and infection risk — can co-exist in a single population (Wolf and Weissing 2012; Webber and Vander Wal 2018; Gartland et al. 2021; Webber et al. 2022).

Social Information Use and Pathogen Introduction

Prior to pathogen introduction, the value of social information influenced which social movement strategies were evolved. Individuals initialised ('born') near their parent's final location may benefit from 'ecological inheritance' (Badyaev and Uller 2009) of their parent's favourable position near resource clusters (see *SI Appendix Fig. S2, S4*). Avoiding potential competitors (and kin) thus correlates with avoiding profitable areas, and this leads to the persistence of the indiscriminately social agent tracking strategy, despite the evident costs of exploitation competition. In an alternative implementation with large-scale natal dispersal, handler tracking is the commonest strategy prior to pathogen introduction (see

SI Appendix). Following pathogen introduction, the agent tracking strategy of our default scenario allows the disease to spread very easily among entire lineages of social individuals (see Fig. 5.3A) (Kurvers et al. 2014). This neatly demonstrates why the risk of infection or parasitism could be among the mechanisms underlying density dependence in natal dispersal decisions (Travis et al. 1999).

Following pathogen introduction, the evolutionary shift in social movement strategies is much more rapid than the timescales usually associated with the evolution of complex traits such as sociality (about 25 generations). Avoiding potentially infectious individuals is a key component of navigating the 'landscape of disgust' (Weinstein et al. 2018). Our results show that sensitivity to cues of high pathogen transmission risk can rapidly evolve following the introduction of a novel pathogen, with a complete replacement of the hitherto dominant social strategy. The emergence of qualitative individual variation in social movement strategies, and especially the trade-off between movement, associations, and infection risk also demonstrates the evolution of 'sociability as a personality trait' (Gartland et al. 2021).

We also find substantial individual variation in the quantitative importance of social cues overall, which is a key component of the evolution of large-scale collective behaviours, such as migration (Guttal and Couzin 2010). Our work suggests how, by leading to the necessary diversity in social movement strategies, a novel pathogen may actually lay the groundwork for the evolution of more complex collective behaviour. Nonetheless, the rapid decreases in social interactions should primarily prompt concern that the evolutionary consequences of pathogen introduction could slow the transmission of, and erode, animal culture (Cantor et al. 2021) — including foraging (Klump et al. 2021) and migration behaviours (Guttal and Couzin 2010; Jesmer et al. 2018). Pathogens themselves typically have shorter generation times than their hosts, and may also evolve rapidly in response to changes in host sociality (Ashby and Farine 2022). Although not examined here, a mixture of social strategies could allow for the maintenance of a corresponding diversity in pathogen strategies as well (Prado et al. 2009; Ashby and Farine 2022).

Ecological Causes and Consequences of Social Movement Strategies

In our model, landscape productivity (R), is a proxy for the usefulness of sociality overall, as social information is less useful when direct resource cues are abundant (high R). Social information benefits in disease models often have no mechanistic relationship with the subject of the information (e.g. food or predators) (Ashby and Farine 2022). In contrast, social information benefits in our model are emergent outcomes of animal movement and foraging behaviour. Our predictions may help explain intra- and inter-specific diversity in social systems across gradients of infection risk and the usefulness of social information (Altizer et al. 2003; Sah et al. 2018), and studies tracking social movements and potential for disease spread could form initial tests of our basic predictions (Wilber et al. 2022). While our individuals do not die, the evolved pathogen-risk adapted, dynamic social distancing strategies (Stockmaier et al. 2021) lead to a significant worsening (equivalent to a halving) of individuals' intake. In real systems, this could increase populations' susceptibility to extreme climate change related mortality events (Fey et al. 2015).

More positively, animals may be able to adapt relatively quickly to the spillover and eventual persistence of infectious pathogens, even when they cannot specifically detect and avoid infected individuals (Altizer et al. 2003; Stroeymeyt et al. 2018; Pusceddu et al. 2021; Stockmaier et al. 2021). While the most noticeable effect of pathogen outbreaks is mass mortality (Fey et al. 2015), even quite serious pathogens — Sarcoptic mange (Almberg et al. 2015), foot-and-mouth disease (Bastos et al. 2000; Vosloo et al. 2009; Jolles et al. 2021), SARS-CoV-2 (Chandler et al. 2021; Kuchipudi et al. 2022), and avian influenza (Global Consortium for H5N8 and Related Influenza Viruses 2016; Wille and Barr 2022) among others — appear to spread at sub-lethal levels for many years between lethal outbreaks. Our model shows how disease-dominated ecological cascades (Monk et al. 2022) could occur even without mortality effects, due to evolutionary shifts in sociality alone. The altered ecological state (here, less resource consumption, as in Monk et al. 2022) may be maintained long after — and indeed because — a population has adapted to be less social in the presence of a pathogen. Our work suggests that decreased sociality resulting from adaptation to a novel pathogen could slow the transmission of future novel pathogens. While decreased sociality could also reduce the prevalence of previously endemic pathogens adapted to a more social host, it may also degrade 'social immunity' through reduced sharing of beneficial commensal microbes, or of low, immunising doses of pathogens (Almberg et al. 2015; Ezenwa et al. 2016).

Feedbacks with Pathogen Chracteristics

Our model results are contingent upon sustained introduction of the pathogen (or its novel strains) to host populations. More sporadic introductions (once every few generations) apparently do not cause evolutionary shifts in social movement (*SI Appendix*). Yet repeated pathogen and parasite introductions among susceptible populations appear to be quite common (Bastos et al. 2000; Vosloo et al. 2009; Levi et al. 2012; Global Consortium for H5N8 and Related Influenza Viruses 2016; Scherer et al. 2020; Jolles et al. 2021; Wille and Barr 2022). Such introductions are often detected only among easily observed groups such as birds (Wille and Barr 2022), or after evident mass mortality events (Fey et al. 2015; Fereidouni et al. 2019). Seasonal host-pathogen dynamics could and do keep pathogens circulating in reservoir hosts, with regular pulses in primary infections similar to our model (e.g. due to new calves in African buffalo hosting foot-and-mouth disease: Jolles et al. 2021, or winter peaks in mange among wolves: Almberg et al. 2015). Existing host-pathogen dynamics, and potential pathogen range expansions, could thus provide more frequent opportunities for novel transmissions to overlapping species than previously guessed. Our model shows how this provides a powerful selective force in favour of detecting and avoiding infection risk cues (Weinstein et al. 2018).

Pathogens also typically have much shorter generation times than their hosts. Analytical models expect pathogen attributes to rapidly co-evolve to match host population attributes (e.g. sociality and immune resistance) (Bonds et al. 2005; Prado et al. 2009; Ashby and Farine 2022). Such models treat pathogens — just as they do host animals — in relatively simple, non-mechanistic ways. Pathogens are primarily expected to evolve to a virulence that promotes between-host transmission (Bonds et al. 2005). Our mechanistic model does not explicitly consider host-pathogen co-evolutionary dynamics, as this complexity was beyond the scope of our general, conceptual model. Adding pathogen evolutionary dynamics to a mechanistic individual-based model would require careful consideration of *(i)* the costs the pathogen imposes on its hosts, and *(ii)* how it transmits between hosts, both within and between generations. We expect that multiple pathogen strategies could coexist in a host population that itself has multiple social movement strategies.

Towards Hypothesis-testing and Predictive Modelling

In order to be widely applicable to diverse novel host-pathogen introduction scenarios, our model is necessarily quite general. A wide diversity of pathogens and their dynamics remains to be accurately represented in individual-based models (White et al. 2017; 2018*b*; Scherer et al. 2020; Lunn et al. 2021). Our framework can be expanded and specifically tailored to real-world situations in which populations are repeatedly exposed to novel pathogens (or strains) (Bastos et al. 2000; Scherer et al. 2020; Chandler et al. 2021; Jolles et al. 2021; Kuchipudi et al. 2022; Wille and Barr 2022). Such detailed implementations could include aspects of the pathogen life-cycle (White et al. 2017; 2018*a*), account for sociality as a counter to infection costs (Almberg et al. 2015; Ezenwa et al. 2016), or model host-pathogen sociality-virulence co-evolution (Bonds et al. 2005; Prado et al. 2009; Ashby and Farine 2022). We generate consistent predictions of marked and swift evolutionary shifts in social movement strategies that could plausibly be tested over the timescales of some long-term animal tracking studies (Wilber et al. 2022).

Importantly, our social information-based movement strategies are made up of continuous values that place individuals on a two-dimensional trait space of relative preferences (or aversions) for successful and unsuccessful foragers (see *Model and Analysis*; Bastille-Rousseau and Wittemyer 2019). Such social movement strategies could already be revealed for free-living animals using newer step-selection approaches (Avgar et al. 2016), combined with the simultaneous, high-throughput tracking of many hundreds of animals in an area (Nathan et al. 2022). Future work would ideally combine wildlife monitoring and movement tracking across gradients of pathogen prevalence, to detect novel cross-species spillovers (Chandler et al. 2021; Kuchipudi et al. 2022) and study the spatial and epidemiological consequently of animal movement strategies (Bastille-Rousseau and Wittemyer 2019; Monk et al. 2022; Wilber et al. 2022). Given that infection patterns can change rapidly in space even in small, well-mixed populations (Albery et al. 2022), the systems that could be used to test these phenomena may be widespread and easily available. Finally, our model shows why it is important to consider evolutionary responses in movement-disease studies, and provides a general framework to further the integration of evolutionary approaches in wildlife spatial epidemiology.

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Supplementary Information for Chapter 5

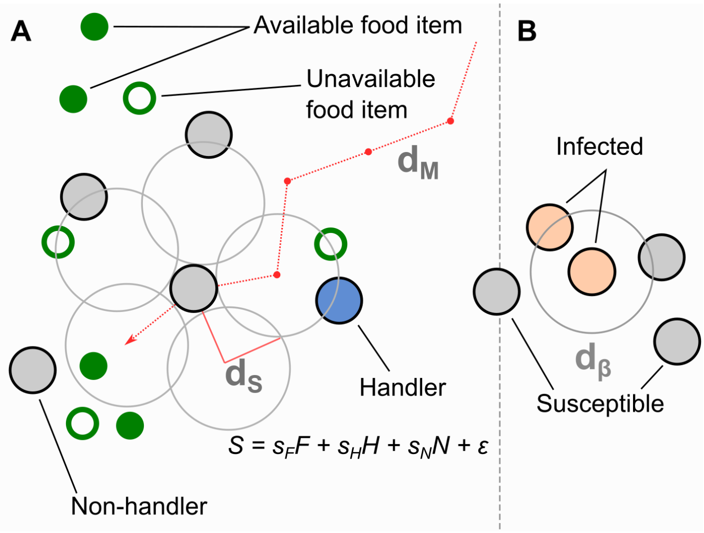

Figure 5.5: Model implementation of discrete movement steps in continuous space, with movement steps selected based on inherited preferences for environmental cues. In our model, **(A)** individuals search for food items (**green circles**), which may be immediately available (**filled green circles**; F), or may be available only in the future (**open green circles**). Individuals can sense only available items, and not unavailable ones. However, given our landscape structure, food items are clustered, making available items a good indicator of where resource clusters are (see next figure). Individuals can also sense other foraging individuals, and can sense whether they have successfully found, and are handling, a food item (handlers; **blue circles**), or whether they are unsuccessful foragers still searching for food (non-handlers; **filled grey circles**; N). To decide where to move, individuals sample their environment for these three cues (F, H, N) at 5 locations around themselves (**large open grey circles**), and have a sensory range of d_S. When the sensory range is relatively large (default = 1.0 units), there is some small overlap in samples. Individuals assign each potential direction a *suitability*, $S = s_F F + s_H H + s_N N + \epsilon$, where the coefficients s_F, s_H, s_N are inherited preferences for environmental cues, and ϵ is a small error term that helps break ties between locations. In our implementation, the sensory distance (d_S) and the movement distance (d_M) are the same, 1.0 units. **(B)** Our infectious pathogen is transmitted between infected (**orange circles**) and susceptible (**filled grey circles**) individuals, with a probability $p = 0.05$, when they are within a distance d_β of each other. In our implementation, d_β is the same as d_S, d_M = 1.0 units.

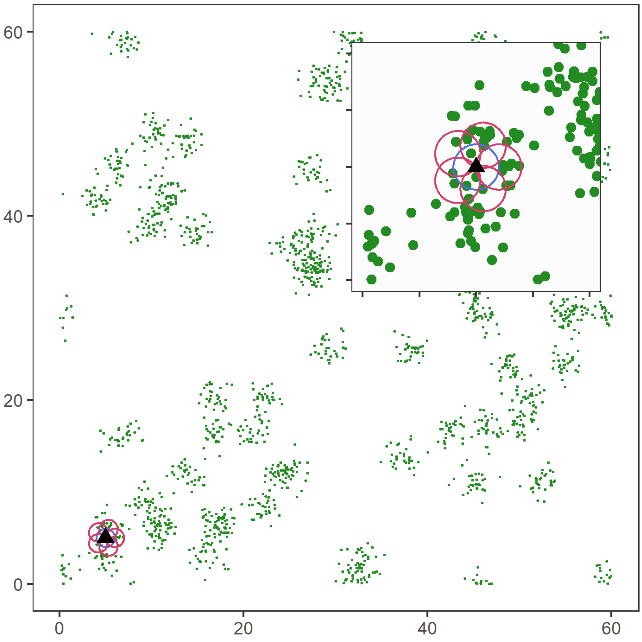

Figure 5.6: An example of the resource landscape used in our simulations. Our simulation's resource landscape consists of 60 randomly distributed clusters of food items ('resource patches'), with 1800 discrete food items divided among the clusters (30 items per cluster). The landscape is a square of 60 units per side, with wrapped boundaries (i.e., a torus). The food item density in our scenarios is 0.5 food items per unit area. Items are distributed around the centre of each cluster, within a standard deviation of 1.0 unit. Items, once consumed by foragers, are unavailable for a fixed number of timesteps (the regeneration time R, expressed in terms of the foragers' generation time), after which they regenerate in the same location. While regenerating (i.e., unavailable). While regenerating, items cannot be sensed by foragers. The sensory ranges of individuals (d_S) are shown for each potential step (**red circles**, including the current location: **blue circle**). Food item clustering means that available items, as well as foragers handling a food item (handlers) are good indicators of the location of a resource cluster.

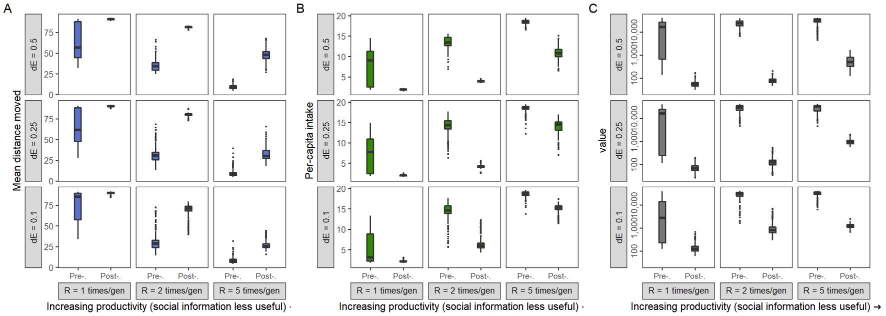

Figure 5.7: Rapid changes in ecological outcomes following pathogen introduction. The introduction of the infectious pathogen leads to rapid evolutionary changes in movement strategies (see Figures 1 and 5; main text) across most combinations of landscape productivity and infection cost. In all combinations where there is rapid evolutionary shift in social-movement strategies, there is a similar change in the population's ecological outcomes: more movement, less intake, and fewer associations. Only in scenarios where the mix of social-movement strategies does not change ($R \in 2, 5$; $\delta E = 0.1$), is there broadly no change in population ecological outcomes. Each subplot in each panel shows the mean and standard error of the per-capita values for **(A)** distance moved, **(B)** intake, **(C)** number of associations, or encounters, with other individuals. Means and standard deviations are shown before (G = 3,000) and after (G = 3,500) pathogen introduction; each data point represents 10 replicates of the relevant parameter combination.

Effect of Modelling Choices

Modelling choices can have a substantial effect on the outcomes of simulations with multiple, complex interactions among components (Scherer et al. 2020; Gupte et al. 2021; Netz et al. 2021*b*). We show the effect of varying implementation on two key aspects of our model: *(1)* where individuals are initialised, or 'born', on the landscape (natal dispersal), *(2)* how the infectious pathogen imposes fitness costs.

Global Natal Dispersal of Individuals

Some models initialise the individuals in each new generation at random locations on the landscape (see e.g. 2021; Chapter 4); this can be called 'global' natal dispersal. This is a reasonable choice when modelling animals during a specific stage of their life cycle, such as after arriving on a wintering or breeding site after migration. Our default choice, on the other hand, is 'local' natal dispersal, where individuals are initialised close to their parent's last position. This is also defensible, as many organisms do not disperse very far from their ancestors. When animals do not disperse very far, they may not evolve movement rules that can be generalised across all landscape conditions, especially when the landscape is ecologically heterogeneous. Instead, animals may adapt their strategies to the local conditions which they inherit from their parents (‘ecological inheritance’; Badyaev and Uller 2009).

Successful individuals are likely to have more offspring than unsuccessful individuals, and successful individuals are likely to be found — in our simulation and in real natural systems — on or near profitable resource patches. This means that many individuals are initialised near profitable patches. In this case, and because of the sparse distribution of resource patches on the landscape, individuals adapt to tolerate their many neighbours (who are often kin), as avoiding them would lead to also moving away from a profitable patch.

By forcing animals in each new generation to encounter ecological circumstances potentially different from those of their parents, implementing global dispersal can help investigate whether animals’ evolved movement strategies are truly ‘optimal’ at the global scale. We implementated global dispersal by running 10 replicates of each parameter combination (9 combinations of $\delta\ E$ and R; 90 simulations in all), with dispersal set to 10. This means that individuals’ initial positions are drawn from a normal distribution with standard deviation = 10, centred on the location of their parent (see Fig. 5.8; blue circles).

Evolutionary Outcomes of the Global Dispersal Implementation

In the global dispersal scenario (see Fig. 5.8), there is a marked difference in which social movement strategy is evolved before pathogen introduction. Since individuals are initialised relatively far away from their parent’s position, they encounter potentially very different ecological conditions, both in terms of the number of other individuals, and the local availability of food items.

As a result, most individuals evolve a ‘handler tracking’ social movement strategy before the introduction of the novel pathogen. This strategy allows individuals to gain the benefits of social information on the location of a resource patch (of which handlers are an indirect cue), while avoiding potential competitors, as well as potentially moving away from areas without many food items.

After pathogen introduction, there is a rapid evolutionary shift in social movement strategies, similar to the shift seen in our default implementation of local dispersal. However, these shifts only occur under conditions where the cost of infection is apparently greater than the value of using social information to find food items. In brief, *(1)* when the benefits of social information cannot compensate for the costs of infection risk (δE = 0.5; δE = 0.25, and R = 1, 2), the agent avoiding strategy becomes more prevalent, similar to the local dispersal case. *(2)* When the costs of infection are lower than the benefits of social information, or when the resource landscape’s productivity can offset the cost of infection, the handler tracking strategy persists as the dominant strategy (see Fig. 5.9).

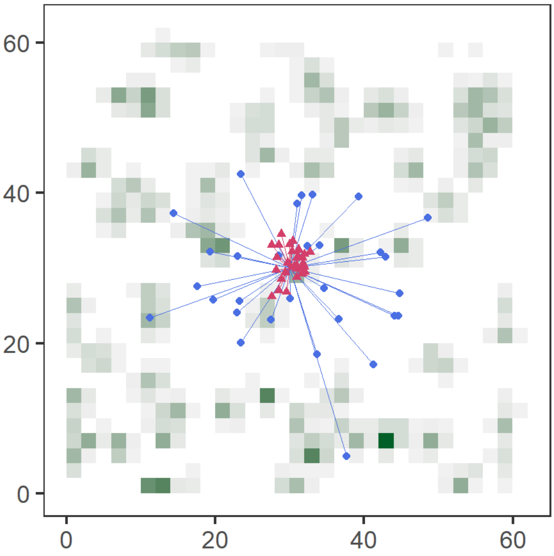

Figure 5.8: Differences between local and global dispersal. Initialising individuals in each new generation within a standard deviation of 10 units around their parent (**blue**; parent at [30, 30]) places can lead them to encounter potentially very different ecological, and social, circumstances from those of their parent. In contrast, individuals initialised close to their parents (within a standard deviation of 2 units; **red**) encounter very similar conditions as their parent. The latter also leads to substantial competition among kin. We used 10 units to represent (nearly) global dispersal, and 2 units to represent local dispersal; this is controlled by the simulation parameter *dispersal*, which takes a numeric argument.

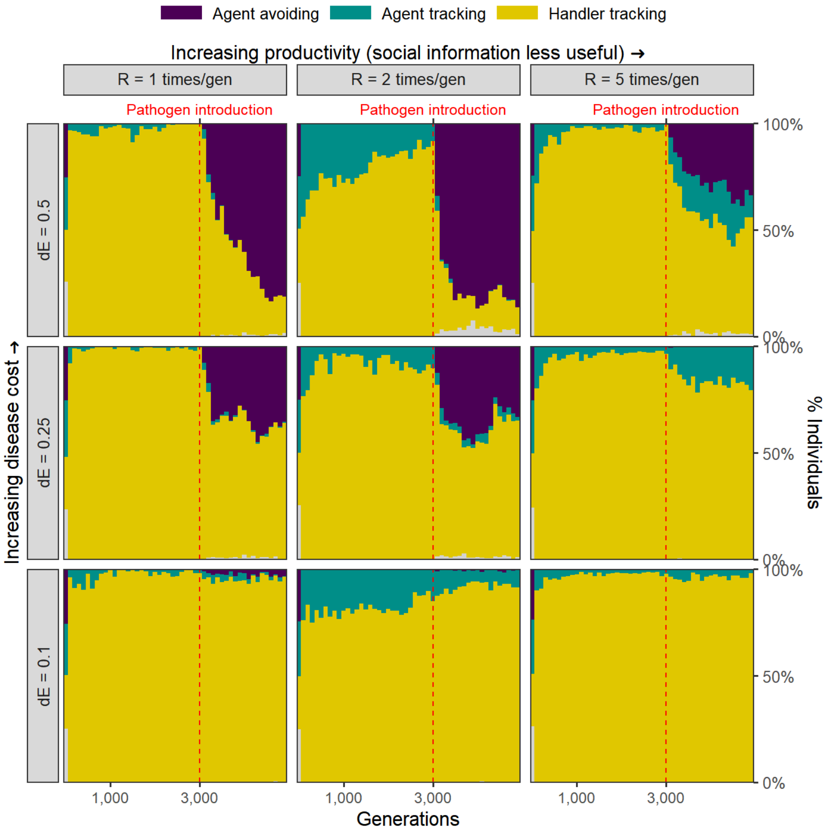

Figure 5.9: Pathogen introduction triggers similar evolutionary changes under global dispersal as under local dispersal. In our alternative, global natal dispersal implementation, the handler tracking strategy is the dominant strategy across most parameter combinations prior to pathogen introduction. Following pathogen introduction, there is a rapid shift in the mix of movement strategies under some ecological conditions. When the cost of infection is greater than the apparent benefit of social information, the agent avoiding strategy becomes more common. When infection costs are low ($\delta E = 0.1$), pathogen introduction does not alter the mix of movement strategies, and the handler tracking strategy continues to be the most common strategy.

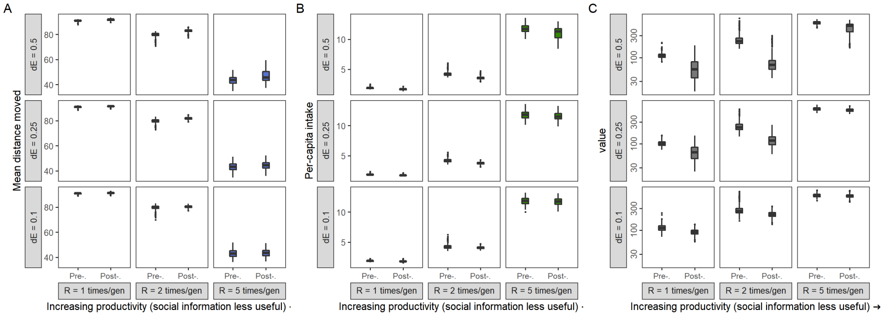

Figure 5.10: Little to no change in ecological outcomes when implementing global dispersal. Despite strong and rapid evolutionary shifts in social movement strategies, the ecological outcomes for populations with global natal dispersal are very similar before and after the introduction of the infectious pathogen. Each subplot in each panel shows the mean and standard error of the per-capita values for **(A)** distance moved, **(B)** intake, **(C)** number of associations, or encounters, with other individuals. Means and standard deviations are shown before (G = 3,000) and after (G = 3,500) pathogen introduction; each data point represents 10 replicates of the relevant parameter combination.

Ecological Consequences in the Global Dispersal Implementation

In the global dispersal implementation, there is little to no change in population-level ecological outcomes — mean distance moved, mean per-capita intake, and the mean number of associations — following pathogen introduction (Fig. 5.10). This is despite the drastic shift in evolved social movement strategies. This is likely because a large part of individual's lifetimes (at low R, up to 90 timesteps), are spent moving, likely to find resource clusters. Since intake depends on finding these clusters, and associations mostly take place at or near resource clusters, these are also reduced compared to our local dispersal implementation.

Infection Cost as a Percentage of Intake

In our model's default implementation, the infectious pathogen imposes a direct cost, δE, on individuals, in each timestep that they are infected. For an individual with intake N, the net energetic gain E after being infected by a pathogen for t timesteps is $E = N - (\delta E \times t)$. In this scenario, *infection costs are independent of intake*.

In an alternative implementation, the infectious pathogen may be considered to reduce an animal's ability to process intake, or to require a portion of daily intake to resist. Such an implementation is used in ... For an individual with intake N, the net energetic gain E after being infected by a pathogen for t timesteps is $E = N \times (1 - \delta E)^t$. Naturally, the two cost structures are not easy to compare, but a comparison of the potential outcomes is shown in Fig. 5.11.

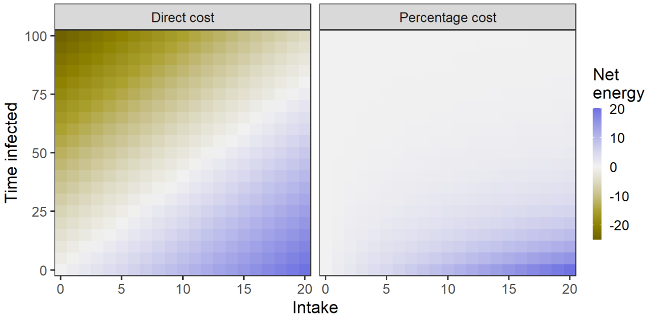

Figure 5.11: Calculated net energy for different combinations of intake and time infected. In the *Direct cost* scenario, and with a δE of 0.25 (shown here), which is our default implementation, an individual foraging on an item (handling time = 5 timesteps) would gain 1.0 unit of intake, and lose 1.25 units of energy in that same period if it were infected, for a net energy balance in that period of -0.25. Individuals' energetic balance is normalised (0 – 1) with reference to the lowest value in each generation. Here, individuals' infection cost is *independent* of their intake. In the *percentage cost* scenario, individuals' infection costs are linked to their intake. For a per-timestep 5% loss of intake (shown here), individuals infected for >25 timesteps already have a net energy balance close to, but never less than, zero. In this implementation, individuals' energy balances are *not normalised* with reference to the lowest net energy, as no individual's energy is ever less than zero.

Evolutionary Outcomes of the Percentage Cost Implementation

The social movement strategies evolved prior to pathogen introduction are identical to those seen in our default implementation. This is because the percentage cost implementation differs from the default only after the pathogen is introduced. After pathogen introduction, there is a rapid evolutionary shift in movement strategies. This shift is similar to that in our default implementation, but the strategies evolved are different. The handler tracking strategy becomes common across parameter combinations. However, when the costs of infection are relatively high (7.5%), and the usefulness of social information is limited by the abundance of food items (R = 5), the agent avoiding strategy forms about one fourth of the population mixture of social movement strategies

Ecological Consequences in the Percentage Cost Implementation

Surprisingly, the implementation of a different cost structure for the novel, infectious pathogen does not affect ecological, population level outcomes when compared with outcomes in our default implementation of direct costs. Across parameter combinations where there is a rapid evolutionary transition from agent tracking to handler tracking as the dominant strategy, there is also an increase in distance moved, a reduction in intake, and a reduction in associations. Notably, the reductions in per-capita intake following pathogen introduction are similar to

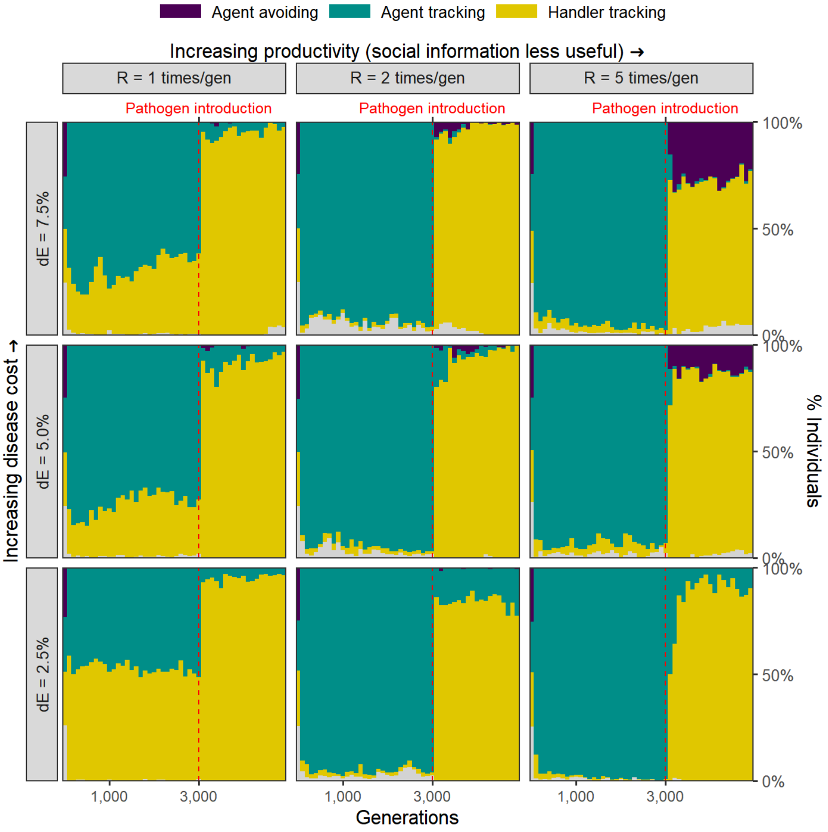

Figure 5.12: Rapid evolutionary change, but different evolutionary outcomes, in an alternative implementation of disease costs. In our alternative, percentage costs implementation of the infectious pathogen, there is a rapid shift in the mix of movement strategies after pathogen introduction. The handler tracking strategy becomes common across all parameter combinations. Only when the costs of infection are relatively high (7.5%), and the usefulness of social information is limited by the abundance of food items (R = 5), does the agent avoiding strategy form about one fourth of the population mixture of social movement strategies.

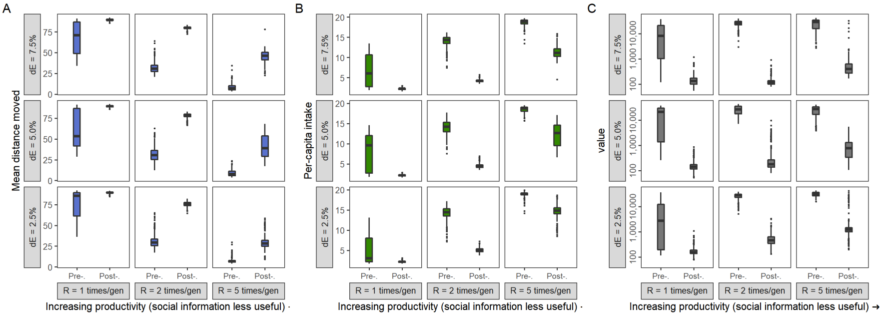

Figure 5.13: Rapid ecological changes accompany evolutionary shifts in an alternative implementation of disease costs, and are similar to the default implementation. In the alternative percentage-costs implementation of the infectious pathogen, the outcomes are very similar to those in our default implementation of direct costs. Across most parameter combinations, there is an increase in movement, a reduction in intake, and a reduction in associations with other foragers. Each subplot in each panel shows the mean and standard error of the per-capita values for **(A)** distance moved, **(B)** intake, **(C)** number of associations, or encounters, with other individuals. Means and standard deviations are shown before (G = 3,000) and after (G = 3,500) pathogen introduction; each data point represents 10 replicates of the relevant parameter combination.

a halving of landscape productivity (as in the default implementation), and there is a comparable drop in the number of pairwise associations among individuals.

Sporadic Introduction of Infectious Pathogens

We implemented a variant of our main model, in which the infectious pathogen is introduced only sporadically after the first introduction event (at G = 3,000). Specifically, we modelled probabilistic introduction of the pathogen in each generation following the initial introduction. We call the per-generation probability of a novel pathogen introduction event the 'spillover rate'. We ran 10 replicates each of this model variant and examined whether there was a similar evolutionary shift in social movement strategies as seen in our default implementation. Since it is the main parameter of interest, we ran this model variant for three values of the spillover rate: 0.05, 0.1, and 0.25. Instead of examining the joint effect of landscape productivity and cost of infection as well, we only examined the effect of infection cost, implementing three different variants with an infection cost δE of 0.1, 0.25, and 0.5. We kept all other model parameters similar to the default scenario of our main model, and importantly, considered only a landscape productivity R of 2. Cross-species novel pathogen introductions are likely to become more common with climate change, and so we chose these spillover rate values to represent different scenarios under altered global regimes of pathogen transfer. Our model's default implementation may be seen as an extreme case of the models considered here, with a spillover rate of 1.0.

In our model code, the sporadic introduction is implemented by drawing the number of generations until the next pathogen introduction event from a geometric distribution whose probability parameter is given by the spillover rates described above. Zero values are handled by converting them into ones. At our lowest spillover rate, up to 100 generations could pass between pathogen introductions, while at our highest rates, there are rarely more than 10 generations between introductions.

The social movement strategies evolved prior to pathogen introduction are identical to those seen in our default implementation, as expected. However, following pathogen introduction, we found that there was little to change in the population-level mixture of movement strategies in this model variant (see figure). This is regardless of the probability of a novel pathogen introduction (our so-called 'spillover rate'), and the cost of infection by a pathogen. Across the simulation, the commonest social movement strategy remains 'agent tracking', i.e., preferring locations with multiple individuals regardless of their foraging status. Since there is little to no change in social movement strategies, we did not expect nor find changes in ecological outcomes.

* * *

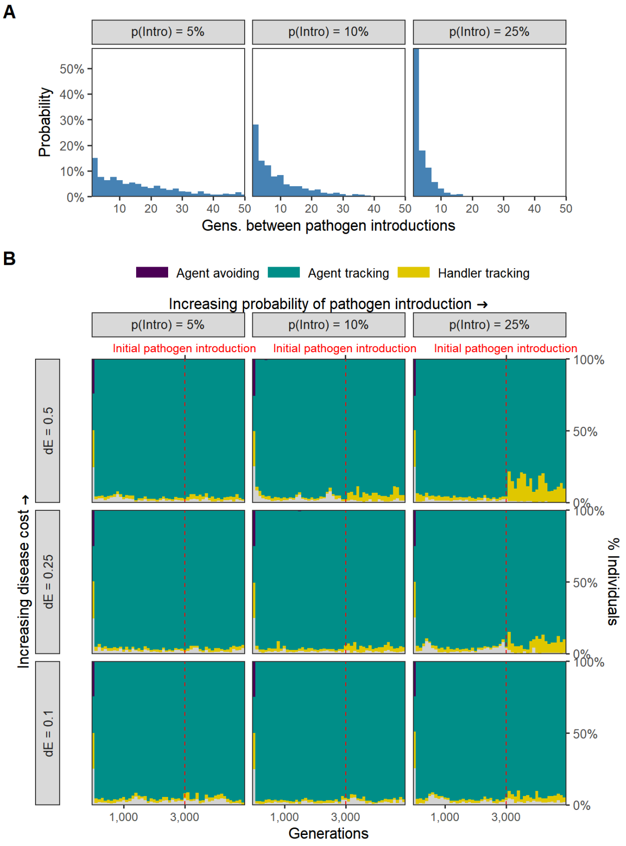

Figure 5.14: No evolutionary change in social movement strategies when novel pathogen introduction events are relatively uncommon. (A) In our alternative implementation of the model, the pathogen is only introduced sporadically after the initial introduction (G = 3,000; red line in panel B). **(B)** When the introductions are relatively rare and sporadic, there is no shift in the mixture of movement strategies after pathogen introduction. The agent tracking strategy remains common across parameter combinations.

Chapter 6

Using a Mechanistic Model to Probe Statistical Methods in Animal Movement

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We can only see a short distance ahead, but we can see plenty there that needs to be done.

– from Computing Machinery and Intelligence, by Alan Turing.

Abstract

Movement ecologists have taken up the challenge of inferring animals' decision-making mechanisms in a spatial context from individual tracking data. The implicit assumption is that differences in the movement paths of animals reflect differences in individual decision-making mechanisms. However, animal movement takes place in complex and rapidly changing environments, where movement cues are not always available, and animals may differ along multiple axes of behaviour. Mechanistic, individual-based modelling of animal decision-making can help investigate whether differences in decision-making mechanisms actually translate into differences in movement paths, and the insights gained by parsing animal tracking data using contemporary statistical methods. To show how such a model can be used to investigate statistical methods, we explore a contemporary question in movement ecology: Can individual differences in movement decision-making mechanisms be detected from the emergent properties of the resulting movement paths? Using data on the movement of evolved model agents, we show how adopting a repeatability framework to quantify individual-differences in movement is sensitive to the evolutionary context in which movement rules evolve. We also find that repeatability analysis can yield very different conclusions depending on how individuals' behavioural types are accounted for. We also show that step-selection analysis can indicate differences between competition strategies, but rarely captures differences between movement types of the same competition strategy. Overall, using a plausible eco-evolutionary model of animal decision-making, we highlight some challenges in using contemporary statistical methods to infer individual differences in animals' decision-making mechanisms from positioning data.

Introduction

Animal movement is understood to be an individual response that integrates multiple internal and external stimuli, including environmental conditions and the presence of other animals (Nathan et al. 2008). Various aspects of animal movement, such as the distance moved over time (speed), or the tortuosity of an animal's path, are now readily measured and quantified in free-living individuals, given significant advances in animal tracking technology (Cagnacci et al. 2010: see Nathan et al. *in prep.*). This makes movement a sort of 'model behaviour' that allows investigation of the underlying mechanisms — the 'how' and 'why' of animal decision-making — under natural conditions that cannot be replicated in experimental settings. For example, tracking individual greenbuls *Phyllastrephus sp.* in forested landscapes revealed that greenbuls moved more frequently to trees that were actually visible from their position, rather than trees that were obscured from view, indicating that visual cues are important in the movement decisions of forest birds (Aben et al. 2021: see also). This illustrates a general tactic in animal movement studies, which is to treat an animal's use of a resource disproportionate to its availability (Fortin et al. 2005; Manly et al. 2007; Signer et al. 2019), or prolonged residence in an area (Bracis et al. 2018) as indicators of adaptive movement decision-making mechanisms. Simple simulation models show that differences in movement patterns — such as path metrics, or emergent social interactions — may reflect underlying differences in movement strategies (Spiegel et al. 2017; Spiegel and Pinter-Wollman 2022; Stuber et al. 2022).

Both differences in movement strategies, or the mechanisms controlling movement (Spiegel et al. 2017), and differences in movement paths, which are the outcomes of movement mechansims (Abrahms et al. 2017; Hertel et al. 2021), are interpreted as facets of animal personality (Sih et al. 2004*a*,*b*). Increasingly however, animal personality, or consistent individual differences in behaviour, are studied in empirical terms, and considered to be detected in a population when its behavioural responses possess certain statistical properties (Sanchez-Tojar et al. 2021). In the context of animal movement, researchers apply sophisticated variance-partitioning approaches to common movement metrics — such as daily distance moved — and aim to determine how much behavioural variation in a population is explained by individual identity, rather than conditions that directly influence behaviour (e.g. diel cycle, temperature), or variation due to other, un-examined factors (e.g. weather differences between intervals) (Hertel et al. 2019; 2020; 2021). Another approach to investigate individual animals' decision-making mechanisms is to estimate their relative preferences for environmental conditions using step-selection analysis (Fortin et al. 2005; Thurfjell et al. 2014; Avgar et al. 2016; Signer et al. 2019; Fieberg et al. 2021: see also resource selection analysis:). Step-selection analysis compares environmental cues between animals' real steps — the movements actually made, and their alternatives — the movements that *could have been made*, from the same starting location (Thurfjell et al. 2014; Fieberg et al. 2021). The relative selection strengths, which are the coefficients of a step-selection function, can be compared between individuals (Thurfjell et al. 2014), and should be expected to be different for individuals with different movement decision-making mechanisms.

However, it is unclear whether individual consistency in the mechanisms underlying movement strategies can really be identified using current statistical tools (Spiegel and Pinter-Wollman 2022; Stuber et al. 2022). Most researchers realise that there is a substantial gap between the environment animals perceive and to which they respond, and the often static representation of that environment that is measured in tracking studies (Spiegel and Pinter-Wollman 2022). For example, resources that are critical to animals are often ephemeral, and difficult to measure with both a high spatio-temporal extent and resolution using existing technologies such as remote sensing, leading researchers to fall back on more long-term resource proxies such as vegetation indices (Pettorelli et al. 2011). This issue is likely even more acute in the case of movements that have a social context, such as competition, as the social environment is expected to change even more rapidly than resource distributions, and to be even more sensitive to local consumer densities. Consequently, it may be difficult to determine whether differences in movement reflect underlying differences in decision-making mechanisms, or whether they better represent stochastic differences in environmental conditions encountered by animals (Spiegel and Pinter-Wollman 2022). Applying current methods in animal movement ecology to individual-based simulation models of animal movement strategies (see e.g. Getz et al. 2015; 2016; Netz et al. 2021*b*) can help explore whether these methods can reliably detect individual differences in movement decision-making mechanisms.

Mechanistic models of intermediate complexity can simulate the main features of many spatial systems, such as heterogeneity in landscape productivity, and resource depletion due to mobile consumers (Getz et al. 2015; White et al. 2018*b*; DeAngelis and Diaz 2019; Diaz et al. 2021; Netz et al. 2021*b*). Here, we work with an evolutionary, individual-based model of agent movement in the context of intraspecific competition (both exploitation and interference, as described in Chapter 4). In our model, agent movement is the outcome of the interplay of simple movement decision-making mechanisms, a fluctuating resource landscape, and due to agent movement, a variable social landscape. Agent movement strategies are controlled by their preferences for environmental cues, such as resource and competitor densities (see e.g. Getz et al. 2015; White et al. 2018*b*; Netz et al. 2021*b*). These preferences may be thought of as the coefficients of resource- or step-selection functions (White et al. 2018*b*). Importantly, in contrast with purely ecological models (e.g. White et al. 2018*b*), agents' preferences are outcomes of many generations of natural selection (see also Getz et al. 2015; Netz et al. 2021*b*). We previously showed that in two scenarios of exploitation and interference competition, differences among individuals in how they assess local environmental cues evolve.

We tackle three specific aspects of a general question in animal movement: what can applying statistical tools to animal tracking data tell us about individual differences in the movement decision-making mechanisms? *(1)* We first examine whether different movement types are indicated by simple exploratory data analysis. *(2)* We then investigate the results of a variance-partitioning approach (repeatability analysis; Nakagawa and Schielzeth 2010; Hertel et al. 2019) to detecting individual differences in populations with different movement types *and* competition strategies. *(3)* Finally, we attempt a novel application of step-selection analysis to the study of consistent individual differences in movement strategies. Overall, by treating a simulation model with simple movement rules as we would empirical animal-tracking data, we aim to explore whether individual differences in movement decision-making mechanisms can be reliably inferred from the emergent structure of animal movement paths.

Methods

Basic Model Setup

We worked with an individual-based evolutionary simulation model of animal movement in a foraging context, previously developed for use in Chapter 4. We describe the model's ecological dynamics in brief here, and refer readers to Chapter 4 for a more detailed exploration of the evolutionary outcomes. Our model simulates a population with a fixed size (10,000 individuals), moving on a finely gridded landscape of 512^2 cells; this is a population density of 1 individual for every 26 cells. The landscape is wrapped at the boundaries so that individuals passing beyond the bounds at one end re-appear on the diametrically opposite side. The model consists of G generations (default = 250) of T timesteps (default = 400); in each generation, individuals move and make foraging decisions to gain intake. At the end of each generation, individuals reproduce and pass on their movement and foraging strategies to their offspring, the number of which is proportional to their intake in the 400 timesteps of their 'lifetime'.

The cells of the gridded landscape each have a cell-specific probability r of generating a discrete resource, which we refer to as 'prey items' (e.g. a mussel). The cells are arranged into 1,024 regularly spaced clusters, or 'resource peaks', in which the productivity of cells at the centre of the peak (called r_{max}) is five times greater than the cells at the periphery of the peak; resource peaks are approximately 16 cells away from each other. We ran the model with a default r_{max} of 0.01, and also at r_{max} values between 0.001 and 0.03, to examine the effect of landscape. For an r_{max} = 0.01, the most productive cells (at the centres of a cluster) are likely to generate one item per 100 timesteps (or four items per generation, for T = 400), while the least productive cells (at cluster peripheries) are likely to generate one item every 500 timesteps (< than one item per generation, for T = 400). Cells in our landscape were modelled as having a uniform carrying capacity K of 5 prey items, and while a cell is at carrying capacity its r is 0.

Individual Foraging and Movement

Agents can perceive a cue indicating the number of all prey items P in a cell, but have a probability q of failing to detect a prey item, and a probability q^P of not detecting any of P prey items; foragers are thus successful in finding a prey item with a probability $1 - q^P$. Individuals on a cell forage in a randomised sequence, and the probability of finding a prey item $(1-q^P)$ is updated as individuals find prey, reducing P. Foragers that are assigned a prey item in timestep t begin handling it, and are considered to be handlers for the next T_H timesteps, during which they are immobile: this creates opportunities for kleptoparasitism (Holmgren 1995). Foragers that are not assigned a prey item are considered idle, and are counted as non-handlers.

Agent movement is a fine-scale process comprised of small, discrete steps of fixed size. These steps are the outcome of short-term individual movement decisions, in which the agent selects a destination cell, after assessing potential destinations based on available cues (similar to step selection or resource selection Fortin et al. 2005; Manly et al. 2007), an approach used previously by Getz et al. 2015 and White et al. 2018*b*. In brief, individuals scan the nine cells of their Moore neighbourhood for three environmental cues, *(1)* an indication of the number of discrete prey items P, *(2)* the number of individuals handling prey H (called ‘handlers’), and *(3)* the number of individuals not handling prey N (called ‘non-handlers’). Based on these cues, agents rank their neighbouring cells by their ‘suitability score’ S, where $S = s_P P + s_H H + s_N N$, and move to the cell to which they have individually assigned the highest suitability. The weighing factors for each cue, s_P, s_H, and s_N, are genetically encoded and and transmitted from parents to their offspring. All individuals move simultaneously, and then implement their foraging strategy to acquire prey.

Scenarios of Intraspecific Competition

We considered two scenarios of intraspecific foraging competition, a process that can strongly shape animal movement and population distributions (Fretwell and Lucas 1970; Parker 1978). In the exploitation competition **scenario 1**, agents move about on the landscape according to their movement rules, and find, handle, and consume prey. Agents must handle each prey item for a fixed handling time T_H (default = 5) before they gain its energetic value. Agents can be either in the handling or searching state (Holmgren 1995). While handling, agents are immobile and do not make any movements. Since there are no direct interactions among agents, the only way in which agents can affect each others' intake is by acquiring prey items before their competitors. In this scenario, the only evolvable properties are the environmental cue weighing factors which determine the suitability scores and hence agent movement (s_P, s_H and s_N).

In **scenario 2**, agents can either search for prey items (foraging), or steal a prey item from a handler (kleptoparasitism). Agents make movement decisions as in the exploitation competition scenario, but their competition strategy (foraging or kleptoparasitism) is fixed through life, genetically encoded, and heritable between generations. For simplicity, agents are always successful in stealing from a handler; however, if multiple agents target the same handler, only one of them, randomly selected, is considered successful — thus kleptoparasitic agents also compete exploitatively among themselves. Handlers that have been stolen from subsequently 'flee' and are moved to a random cell within a Chebyshev distance of 5. Having acquired prey, a kleptoparasite converts into a handler, but need only handle prey for $T_H - t_h$ timesteps, where t_h is the time that the prey has already been handled by the previous handler; thus kleptoparasites save time on handling compared to a forager. Unsuccessful kleptoparasites are considered idle, and are also counted as non-handlers. Handlers that finish processing their prey in timestep t return to the non-handler state and are assessed as such by other individuals when determining their movements.

Inheritance of Movement and Competition Rules

For simplicity, we modelled discrete, non-overlapping generations, with haploid, asexually reproducing individuals. In the exploitation competition scenario, individuals have three active gene loci that encode the decision-making weights which control individual movement (s_P, s_H, s_N). In scenario 2, individuals additionally inherit their competition strategy from their parent. We assume that the expected number of offspring per individual is proportional to the individual's total lifetime intake of resources (hence resource intake is used as a proxy for fitness). This is implemented as a weighted lottery (with weights proportional to lifetime resource intake) that selects a parent for each offspring in the subsequent generation (see prior implementation in Netz et al. 2021*b*). Across scenarios, the movement decision-making weights are subject to independent random mutations with a probability of 0.001. The mutational step size (either positive or negative) is drawn from a Cauchy distribution with a scale of 0.01 centred on zero. This allows for a small number of very large mutations while the majority of mutations are small. In scenario 2, agents have a probability of 0.001 of a mutation on their competition strategy, i.e., of transforming from a forager to a kleptoparasite, or vice versa. Agents are intialised at a random location on the landscape, potentially forcing individuals to contend with different environmental conditions from those experienced by their parent.

Agent Positions, Agent Preferences, and Landscape Data

We previously established that in our model, the mean per-capita intake stabilises within 50 generations, and the fixation of certain movement rules (such as the preference for handlers) is complete by generation 100 (see Fig. 1). We wanted to determine whether agent path structure, and specifically, the distance moved, also has a clear trajectory over generations. In order to do this, we focused on the positions of 1% of the agents (N = 100) in each timestep, for every 10th generation, up to generation 249 (25 generations, including $G = 249$). Overall, we collected 400 × 100 × 25 = 1,000,000 positions over each simulation run. To apply methods commonly used in movement analyses, we let the final generation ($G = 250$) run for 10,000 timesteps, and exported the positions of 100 agents in each timestep, for a further 10,000 × 100 = 1,000,000 positions. We also exported the decision-making weights for movement (s_P, s_H, s_N) for each agent in the exploitation competition scenario, as well as the foraging strategy-decision weights (w_P, w_H, w_N, w_0) for agents in the interference competition scenario; we aimed to later relate these weights to the structure of movement paths.

Animal movement is strongly influenced by the landscape, and must be taken into account to accurately compare among individuals. The cell r values may be seen as analogous to empirically measured long-term indicators of productivity, such as the normalised-difference vegetation index (NDVI; Pettorelli et al. 2011). We took the known, fixed r values for each cell, and linked them to agent positions as environmental covariates. Animals likely cannot always sense underlying differences in the drivers of productivity of a resource landscape, but only an indicator of that productivity, such as prey items. Nonetheless, long-term measures are frequently used as predictors in step-selection functions, because they are often easy to measure, and do have a mechanistic link with animal movement.

Quantifying Model Ecological Outcomes

We first plotted the frequencies of the decision-making weights, scaled between -1 and +1 using a hyperbolic tangent tranform, over the 250 generations of each model run (see Fig. 6.1A). We then visually examined the population at the evolutionary equilibrium for functional differences in movement rules. Since distinct values, or morphs, of each weight might be correlated with distinct values of the other two weights, agents with seemingly different absolute values of the three weights could have the same relative preference for, or aversion to, a movement cue. We did this by normalising each of the agents' three movement weights relative to the sum of the absolute values of the weights: $W_i = W_i / (|s_P| + |s_H| + |s_N|)$, where W_i is any one of the movement weights, s_P, s_H or s_N. We refer to these normalised weight values (ranging from -1, avoidance, to +1 preference) as the relative preferences. Thus, for example, an agent prioritising movement towards handlers would have a normalised value for s_H close to +1, and s_P and $s_H \equiv 0$. To visualise the spread of agents over the trait space, we plotted the scaled values of s_H against the scaled values of s_P, colouring points by the scaled value of s_N (see Fig. 6.1A).

We classified the 100 agent paths exported in each simulation run based on the agents' relative preferences: (1) *prey tracking*, if $s_P > 0.55$; (2) *handler tracking*, if $s_H > 0.5$; (3) *prey & handler tracking*, if $s_P > 0,\ s_H > 0,\ |s_P - s_H| > 0$; (4) *non-handler avoiding*, if $s_N < -0.5$; (5) *handler avoiding*, if $s_H < -0.5$; and (6) *mixed*, for all other combinations. We plotted the distribution of total distance moved across equal intervals for each of these five strategies (or those present in the evolved populations; see Fig. 6.3). We also plotted the movement paths of individuals from the strategies for a visual comparison of path structure and distance moved.

Repeatability of Agent Movement

When animals are challenging to assay in captivity, researchers may attempt to detect individual consistency in movement behaviour from animal tracking data alone (see a review in Hertel et al. 2020: see for an example). In this approach, a population is understood to comprise of 'repeatable' individuals if the between-individual variance in behaviour is a substantial proportion of the total variation that is not explained by the fixed effects of a linear mixed model (LMM Hertel et al. 2019). Individuals differing in behavioural mechanisms are expected to make differing movement decisions when presented with the same environmental cues; the cumulative and emergent effects of these decisions are thus expected to be reflected in the tracking data. Consequently, a population with differences among individuals in movement decision-making mechanisms ('movement types') should be expected to be 'repeatable' in movement behaviour.

This approach relies on repeated measures of an individual behaviour, such as daily distance moved (Niemelä and Dingemanse 2018; Hertel et al. 2020). One way of obtaining such repeated measures is by summarising behaviour over equal time-intervals of an animal's track (see e.g. Hertel et al. 2019). We investigated whether our agents' fixed movement decision-making weights would result in high population-wide repeatability in movement behaviour, and specifically, in the mean distance moved.

We tried to determine whether repeatability analysis could detect that there was wide functional variation in the movement decision-making rules of our evolved agents. To implement this approach, we divided agent paths from the final generation of 10,000 timesteps into 10 consecutive intervals of equal duration (1,000 timesteps each; similar to weeks), and calculated the mean distance travelled over 100 timestep-long segments (similar to days) in each interval. Following Hertel et al. 2019, we calculated the between-individual variance using linear mixed models (LMMs) of the form

$$\text{mean distance} \sim \bar{r} + (1|\text{identity}) + (1|\text{interval}) \tag{6.1}$$

where the mean cell productivity $\bar{r}$ was taken as fixed effects to account for differences in the environment experienced by each agent.

Knowing that our scenario 2 reliably results in a population with both fixed-strategy foragers and kleptoparasites, we examined three ways of taking individuals' competition strategy into account when estimating repeatability. *First*, in the basic model, we used the repeatability model specified above, in which we ignored the differences in competition strategy among our agents. *Second*, in the fixed effect model, we included the competition strategy of each agent (forager or kleptoparasite) as a fixed effect in the model. *Third*, in the separate modelling approach, we fit the basic model to the data from foragers and kleptoparasites separately.

Across model formulations, We scaled the movement distance and the predictor variables between 0 and 1, for each interval of each simulation run. We set individual identity and the time interval to be random intercepts, following (Hertel et al. 2020). We fit separate GLMMs for each simulation run, and used the *rptr* package in R (Nakagawa and Schielzeth 2010) to estimate the repeatability of total distance in our agent population (bootstraps = 100; permutations = 10).

Individual Differences in Habitat Selection

Finally, we investigated whether individual differences in movement rules would translate to differences in habitat selection, using a step-selection function framework. Step-selection analysis essentially aims to determine why animals move where they do, given the alternative steps they could have made, by relating the animal's choice of step to differences in environmental conditions among the alternatives (Thurfjell et al. 2014; Avgar et al. 2016; Signer et al. 2019; Fieberg et al. 2021). When an SSF is fit to each individual's tracking data, the estimated coefficients of a step-selection function (SSF) are analogous to the agent movement decision-making weights in our model (see previous interpretation in White et al. 2018*b*). In empirical studies, it is difficult to measure the availability of fine-scale environmental cues, such as the abundance of depleteable resources, or the densities of conspecifics. One common solution to this challenge is to compare selected and alternative steps on the basis of a slowly-changing environmental measure such as productivity (e.g. NDVI, analogous to r Pettorelli et al. 2011), that is broadly correlated with other phenomena. When correctly chosen, productivity has a mechanistic relationship with other environmental cues: cells with higher r should be expected to have more prey items by definition, and to attract more competitors, following expectations from Ideal Free Distribution theory (Fretwell and Lucas 1970; Parker 1978). Though animals likely cannot sense landscape productivity directly (and our agents cannot sense r), analysing step-selection in relation to productivity is still a common practice, and could help reveal relative differences among individuals' selection for habitats, potentially indicating variation in the underlying behavioural mechanisms.

We prepared the data for SSF fitting by reducing data volumes to make computation faster: we thinned agent tracks to select only every 10th position, and selected 8 alternative positions for each 'true' step. We customised the method of selecting alternative steps from the default implementation in *amt* (Signer et al. 2019): while accounting for the wrapped landscape, we selected eight cells within a distance of 10 units from the agent position, since these are only locations to which an agent could voluntarily move in 10 timesteps. We excluded the true step end-point from among the alternatives, and considered remaining in place to be a valid option. The resulting dataset consisted of the true and alternative step coordinates for each step, to which we linked the the cell-specific r. We fit a step-selection function for each individual separately in each simulation run, relating whether a step was taken or not (the *case*, in *amt* parlance) to the value of r. We used an SSF of the form:

$$\text{case} \sim r + \text{strata}(\text{step identity}) \tag{6.2}$$

We visually investigated whether differences in selection strength for r were revealed for populations with substantial polymorphisms in movement weights. During earlier analyses, we had found that agents in the exploitation competition scenario could be classified into three 'movement types', based on which weight (sP, sN, sH) had the largest absolute value. We expected that agents whose largest weight was s_P, the preference for prey-items, would have larger selection strengths for cell r.

Results

Model Eco-Evolutionary Equilibrium

Both scenarios of our model — as expected from previous analysis — reached an evolutionary equilibrium: a stabilisation of mean per-capita intake within 50 generations (index r_{max} = 0.01). The two scenarios differed strongly in terms of the evolution of movement decision-making weights, again, as we already knew from earlier investigation in Chapter 4. Briefly, in **scenario 1**, populations across replicates rapidly and consistently evolved to prefer moving to cells with prey-items (positive values of sP) and cells with handlers (positive values of sH) within 100 generations (Fig. 6.1A1). Populations also evolved to avoid non-handlers (negative values of sN; Fig. 6.1A1). All replicates showed substantial variation in the movement decision-making weights (Fig. 6.1A1). In **scenario 2**, we found an eco-evolutionary equilibrium with stable proportions of the two competition strategies. As might be expected then, the evolution of populations' decision-making weights was quite different from that of scenario 1. Agents had an evolved preference for moving to cells with prey-items, and an avoidance of cells with non-handlers (Fig. 6.1A2). However, there was a strong dimorphism in the response to handlers, with most agents showing a strong preference for handlers, but with a sizeable minority of agents showing an avoidance of handlers (Fig. 6.1A2).

The differences in evolved movement rules also translated to functional variation in relative preferences for the three environmental cues. In **scenario 1**, most agents had a strong preference for prey-items, with a number of agents neutral to the other two cues (large values of s_P, see Fig. 6.1B1). Nonetheless, many scenario 1 agents' movement rules also incorporated social information in the form of the presence of competitors, and these agents either avoided non-handlers (large negative values of s_N), or preferred to move towards handlers (positive values of s_H). In **scenario 2**, the two competition strategies differed dramatically in their relative preferences for movement cues. Overall, most agents relied entirely on social information — the presence and foraging status of competitors — and on the abundance of prey-items almost not at all, when making movement decisions (Fig. 6.1B2). Foragers sought to avoid all agents, with negative values for s_H and s_H, but differed strongly in *which*, of handlers and non-handlers, were most avoided. Kleptoparasites, on the other hand, were almost exclusively handler-preferring, with strong positive values of s_P. A small number of both foragers and kleptoparasites followed the movement rules of the opposite strategy; these likely represented a strategy mutation during reproduction, rather than a viable combination of movement and competition strategies.

Our classification of agents based on evolved relative preferences for movement cues revealed that most agents in scenario 1 were either prey-tracking, prey and handler tracking, non-handler avoiding, or used a mixed strategy (Fig. 6.2A1). On the other hand, agents in scenario 2 had a movement type strongly correlated with their competition strategy: most foragers were either handler- or non-handler-avoiding, while kleptoparasites were all handler-tracking (Fig. 6.2A2). We found that movement distance was strongly linked to competition strategy, and did not correlate with movement type, as foragers in both scenarios 1 and 2 had very similar movement distances, regardless of their movement type (Fig. 6.2B1, B2). Kleptoparasites, however, moved nearly twice as much as foragers in scenario 2 (Fig. 6.2B2).

Movement Cues, Competition Strategies, and Repeatability of Movement Distance

Our simulation's populations, at the eco-evolutionary equilibrium ($G = 250$) were comprised of individuals with a broad range of movement strategies (Fig. 6.3A). In **scenario 1**, a wider range of movement strategies were evolved on higher productivity landscapes ($r_{max} \in 0.02, 0.03$), than on lower productivity landscapes ($r_{max} = 0.01$); the pure handler-tracking and handler avoiding strategies were seen only at at higher growth rates (Fig. 6.3A1). This suggests that on higher productivity landscapes, a wider range of movement types have equivalent fitness. The mechanism enabling this is the increased abundance of prey-items: as more agents find prey more easily and become handlers, the relative strength and frequency of the handler cue increases, and navigating using this social information alone becomes a viable movement strategy.

The repeatability of movement distance is nearly five times as high on more productive landscapes ($r_{max} \in 0.02, 0.03$; repeatability ≈ 0.70), as on low productivity landscapes ($r_{max} = 0.01$; repeatability ≈ 0.15; Fig. 6.3B1). This large difference may be because there are more movement types on high-productivity landscapes (Fig. 6.3A1), with subtle differences in distance moved among them. Yet, another plausible explanation is that on high productivity landscapes, there are simply more movement cues, in the form of prey-items and handlers. Since the movement types differ in how they process and respond to cues, movement on landscapes with more cues might better reveal subtle differences among the behavioural types.

In **scenario 2**, increasing productivity also allows a wider range of forager, but not kleptoparasite, movement strategies (Fig. 6.3A2). At the index r_{max} of 0.01, foragers are mostly agent avoiding, while kleptoparasites are handler tracking.

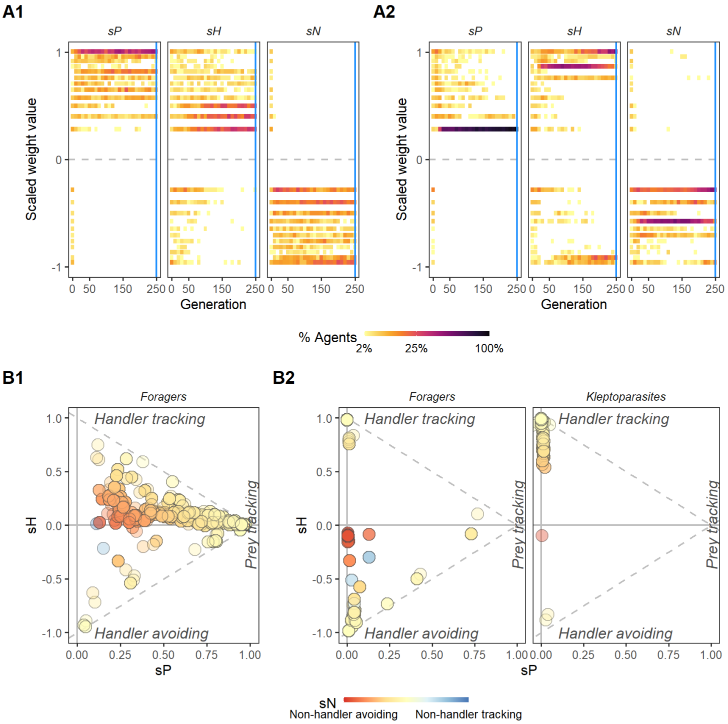

Figure 6.1: Evolutionary equilibrium and functional variation in movement rules in a spatially explicit, individual-based model of animal movement. We find substantial polymorphism in movement rules in both scenarios of our spatially explicit, individual-based model of the joint evolution of animal movement and competition strategies. Agents in both **(A1)** scenario 1 (exploitation competition only), and in **(A2)** scenario 2 (fixed, individual competition strategies), evolve multiple, distinct, co-existing values of each of the weights controlling movement rules in the forms of preferences for each cue: s_P (prey-items), s_H (agents handling prey, 'handlers'), and s_N (idle agents, 'non-handlers'). The morphs persist across generations, indicating that they likely have equivalent foraging success, and hence, fitness outcomes. **(B1)** In the exploitation competition scenario, the evolved population (at G = 250; blue line in panels A1 and A2) has wide individual variation in their relative preferences for environmental cues (the scaled weights s_P, s_H, s_N). Most agents trade a preference for prey-items against either an avoidance of non-handlers (orange points), or a preference for handlers (yellow points with $s_H > 0.5$). **(B2)** In the fixed-strategy scenario 2, agents of the two competition strategies (foragers and kleptoparasites) have very different relative preferences for environmental cues. While foragers largely either avoid handlers (yellow points, $s_H < -0.5$), or avoid non-handlers (red points), most kleptoparasites prefer moving towards handlers, their direct resource. A small number of both foragers and kleptoparasites follow the movement rules of the opposite strategy; these likely represent a strategy mutation during reproduction. All panels show simulation runs with $r_{max} = 0.01$, and show a single replicate for clarity.

However, with increasing growth rates, the frequency of kleptoparasites decreases, until, at $r_{max} = 0.03$, kleptoparasites are extinct in nearly all simulation replicates.

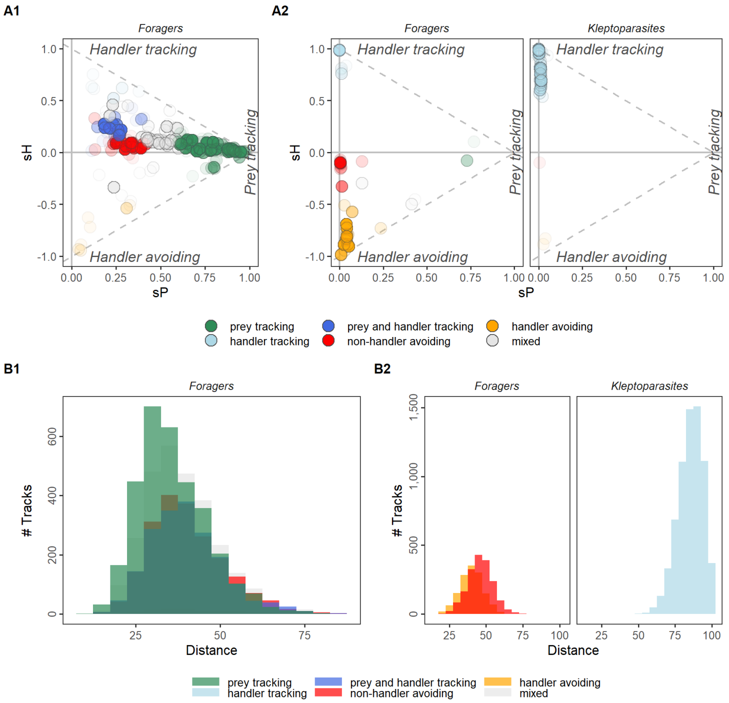

Figure 6.2: Movement types and competition strategies, and differences in movement paths. We classified agents in both scenario 1 **(A1)** and scenario 2 **(A2)** into intuitive 'movement types', based on their relative preferences for environmental cues (see Fig. 1 and Main Text). We plotted them based on their weights for prey-items and handlers, adding a transparency to show the frequencies of the types. By this simple classification, agents in scenario 1 **(A1)** mostly track prey-items, or both prey-items and handlers, while avoiding non-handlers. Agents in the 'mixed' strategy mostly track prey-items and avoid non-handlers. In scenario 2 **(A2)**, most foragers avoid other agents, either handlers or non-handlers; meanwhile, kleptoparasites, as expected, track their primary resource, handlers. Regardless of their movement type, agents in **(B1)** the exploitation scenario all move roughly the same distance in each interval. **(B2)** However, in the kleptoparasitism scenario, the competition strategies differ strongly, with kleptoparasites moving nearly twice as much as foragers. Despite moving according to quite different rules (avoid handlers, or avoid non-handlers), both types of foragers move nearly the same distance on average. While kleptoparasites' greater movement should be expected to lead to less time for handling prey, and hence lower intake, they save on this time by taking advantage of pre-handled items stolen from foragers. Panels A1 and A2 show 5,000 individuals from a single replicate of each scenario, while panels B1 and B2 show the mean movement distance of 100 agents over segments of 100 timesteps from all 10 replicates.

Thus, on high productivity landscapes, the scenario 2 population is functionally identical to the scenario 1 population, and all individuals follow a forager strategy.

Repeatability analyses on the movement distances of scenario 2 populations is sensitive to how the differences in competition strategy are treated, but not to

landscape productivity (Fig. 6.3B2). Specifically, *(1)* When repeatability analysis ignores differences in competition strategy, our populations, comprised largely of handler and non-handler avoiding foragers, and handler tracking kleptoparasites, had repeatability scores > 0.8 (Fig. 6.3B2a). This would suggest that nearly all the variance in movement distance not explained by the fixed effect of environmental productivity is due to between-individual differences (which we know to be primarily differences in competition strategy).
(2) When competition strategy is included as a fixed effect in repeatability analysis, repeatability scores drop substantially to < 0.5 (Fig. 6.3B2b). This suggests that while competition strategies are important in explaining differences in movement distance, a substantial chunk of the unexplained variance is comprised of between-individual variance.
(3) Finally, in another plausible way of treating data when the existence of competition strategies is known, running separate repeatability analyses for foragers and kleptoparasites reveals very different repeatability scores for the two strategies (Fig. 6.3B2c). While foragers have repeatabilities betwen 0.0 and 0.75, depending on the growth rate, kleptoparasites have repeatabilities close to zero.

There did not appear to be an effect of landscape productivity as in scenario 1. This may be because, in scenario 2, the presence of kleptoparasites (indeed, as the majority strategy) reduces prey-item extraction from the resource landscape. Consequently, all scenario 2 landscapes eventually resemble scenario 1 landscapes at $r_{max} = 0.03$. We ran analyses only on growth rates of 0.01 and 0.02, as kleptoparasites rapidly go extinct early on in simulations with a growth rate of 0.03 (see Chapter 4 for an explanation of the evolutionary dynamics).

Individual Differences in Habitat Selection

We fit 6,000 step-selection functions to thinned movement data from 60 simulation runs, with 10 replicates for each r_{max} value (0.01, 0.02, 0.03) and scenario (1 and 2). In **scenario 1**, all agents forage and have a substantial preference for moving towards prey-items. Consequently, the estimated coefficients of their apparent selection for cell productivity r are all positive, with no differences among the movement strategies (Fig. 6.4A1, B1). On the other hand, in **scenario 2**, the dramatic difference in competition strategies is reflected in the estimated coefficients of apparent selection for cell r; foragers have substantially lower (and even negative) selection for r than kleptoparasites (Fig. 6.4A2). However, there is little difference between foragers moving mostly to avoid handlers or to avoid non-handlers (Fig. 6.4B2). As landscape productivity increases, scenario 2 populations, but not scenario 1 agents, show a shift in their selection for cell r. At higher growth rates ($r = 0.02$), scenario 2 populations — still comprised of about equal proportions of foragers and kelptoparasites (see Fig. 6.3) — show substan-

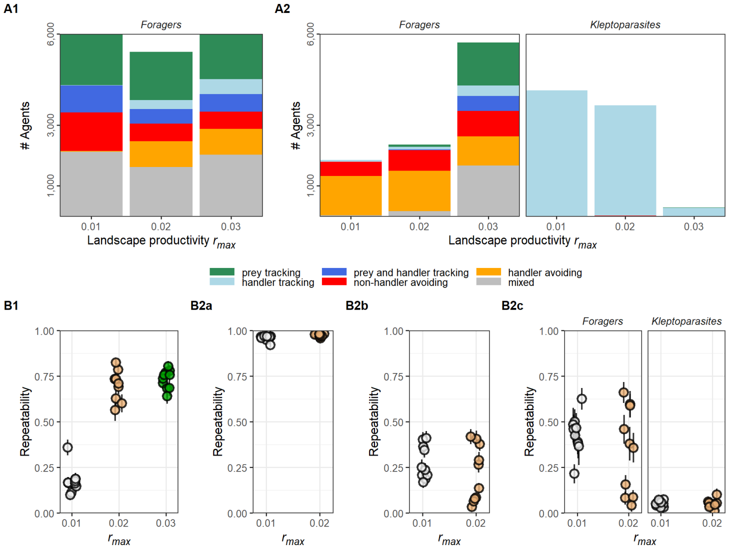

Figure 6.3: Frequency of movement types, competition strategies, and environmental cues, and consequences for repeatability analyses to detect individual differences in movement. Increasing landscape productivity (r_{max}) beyond the index value of 0.01 leads to more prey-items on the landscape, and hence more available cues for movement decisions. In **(A1)** scenario 1, this leads to a change in the frequencies of movement types, with the persistence of handler-avoiding and pure handler-tracking types. In **(A2)** scenario 2, the frequencies of both movement types and competition types change with the increased availability of prey-items: at higher r_{max} (0.03), foragers are both more common, and use more movement strategies, than at lower r_{max} (0.01). The repeatability of movement distance is greater for scenario 1 populations on landscapes with higher r_{max}, and hence more available movement cues **(B1)**. This suggests that individual differences in movement decision-making mechanisms may be more readily detected when agents are actually able to process environmental cues using those mechanisms, rather than when agents move on relatively 'clueless landscapes'. When agents' competitive strategy strongly influences their movement, as in scenario 2 **(B2 panels)**, repeatability analyses are strongly affected by how this difference is treated. **(B2a)** If differences in competitive strategies are not included in the model formulation, repeatability scores are consistently high (> 0.9). **(B2b)** When agents' competitive strategy is included as a fixed effect, repeatability scores are substantially lower (< 0.5). Finally, **(B2c)**, repeatability models run separately for each of the competitive strategies would essentially reveal that competitive types with strong dimorphism (or clustering) in movement types (here, foragers) have a higher repeatability than competitive types with a monomorphic movement strategy (here, kleptoparasites). Panels A1 and A2 show frequencies pooled over 100 agents from 10 replicate simulations, with agent data exported at G = 200, 210, ...249. Panels B1 and B2 used long-term movement paths from 100 agents in generation 250, over 10 replicates. B2 omits r_{max} = 0.03, as kleptoparasites are often extinct.

tially more overlap between the two strategies' selection for r (Fig. 6.4A2). This is carried over as an overlap between the three main movement types (Fig. 6.4B2). At the highest growth rates, scenario 1 and scenario 2 populations are essentially identical, and the few kleptoparasites remaining in scenario 2 apparently select for r similar to foragers. Overall, applying step-selection analysis to our model output suggests that differences between competition strategies, when associated with different movement types, could be revealed under certain conditions from animal movement paths.

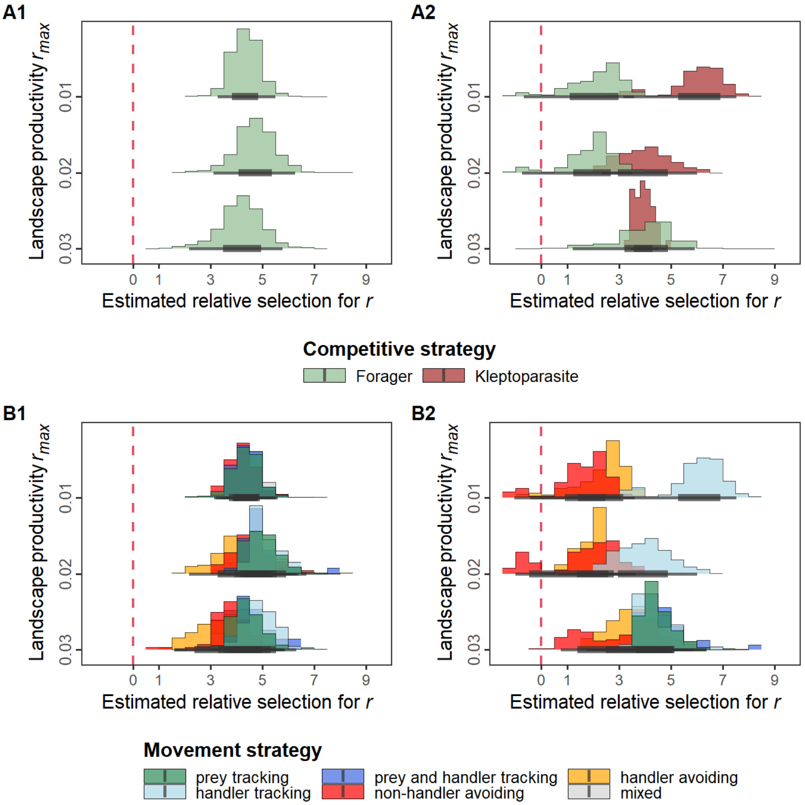

Figure 6.4: Movement types and competition strategies revealed in step-selection analyses. Applying step-selection analysis to long-term movement paths from **(A1)** scenario 1, and **(A2)** scenario 2 reveals strong differences in apparent selection for landscape productivity between competition strategies (r_{max} = 0.01). In **(B1)** scenario 1 and **(B2)** scenario 2, the apparent selection strengths for productivity r of foragers of different movement types overlaps. Handler-tracking kleptoparasites in scenario 2, too, have apparent selection strengths for r that overlap with those of some foragers, but which are substantially higher than those of most foragers, which avoid both handlers and non-handlers. These essentially opposing movement strategies are picked up as differences in selection for r. Kleptoparasites track handlers, and the probability of a forager finding prey and handling are higher at the centres of resource peaks, i.e, cells with high r. Conversely, foragers avoid other agents, and since high-productivity cells are more likely to have agents, they apparently select *against* high productivity cells. All panels show selection coefficients from 100 agents' long-term movement paths at G = 250, from 10 replicates of each simulation; only coefficients with $p \leq 0.05$ are shown.

Lessons for Data Analysis from the Performance of Statistical Methods on Simulated Data

We used an evolutionary individual-based model of animal movement decision-making under two scenarios of foraging competition (*Kleptomove*; as described here and in Chapter 4), to investigate what we can learn about individual-differences by applying statistical analyses to animal movement data. Our evolved agent populations showed substantial between-individual differences in their relative preferences for environmental cues ('movement types'; Getz et al. 2015): when presented with the same cues, agents could make substantially different decisions about where to move. We showed that despite very different relative differences among the movement types for environmental cues, the types did not consistently differ in their movement distance. However, in our scenario 2, in which individuals had a fixed competition strategy (forager or kleptoparasite), kleptoparasites moved much more than foragers. With few between-type differences in movement distance, the repeatability of movement distance was low in scenario 1 at low growth rates, but increased substantially at higher growth rates. In scenario 2, not accounting for differences in competition strategy led to repeatability scores ≈ 1.0, but correcting for these differences led to lower repeatability scores. Finally, applying step-selection analysis to estimate agents' apparent selection for landscape productivity showed no differences among movement types in scenario 1, but revealed clear differences between competition strategies (and their correlated movement types) in scenario 2.

Variation Among Movement Types and Competition Strategies

The co-existence of multiple movement types across multiple generations of scenario 1 suggests that multiple alternative movement rules are equally good for navigating our fluctuating resource and social landscapes (see also Getz et al. 2015; Netz et al. 2021*b*). That movement types travel roughly the same distances is not surprising, as they must spend the same time handling, and gaining intake, to have equivalent fitness. In scenario 2, there are essentially only two viable movement types that are strongly correlated with competition strategies at low growth rates (r_{max} = 0.01). Here, the handler-tracking kleptoparasites move more because their primary resource, handlers, are scarce; conversely, foragers move less, as prey-items are abundant. Yet both strategies have equivalent fitness because kleptoparasites make up for lost time by having to handle stolen prey-items for a shorter duration. We suggest that for movement types to differ in their path metrics (e.g. distance, or speed; see Abrahms et al. 2017), between-individual variation and within-individual consistency along a further axis of behaviour that equalises fitness between the types is likely necessary.

Repeatability Analysis

Repeatability analysis of the scenario 1 movement paths showed that populations evolved on higher productivity landscapes had significantly higher repeatability scores. The major difference between lower (r_{max} = 0.01) and higher productivity landscapes (r_{max} = 0.03) is that the latter have many more prey-items per cell. While agents on low growth rate landscapes often encounter areas with few or no movement cues ('clueless regions'; Perkins 1992), this is much more rarely the case on high productivity landscapes. Since our agents' decision-making mechanisms — in common with animal cognitive systems — require environmental cues to make movement decisions, between-individual differences in movement are more readily detected on landscapes with more movement cues (see Carter et al. 2013*b*). Our result might suggest that populations with different movement types transplanted between information-poor and information-rich landscapes would show a marked increase in behavioural consistency. We caution against this interpretation, as our populations have *evolved*, rather than simply been tested on, landscapes across a productivity gradient. On high productivity landscapes, a wider range of movement types is evolved, highlighting how measures such as repeatability are linked to the evolutionary trajectory of populations.

Using scenario 2, we illustrated three different ways of implementing repeatability analysis for a population with correlated differences in movement type and competition strategy. When differences in competition strategy were ignored, repeatability scores were close to 1.0, as the variance in movement distance due to competition strategy was picked up as between-individual variance instead. Adding competition strategy as a fixed effect to the analysis resulted in lower repeatability values; this was expected, as differences among competition strategies explain the bulk of the variance. Finally, performing separate repeatability analyses for foragers and kleptoparasites yielded very low repeatability scores for kleptoparasites, which foragers were still quite repeatable. This last result is potentially because kleptoparasites are solidly monomorphic in their movement type, while foragers may be either handler- or non-handler-avoiding, and this difference in decision-making mechanism could result in subtle differences in movement metrics. Overall, we suggest that extremely high repeatability scores might indicate that an important source of variation is not being taken into account, and should be sought for. Multivariate methods can help identify within-individual behavioural co-variation in movement metrics, such as distance and displacement (Hertel et al. 2019; 2021). This approach could help reveal strong associations between movement types and competition strategies, as in our model, or responsiveness to social cues (Strandburg-Peshkin et al. 2015). Identifying such behaviours from animal movement data is likely to require very high-resolution tracking and associated computational methods (Nathan et al. *in prep.*).

Individual Differences in Habitat Selection

In a novel application of step-selection analysis to the study of individual differences, we showed that agents of different competition strategies (scenario 2), but not of different movement types (both scenarios 1 and 2), had diverging selection for environmental conditions. An important reminder is that our model's agents cannot actually detect cell productivity r, and therefore the preference for r values is more correctly termed apparent selection. This situation parallels empirical analysis of animal tracking data, in which researchers commonly use long-term indices of environmental conditions (e.g. NDVI; Pettorelli et al. 2011) to approximate the ephemeral movement cues actually encountered and acted upon by individuals. Nonetheless, strong between-individual differences (here, in competition strategy) are likely to be reflected in animals' apparent selection for environmental conditions. In our model, the difference in apparent selection arises from the distribution of movement cues relative to cell growth r. Handler-tracking kleptoparasites have a higher selection for r because high-r cells are more likely to have handlers, since foragers are more likely to find prey-items there and begin handling. On the other hand, agent-avoiding foragers have a lower selection for r as they avoid resource peaks, which are more likely to have more agents. Some foragers will always be found on high-r cells, as even a forager moving across the landscape at random (which they do not) is more likely to stop and begin handling on a high-r cell than a cell at the periphery of a resource peak.

Individual-based Models as a Check on Statistical Methods

Individual-based models are not new in movement ecology, and are increasingly used and prescribed to better understand animal movement (see a review in DeAngelis and Diaz 2019). Such models have been used to illustrate the importance of animal movement to phenomena such as disease outbreaks (White et al. 2018*b*), and sympatric speciation (Getz et al. 2015), while also showing how individual differences in animal movement strategies can have downstream effects on population-level phenomena such as habitat-selection and social interactions (Spiegel and Crofoot 2016; Spiegel et al. 2017). There is also a rich tradition of individual-based models being used to assess the performance of methods intended for use on empirical tracking data. For example, Gurarie et al. 2016, Michelot et al. 2016, and Patin et al. 2020 simulated the paths of individuals with different behavioural modes to test the performance of tools to detect behavioural change-points, where the animal switches from one movement mode to another.

However, very few individual-based models that are used as checks on statistical methods actually model the fine-scale decisions — comprising comparisons among, and eventual selection of — steps that comprise animal movement (but see recently Vissat et al. 2021). This is at least partially because few statistical methods seek to estimate animal movement preferences, and by implication, animal cognitive processes, at such fine scales. Step-selection analysis has the potential to be among these methods, as it directly links what animals actually perceive, to where they go (see recently Aben et al. 2021). This allows a fine-scale comparison between selected and alternative steps, which, at certain scales, may functionally approximate individuals' cognitive processes, at least in terms of preference or avoidance.

Our model and other mechanistic individual-based models that follow similar principles (Getz et al. 2015; 2016; Netz et al. 2021*b*), allow for the implementation of different movement decision-making mechanisms at very fine scales, in biologically plausible ways. Our agents' movement decisions integrate locally available cues to make adaptive movement decisions, just as real animals are expected to do (Nathan et al. 2008). While our agent responses are linear, they can in principle be much more complex, including convoluted relationships between the environmental cues, as well as separate weights for each cue combination. Coupled with the ability to know the state of the environment, and of each agent, at any point in the simulation, we believe this and other similar models are suitable for the testing of a range of empirical methods. For example, a better test of whether step-selection analysis can determine agent preferences for environmental cues, and individual differences therein, could involve the dynamic logging of selected and alternative steps, as well as the environmental covariates (prey-items and competitors) at those steps, in order to compare between them at fine scales. Such logging would immediately reveal that often, agents have either very few direct local cues, or very few differences between conditions at alternative and selected steps, on which to base movement decisions at fine timescales relatively clueless regions, per Perkins 1992. This highlights a potential challenge to such analyses from the ever increasing resolution of animal tracking and environmental monitoring data; for example, how should step-selection analysis be adapted to account for high spatial- and temporal-autocorrelation in animals' environments, while still taking advantage of high sampling frequencies.

Conclusion

The analysis of our model's agent movement paths using contemporary statistical tools from movement ecology showed that it is often challenging to infer animals' decision-making processes, or even relative differences among individuals, from tracking data alone. First, when seeking to assess individual consistency and between-individual differences from animal tracking data, it is key to include predictors that have a mechanistic relationship with the behavioural response being studied. For species that are only poorly known, or difficult to study in captivity, this requires first collecting substantial knowledge on natural history and behavioural biology. Researchers could potentially apply a model selection approach (Burnham et al. 2011), to determine which fixed effects are best suited to their study species. Second, uncovering individual behavioural tendencies in captivity may not be sufficient to describe animal movement in natural environments, which is likely to be affected by fine-scale fluctuations in resources, as well as the social environment. Finally, attempting to recover animals' movement preferences at fine scales is a challenging task. In part, this is due to a mismatch of scales: empirical researchers are rarely able to study fine-scale movement decisions, because suitably fine-scale data on the environmental cues that go into these decisions are not available. While increasingly high-resolution animal tracking is becoming more common, there would need to be a concurrent increase in the resolution of environmental monitoring *from the animal's point of view*. The availability of such data sources would make the development of statistical tools that account for particular issues — such as spatio-temporal autocorrelation — a priority in movement ecology. Individual-based models, in which simple mechanisms can give rise to substantial complexity in animal movement and population distributions, could be very useful as test-beds to investigate whether current and upcoming tools are truly capable of parsing patterns to recover the underlying processes.

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Chapter 7

A Brief Reflection on this Thesis

Pratik R. Gupte

Not all those who wander are lost.

– from the works of J. R. R. Tolkien

THIS thesis, as the abstract promises, is relatively episodic, and the various chapters are only loosely tied together inasmuch as they discuss different aspects of animal behaviour. Nonetheless, I hope to have put forward a cogent view of one approach to studying animal movement — this approach is essentially to take as mechanistic a perspective as possible. Here, I reflect upon the findings and methods in this thesis.

Reflections on Part I

Part I of this thesis took an empirical approach to animal movements and space-use. Animal movement ecology has benefited greatly from the adoption of advanced animal tracking technology, and especially from the proliferation of GPS loggers (Cagnacci et al. 2010). Yet the majority of species of birds and mammals (leave alone reptiles or amphibians) cannot currently be tracked because most high-resolution loggers are much too heavy for them to bear safely (Kays et al. 2015). High-throughput tracking systems — which Nathan et al. (2022) described — such as ATLAS with its lightweight tags, can allow researchers to achieve at regional scales a far more detailed understanding of animal movement than sought by Wikelski et al. (2007) when floating the idea of ICARUS (see now Jetz et al. 2022). Yet data from these systems is not as conservatively ‘cleaned’ as that from GPS tracking, and this is because the original end uses of each of these systems are very different.

In Chapter 2, I showed how a set of simple techniques and workflows can be used to substantially improve the quality of raw ATLAS data. Beardsworth et al. (In press) have now shown that the accuracy of ATLAS systems (in this case, the Wadden Sea ATLAS system; Bijleveld et al. 2021) — after applying my cleaning methods — is comparable to GPS tracking, but with a much higher sampling rate. An interconnected network of such high-throughput systems could represent one option for how animals could be tracked at high spatio-temporal resolution at large, continental scales (Nathan et al. 2022). The methods that I set out in Chapter 2 were borrowed from a range of fields that have already made the transition to being ‘big data’ disciplines; among them, remote sensing of the earth, and molecular biology and biochemistry (Peng 2011; Gorelick et al. 2017). It is entirely unclear whether, and to my mind actually unlikely, that the full extent of these recommendations (version control, open science, well tested pipelines) will be adapted by the majority of researchers. This is simply because the correct incentive structures to promote their adoption are currently quite weak.

In Chapter 3, I used data from the original ATLAS system deployed in the Hula Valley in Israel, to study how moult — the loss and regrowth of flight feathers — affects bird movement and habitat selection. This project demonstrates how data from more developmental versions of high-throughput systems can be made usable by robust filtering and cleaning. I found that birds, regardless of their moult status, strongly avoid open areas which they presumably perceive as having a higher risk of predation. This finding is interestingly in contrast with an example presented in the Introduction: small southern African herbivores actually prefer open areas when seeking to avoid predation, as unlike with birds, it is mammalian predators rather than prey that use cover to ambush their prey (Le Roux et al. 2018). This highlights the challenges in generalising even broad findings about movement across taxa. Within birds, however, my results are in line with recent findings that flight characteristics affect whether bird species will risk crossing even narrow open tracts, such as forest roads (Claramunt et al. 2022).

The results here suggest that predation risk avoidance could be a possible mechanism by which some areas that appear productive become unsuitable for many bird species — agricultural fields for instance provide little cover from aerial predators. Birds have long been anecdotally known to avoid certain features such as water bodies despite being powerful flyers, to the extent that this has prevented entire groups from colonising archipelagos in the absence of land bridges (Diamond 1981). This effect is now much better quantified by studying the migration of raptors across open water (Nourani et al. 2020). Both road- and water-crossing avoidance seem bizarre to human observers, possibly because as a terrestrial species, we subconsciously think of flight as a certain kind of invulnerability, whether from environmental hazards or active hunters. It is much more likely that we simply do not — and perhaps cannot — really appreciate how complex flight is, and the many risks it holds. One of the main conclusions of Chapter 3 (and of Part II), then, is the importance of adopting the perspective of the study species, the *individual in its context*, when seeking to understand the short- and long-term drivers of animals' behaviour.

Reflections on Part II

In Chapter 4, I showed how animal movement and competition strategies jointly evolve, using an individual-based model with 10,000 individuals moving about on a grid of over 250,000 cells — among the largest IBMs in this field of study. The model demonstrated a number of interesting outcomes that could form the basis for future work. For instance, I showed that individual variation in preferences for environmental cues reliably evolves in simple foraging contexts, without apparent trade-offs in foraging strategies, and that social information is key to moving and foraging in consumer populations. When individuals can adopt a kleptoparasitic strategy, they may do so even when environmental cues indicate that a 'producer' strategy (Beauchamp 2008) might be more suitable. In this sense, certain competition and foraging strategies may actually represent 'personalities' as they were originally conceived of — suboptimal choices despite countervailing information (Sih et al. 2004*a*). Unlike other chapters in this thesis, I cannot be sure that this one will lead to substantial developments in eco-evolutionary theory, and see it more as a culmination of theory in the once-key field of foraging competition studies.

Chapter 6 is a direct development of of Chapter 4, even though it is presented later. Here, I adapted movement paths generated in Chapter 4 to investigate popular statistical tools in movement ecology: repeatability analysis, and step-selection analysis. Inferring processes (mechanisms) from observed patterns (phenomena) is a common pursuit in movement ecology. My analysis shows that there are substantial risks to doing so naively — spatial personalities (Stuber et al. 2022) may actually result from underlying differences in movement and competition strategies. This highlights the importance of a detailed natural history understanding of the study species and its ecological context.

Finally, in Chapter 5, I tackled a scenario that is expected to become increasingly common — the transmission of novel pathogens from one species to another (Carlson et al. 2022*a*). Indeed currently the hitherto poorly known tropical African disease monkeypox is currently breaking out in multiple countries where it is not usually found, with the key risk that it could become endemic in rodent and other animals in those regions. Additionally, SARS-CoV-2 has seen multiple introductions to animals, including abundant wildlife such as deer in the United States (Kuchipudi et al. 2022), and the H5N1 strain of avian influenza has been spreading through multiple temperate species, primarily of shore- and seabirds (Wille and Barr 2022). My relatively simple model of the trade-off between social information use (in a foraging context), and the risk of pathogen transmission generated clear predictions for how such novel pathogen introductions should affect the evolution of host sociality. Worryingly, a cascading effect of decreased host sociality in most scenarios could be poorer ecological performance in terms of harvesting resources from the landscape, leaving populations vulnerable to other environmental risks.

The potential consequences for an ecological community other than the species directly affected by pathogens are borne out by Monk et al. (2022), who studied the effects of the introduction of mange to vicuñas in Patagonia. The scenarios I modelled may actually be too mild, and novel pathogen spillovers could exterminate their hosts, rather than force the evolution of less gregarious social systems. The scale of future work required in this field is daunting: identifying outbreaks as they happen, often in remote areas and involving poorly known species; determining patterns of species' spatial overlap that could aid cross-species transmission beyond the initial spillover; determining which species — for a range of reasons — may be at heightened risk from an epi- or panzootic outbreak; and finally, determining a response that preserves species while minimising risk of further spillover.

The Role of Models in Understanding the Evolution of Movement

The issue of how to use individual-based models to understand the (evolution of) mechanisms underlying empirical data from animal tracking studies is not new. One approach has been to use IBMs to generate ecological patterns ('pattern-oriented modelling'; Grimm et al. 2005), with quasi-evolutionary processes used to fine tune the IBM parameters (Hamblin 2013). In Nathan et al. (2022), a recent review of approaches to modern animal tracking data, we wrote,

> Using *genetic algorithms*, initial candidate rulesets for individual decision-making can evolve into a robust ruleset that is able to reproduce the unique range and quality of spatial and temporal patterns in high-throughput data *("reinforcement learning')* [emphasis mine].

This approach seeks to recover patterns seen in real empirical data from simulations, with the hope that the simulated mechanisms ('candidate rulesets') that produced them are similar to those animating real individuals ('true mechanisms') — this is the essence of 'pattern-oriented modelling' (Grimm et al. 2005). However, a wide range of behavioural mechanisms can produce very similar ecological phenomena, making it difficult to determine whether the 'true' mechanism is approximated by any of the candidate simulated mechanisms. Essentially, it is challenging to determine processes from patterns (as I have alluded to in Chapter 6).

Open questions also remain about how rulesets, or mechanisms, should be encoded in models. Habitat selection rules which are complex functions of the information available to individuals are likely to be challenging to interpret. For example, movement decisions based on outputs computed by artificial neural networks were first proposed over a decade ago (Mueller et al. 2011), but they have not seen widespread adoption in the ecology and evolution literature (but see Netz et al. 2021*b*). One approach to interpreting the strategies encoded by complex functions is to use sophisticated clustering algorithms to detect distinct combinations of function coefficients (weights in a neural network) (Bastille-Rousseau and Wittemyer 2019). The potential stumbling block here is that the methods required for such clustering are also not native to ecology and evolution, and themselves suffer from being much too complex to interpret for a general biologist audience (see e.g. the GigaSOM method for clustering single-cell cytometry data; where SOM is a 'self organised map', a form of machine learning Kratochvíl et al. 2020).

Furthermore, it is also unclear how these mechanisms should undergo evolution — in Nathan et al. (2022), we suggested using both genetic algorithms and reinforcement learning acting on the simulated mechanisms, based on the similarity of simulated movement paths with real animal movements. The concept of genetic algorithms and reinforcement learning is borrowed from the fields of artificial intelligence and computer science, and represents their idea of biological processes (evolution and learning, respectively DeAngelis and Diaz 2019). However, these approaches are explicitly designed with a specific goal in mind, and the success of agents employing these algorithms can be — and is — usually measured using single, simple metrics (e.g. classification accuracy, task completion time). This solution-oriented approach of artificial intelligence is poorly suited to ecology and evolution, in which there *are* no single correct solutions — and in which, moreover, individuals interact not only with the environment, but also with each other, making 'optimal' solutions heavily dependent on local ecological contexts. Consequently, I believe that neither the implementation of genetic algorithms such as 'simulated annealing' (Getz et al. 2015), nor the use of reinforcement learning is a good choice for conceptual eco-evolutionary models.

Throughout the latter part of this thesis, I have proposed a different way forward: rather than working backwards from empirical phenomena to potential mechanisms, to instead *work forwards from plausible mechanisms to potential emergent outcomes*. This first requires a change in perspective on individual-based models, from being highly detailed simulations of specific empirical systems (such as in Stillman and Goss□Custard 2010; Bocedi et al. 2014; Diaz et al. 2021), to being used to obtain broad conceptual insight into 'What if ...?' scenarios. Such conceptual implementations, in addition to being demonstrated below, are also included in Chapters 4 and 5. Second, I suggest beginning with plausible, well-supported movement mechanisms, such as individual perception and integration of local cues when making movement decisions (Nathan et al. 2008). Having selected salient mechanisms, a plausible ecological context is also key — a population foraging on a landscape is a solid starting point. The main feature of these models, however, is to let the ecological outcomes for individuals in one generation (such as intake) determine the mixture of movement decision-making mechanisms in the next generation, through inheritance (with variation arising *via* mutations; see below, or Chapters 4, 5). For simplicity, as seen in the example models here, and in Chapters 4 and 5, some ecological and evolutionary aspects will have to be set aside. In addition to an initial understanding of how mechanisms can lead to unexpected emergent outcomes, the class of models I advocate are well suited to examining how these emergent outcomes could change following perturbations in environmental regimes, as I do in Chapter 5 (see also Botero et al. 2015).

Estimating the Fitness Consequences of Movement Strategies from Tracking Data

A key barrier to achieving a unified evolutionary ecology of animal movement is understanding the evolutionary consequences of animal movement strategies; in short, this requires estimating the 'fitness' outcomes of movement (fitness itself being a challenging term). These consequences may be broken down into two key components, survival, and fecundity; together these determine lifetime fitness. Ecologists, taking a phenomenological approach, have been able to make some headway in examining the evolutionary consequences of some movements, such as annual migrations. For example Sergio et al. (2022) recently showed that compensation for drift in the north-south migration route, caused by lateral east-west winds, improved with age in black kites (*Milvus migrans*), but that this was mainly due to poorly navigating individuals dying while young. While this study highlights the importance of movement for evolutionary dynamics — in this case, conferring a survival benefit to better navigators — the inferences are often specific to particular taxa, and difficult to generalise. However, we currently possess some methods that could be used to link the consequences of movement across temporal scales.

At relatively short temporal scales of a few tracking seasons, one approach is to study movement in the context of a common 'currency', energy. Combined experimental-observational approaches, linking respirometry measures of resting metabolic rate, doubly-labelled water measures for daily metabolic output, and tri-axial accelerometry and movement tracking, have paved the way for robust estimates of daily energy expenditure in free living animals (Stothart et al. 2016). Animals' spatial settings can impose or alleviate metabolic costs, leading to the broader approach of studying 'energy landscapes', i.e., environmental factors that change the "cost of transport" (Shepard et al. 2013). Building off this work, we can now estimate how the cost of navigating through landscapes can affect large-scale patterns of animal space-use (e.g. Gallagher et al. 2017). Yet more recent work is probing how animals' fine-scale movement decisions can be linked directly to the energetic costs of those decisions (Klappstein et al. 2022). Overall then, the frameworks for measuring energetic loss in moving animals are well developed, and this can be linked to reductions in both individual survival and fecundity.

The positive effects of movement are more challenging to measure. Energetic gain, for instance, requires the detection of foraging bouts. Here too, the addition of accelerometry data can be useful in detecting sudden bursts of activity, especially those associated with predation attempts (Williams et al. 2014; Bryce et al. 2017). However, it is still challenging to remotely and automatically determine the energetic gain from a predation event. The task of measuring the calorific value of forage is easier for herbivorous species, as vegetation cover and quality can often be quantified from remote sensing platforms (Pettorelli et al. 2011). The caveat here is that the spatial resolution of remotely sensed data is often low. Movement itself cannot confer increased fecundity, but can indirectly facilitate more or higher quality breeding attempts through increased sampling of breeding opportunities (as in Kempenaers and Valcu 2017). Yet movement data can be very useful in determining whether individuals have bred successfully, and uncover the characteristics of good nesting sites (Picardi et al. 2020). Integrating the analysis of tri-axial acceleration data, could help refine current methods for detecting breeding or nesting outcomes, at least in some taxa (Schreven et al. 2021). At larger temporal scales, individuals' preferences for energy landscapes could be linked to their survival or reproductive success, for global comparisons of the potential evolutionary consequences of movement strategies.

Approaches to Investigating Model Predictions

My class of conceptual models aim to provide broad frameworks for the interpretation of current and future patterns observed in animal tracking data. This is especially important as animal movement ecology becomes a ‘big data’ field through the use of high-throughput tracking (Nathan et al. 2022). As the resolution of tracking data improves, animals’ fine-scale decision-making rules could be revealed, and our framework could help understand the evolutionary causes of these rules — as well as how these rules could shift with environmental change. In this regard, space-time substitutions could help: by studying movement strategies in distinct population of the same or similar species along a moving gradient of environmental conditions, researchers could understand the eco-evolutionary impacts of global changes such as warmer temperature bands moving polewards, or shifts in pathogen prevalence (Blois et al. 2013; Carlson et al. 2022*a*). These could constitute simple initial tests of model predictions for the example scenarios I outline earlier. Such studies would require international collaborative frameworks studying comparable animal populations; fortunately, multiple such networks exist and are growing (Iverson et al. 2019; Davidson et al. 2020; Jetz et al. 2022).

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Nederlandse Samenvatting

Beweging is een fundamenteel proces in de natuur en het ontrafelen van de oorzaken en consequenties van bewegingspatronen is een belangrijke doelstelling van de dierecologie. De posities van individuele dieren in een landschap bepalen wat ze kunnen waarnemen en met welke andere dieren ze interacties kunnen aangaan. De uitkomsten van deze waarnemingen en interacties hebben invloed op beslissingen over waar ze vervolgens heengaan. Dergelijke individuele beslissingen vormen de basis voor grootschalige ecologische verschijnselen, zoals de verspreiding en de ecologische interacties van een soort. In de afgelopen twintig jaar heeft het vakgebied bewegingsecologie, dankzij snelle ontwikkelingen op het gebied van trackingtechnologie, fascinerende en nooit eerder waargenomen relaties tussen de bewegingspatronen van dieren en ecologische processen aangetoond.

Nog steeds is de bewegingsecologie een van de meest dynamische gebieden in de biologie. Dit proefschrift is een episodisch, persoonlijk verslag van twee ontwikkelingen, waarbij ik betrokken ben geweest: *(i)* de ontwikkeling van statistische methoden om uit de enorme tracking datasets ecologisch betekenisvolle inzichten te verkrijgen over de oorzaken en consequenties van bewegingspatronen; en *(ii)* de ontwikkeling van simulatiemodellen om de evolutie van bewegingsstrategieën beter te begrijpen. Beide ontwikkelingen zijn mogelijk gemaakt door methodologische innovaties die in dit proefschrift nader worden beschreven en nader worden uitgewerkt. Mijn proefschrift bevat twee delen, die die overeenkomen met de twee bovengenoemde thema's.

Hoofdstuk 1 biedt een uitgebreide introductie op de twee thema's. Ik leg uit hoe mechanistische, individu-gebaseerde simulatiemodellen kunnen bijdragen aan een beter begrip vande ecologie en evolutie van de dierlijke bewegings- en verdelingspatronen.. Onder meer leg ik uit dat vaak voorkomende bewegingspatronen, zoals de verplaatsingen van dieren tijdens het foerageren, even goed (of zelfs beter) geschikt zijn om de ecologische en evolutionaire oorzaken van dierlijke beweging te begrijpen als grootschalige maar sporadische gebeurtenissen, zoals geboorteverspreiding of jaarlijkse migratie.

In Deel I beschouw ik het probleem hoe de verplaatsingsstrategieën met behulp van de big data van trackingsystemen ontrafeld kunnen worden. Ik was als coauteur betrokken bij een recent overzichtsartikel in Science (niet opgenomen in mijn proefschrift; zie de lijst met publicaties) dat een handige inleiding tot de problematiek geeft.

Hoofdstuk 2 beschrijft een aantal praktische aspecten van het werken met de enorme ruimtelijke datasets die worden gegenereerd door high-throughput trackingsystemen, die de verplaatsingen van honderden dieren met een zeer hoge spatio-temporele resolutie kunnen tracken (met een nauwkeurigheid van een paar meter en met een interval van een paar seconden). Ik behandel het opschonen, aggregeren, segmenteren en clusteren van data, en bespreekmanieren om deze methoden op een reproduceerbare en efficiënte manier te implementeren. Hierbij maak ik gebruik van recentelijk ontwikkelde methoden uit andere vakgebieden (softwareontwikkeling en andere big data vakgebieden zoals genomics). Het ontwikkelen van robuuste en reproduceerbare methoden voor dataverwerking is volgens mij een hoeksteen van de bewegingsecologie van de toekomst.

In Intermezzo A illustreer ik aan de hand van een voorbeeld zowel de technische als de esthetische aspecten van het visualiseren van bewegingsdata. Dit resulteerde in een kaart die in 2021 de Mapping Animal Movements-competitie van de British Ecological Society heeft gewonnen.

In Hoofdstuk 3 laat ik zien hoe een combinatie van fijnmazige bewegingsdata en de analyse van 'gezichtsvelden' (wat een individueel dier daadwerkelijk kan zien vanuit zijn locatie) nieuwe inzichten geeft in de verplaatsingsstrategieën en habitatselectie van ruiende (en dus kwetsbare) vogels. De analyse laat zien dat de beslissingen van ruiende vogels voornamelijk worden bepaald door de toestand van hun verenkleed (dat bepaald hoe makkelijk zij kunnen vluchten) en de vraag of en in hoeverre potentiële bestemmingen zichtbaar zijn voor predatoren.

In Deel II beschrijf ik hoe we met behulp van individu-gebaseerde modellen inzichten kunnen verkrijgen in de evolutie van bewegingsstrategieën en de ecologische consequenties van deze strategieën. In Intermezzo B illustreer ik aan de hand van een eenvoudig voorbeeld hoe dit soort conceptuele modellen kunnen worden geïmplementeerd. Ook laat ik zien dat de evolutionaire en ecologische voorspellingen van dit soort modellen substantieel kunnen verschillen (kwantitatief en kwalitatief) van de uitkomsten van wiskundige modellen.

In Hoofdstuk 4 bestudeer ik een model voor de evolutie van bewegingsstrategieën in het verband van voedselcompetitie. Dit is het eerste, volledig uitgewerkte onderzoek dat gebruikmaakt van het type modellen dat ik in de Inleiding bepleit. In dit model zijn de verplaatsings- en foerageerbeslissingen van individuele dieren afhankelijk van lokale omgevingssignalen (zoals de dichtheid van voedsel en de aanwezigheid van soortgenoten) en leidt evolutie tot een steeds betere aanpassing van deze beslissingen aan de competitieve context. De simulaties laten zien dat verschillende competitiestrategieën geassocieerd raken met verschillende bewegingsstrategieën. Dit leidt tot een verdeling van de concurrerende individuen over de ruimte die sterk afwijkt van de voorspellingen van klassieke modellen. Voor elke competitievorm volgen de bewegingsstrategieën een bepaald patroon, maar binnen dit patroon bestaat een grote diversiteit aan bewegingsstrategieën. Dit heeft belangrijke consequenties, want vanwege deze diversiteit kunnen bewegingsstrategieën zeer snel evolueren als omgevingsfactoren (zoals de voedselverdeling) veranderen.

Intermezzo C is een (gepubliceerd) commentaar op een individu-gebaseerde simulatiestudie die niet voldoende rekening houdt met de door mij voorgestelde principes voor het modelleren van beweging en competitie. We laten zien dat kleine onnauwkeurigheden en fouten bij de implementatie van een simulatiemodel grote consequenties voor het systeemgedrag kunnen hebben.

Hoofdstuk 5 behandelt de evolutie van verplaatsingsstrategieën na de introductie van een besmettelijk pathogeen. Via evolutie moet een nieuwe balans worden gevonden tussen de voordelen van sociale contacten (het verkrijgen van informatie over potentiële voedselbronnen) en de nieuw ontstane risico's van dit soort contacten (de overdracht van het pathogeen). Ik laat zien dat de evolutie verrassend snel verloopt en grote consequenties heeft voor de structuur van sociale netwerken en de foerageerefficiëntie. Een mechanistische modellering van de introductie en verspreiding van een nieuw, besmettelijk pathogeen, een scenario dat wereldwijd tot steeds grotere zorgen leidt, kan dus helpen om de directe en indirecte gevolgen op individueel niveau te voorspellen, evenals de gevolgen voor de ruimtelijk-sociale organisatie van dierengemeenschappen.

Hoofdstuk 6 combineert de methoden van deel I en deel II van mijn proefschrift. Met behulp van de individuele bewegingspatronen in de simulaties in hoofdstuk 4 valideer ik twee populaire statistische methoden in de bewegingsecologie: herhaalbaarheidsanalyse en de analyse van stapselectiefuncties. Ik laat zien dat de in hoofdstuk 4 gevonden aanzienlijke individuele verschillen in verplaatsingsstrategieën door deze methoden vaak niet gedetecteerd worden. Deze studie laat zien dat simulatiegegevens zeer nuttig kunnen zijn om de mogelijkheden en beperkingen van statistische tools in kaart te brengen.

In Hoofdstuk 7 kijk ik ten slotte terug op de bevindingen van dit proefschrift en stel ik voor hoe een energetica-aanpak zou kunnen worden gebruikt om sommige van de fitnessgevolgen van verplaatsingen van dieren in te schatten.

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About the Author

Pratik R. Gupte was born in India in 1993. After schooling in Hyderabad and an undergraduate degree in zoology from St. Xavier's College, Mumbai in 2014, he worked on field projects in southern India, Ladakh, and in South Africa. In 2017 he received a master's degree from the University of Kiel, as part of the International Master's in Applied Ecology, a programme spread over France, Portugal, Germany, and Ecuador. His master's thesis on families of wintering geese saw fieldwork in the Russian Arctic and the Netherlands. In 2018, he began his PhD in Franjo Weissing's lab at the University of Groningen. Pratik is broadly interested in the spatial ecology of animals, especially birds. Recognising that the current model of academic science is unsustainable, he left the academic career track, and is now a research software engineer at the London School of Hygiene and Tropical Medicine, where he develops epidemiological models to inform policy responses to disease outbreaks.

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