

# **Introductory Essay**

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Short term causes and long term consequences of adaptations to environmental change

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## Part I.

### Summary

The **movement of animals** has always fascinated humans, but modern biology has only now come to actively study movement as the linchpin of many processes. As movement studies seek to unify phenomena across scales, they must also contend with the idea that there are **consistent individual differences** within many animal populations. These differences, whose evolution, development, and maintenance are still under debate, are estimated to have population level consequences. One system in which consistent individual differences have been identified is that of **red knots** *Calidris canutus*, which forage on intertidal mudflats and vary along an axis of exploratory behaviour. Knots' and other foragers' movement is often strongly influenced by which **spatio-temporal change** in the often unpredictable resource landscape. This system inspires questions about how movement strategies evolve in such landscapes, how they affect the landscapes on which they evolve, as well as how the interaction of the two gives rise to emergent phenomena such as structured communities. Those questions will be the subject of my thesis.

This essay, an introduction to my work over the next two years, is organised in the following sections: first, the **Introduction** contains key concepts in the fields of *Animal movement*, *Movement as personality*, and *Modelling movement*. The second section, **About this project**, lays out the questions I want to investigate. The third section, **Towards a model of wader movement**, explains the conceptual and practical aspects of the models and empirical methods I propose to implement towards goals in Section 2.

## Part II.

### Introduction

#### Animal movement

Animal movement across spatio-temporal scales – from seasonal migration, to breeding aggregations, to diurnal cycles – have been an important field of human knowledge throughout recorded history, and likely long before. Even in more modern times, the two most successful paradigms of the natural sciences' century of insight, evolution by natural selection (Darwin and Wallace 1858) and island biogeography (MacArthur and Wilson 2001), rely at least in part on the movement of animals to make their point. Explicit treatment of the subject began with theoretical developments on the movement of freely moving and ideally rational agents. This led to nearly simultaneous advances in the understanding of the distribution of foragers at the landscape scale (Fretwell and Lucas 1970), and the topology of groups of selfish agents (Hamilton 1971). Theory on population spatial distributions soon incorporated fine-scale phenomena

such as individual interactions and population structure, and was already a mature field with strong empirical support when reviewed by Sutherland 1996. Theoretical advances in the study of fine-scale movement itself, on the other hand, have lagged behind the measurement of the movement of individual animals (Holyoak et al. 2008).

The recently emerged movement ecology paradigm (MEP; Nathan et al. 2008) has sought to fill this gap, understanding “movement itself as the focal theme...by providing a unifying framework and common tools” (Nathan 2008). This paradigm urges practitioners to attempt to answer three questions: 1. *Why* do organisms move? 2. *Where* do organisms decide to move? 3. *How* do organisms move? This links (1) external stimuli, such as fear of predators (Laundre et al. 2001), (2) sensory capacity, which translates into navigational ability and search strategies (eg. Bartumeus and Levin 2008), and (3) life-history dependent physiology and internal state (eg. Fryxell et al. 2008). Movement ecology’s rise has coincided with the beginning of “a golden age of animal tracking science” in the form of large-scale and high-resolution animal tracking (Hussey et al. 2015, Kays et al. 2015). Biologging, i.e., the remote measurement of instantaneous organism state (Cooke et al. 2004), and high-resolution animal tracking in particular, have led to remarkable insights into the detailed sub-units of movement behaviour, such as the energetics of predation and locomotion (see eg. Williams et al. 2004, Scantlebury et al. 2014).

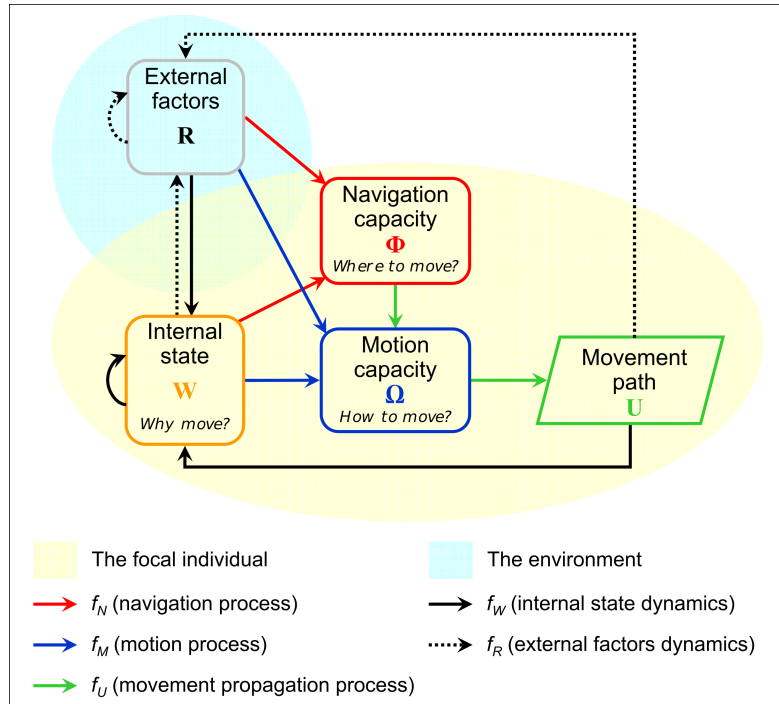


Figure 1: The movement ecology paradigm places observed movement (*path*:  $U$ ) as both a consequence of prior factors, and a contributor to future ones. From Nathan et al. (2008).

Despite advances in empirical methods, animal movement studies are still subject to limitations of scale. Among these are emergent group-size effects (Tunström et al. 2013), which are diffi-

33 cult to quantify empirically notwithstanding recent advances (Handegard et al. 2012, Kays et al.  
 34 2015, Strandburg-Peshkin et al. 2015, Dhanjal-Adams et al. 2018); a distinct problem when ani-  
 35 mal grouping is near-universal (Krause and Ruxton 2002). The impracticality of research across  
 36 scales of organisation (eg. physiology to population) has similarly confined most movement  
 37 studies to answering at most one MEP question at a time (but see Fryxell et al. 2008, Strandburg-  
 38 Peshkin et al. 2015, Curtin et al. 2018). This is linked to the choice of study system, which among  
 39 vertebrates has been restricted by the technical difficulty in hewing to the 3% body-mass rule  
 40 (Naef-Daenzer et al. 2001). Finally, animal movement has been captured by the movement *ecol-*  
 41 *ogy* paradigm because of the difficulty in studying movement at evolutionary timescales. Here,  
 42 simulation models can help to shine “the light of ecology” on evolutionary biology (Grant and  
 43 Grant 2011), by uncovering the importance of individual interactions for emergent phenomena  
 44 (eg. Hildenbrandt et al. 2010, Tunström et al. 2013), the surprising extrinsic drivers of move-  
 45 ment mode (Guttal et al. 2012), the evolutionary effects of higher trophic levels (Ioannou et al.  
 46 2012), and the evolution of movement rules (de Jager et al. 2011, Netz 2017).

## 47 **Movement as personality**

48 The work cited above may be safely claimed to make at least one of two assumptions; the first  
 49 is that of the ‘golden mean’. The second is the assumption of optimality (Fretwell and Lucas  
 50 1970) entailing infinite behavioural plasticity. Neither of these assumptions is very well founded.  
 51 While the first is methodologically convenient, theory from Darwin 1859 onwards has recog-  
 52 nised it as untrue; models find that differences among individuals can have population level  
 53 consequences (eg. Pruitt and Riechert 2011). The second assumption is squarely challenged by  
 54 the study of consistent individual differences in behaviour. The field of animal personality and  
 55 behavioural syndromes (Sih et al. 2004a, b) and its consequences (Dingemanse and Réale 2005)  
 56 seeks to quantify between and within individual consistency in behavioural responses “through  
 57 time or across situations”. Variation along two or more axes of personality (Réale et al. 2007)  
 58 may be correlated into a ‘behavioural type’ (examples in Sih and Bell 2008, Bell et al. 2009); for  
 59 example, ‘boldness’ and ‘aggression’ form two of the major axes of personality, and are often  
 60 quantified together as a syndrome (Carter et al. 2013).

61 Behavioural ecology has only slowly come to terms with the idea that such individual differ-  
 62 ences within populations could be advantageous (Wilson 1998). Individual differences have  
 63 been explained in terms of mechanisms engaged during development (Wolf and Weissing 2010,  
 64 Groothuis and Trillmich 2011), trade-offs in life-history (Wolf et al. 2007a, b), and the feedback  
 65 loops created between individual state and behaviour (Wolf and Weissing 2010) as prominent  
 66 proximate causes. Evolutionary explanations of these differences and especially their consis-  
 67 tency have remained elusive because the default expectation has been that plasticity is more  
 68 adaptive (Wilson 1998). Wolf and Weissing 2010 have since shown that consistent behavioural  
 69 types may yet achieve comparable fitness outcomes if selection is frequency-dependent (May-  
 70 nard Smith 1982), and rarer types have a selective advantage. Spatio-temporal variation, a ubiq-  
 71 uitous feature of environments (Levin 1992), may have a major role to play when it hosts a popu-  
 72 lation where infinite adaptability is costly or habitat choice limited (Wolf and Weissing 2010). In

such cases, individuals may specialise for particular spatial or temporal conditions, maintaining global variability, while local variability may be maintained through imperfect estimation of current habitat state (Wolf and Weissing 2010, 2012). However, there is little doubt that behavioural types have significant eco-evolutionary consequences for populations (Sih et al. 2012, Wolf and Weissing 2012).

The movement ecology paradigm places animal movement at the end of a pipeline fed into by physiology, stimuli, and cognition (*state*, Wolf and Weissing 2010, 2012), and it is unsurprising that populations might have evolved behavioural polymorphisms for movement, or *movement types* (Wolf and Weissing 2010, Getz et al. 2015, Netz 2017). Indeed, movement types are inherent predictions of previous theoretical work that did not necessarily consider movement as its central theme (eg. Watson and Miller 1971, Lima and Zollner 1996). Animal tracking has since confirmed such individual consistency in movement across scales, from local movements (Austin et al. 2004, Leclerc et al. 2016) to dispersal (Duckworth and Badyaev 2007, Clobert et al. 2009, Cote J. et al. 2010, Duckworth and Sockman 2012). While Wolf and Weissing 2010 suggested that some spatio-temporal environmental variability might be causal to consistency evolution, later work showed that such structure can be created from uniformity by individuals themselves, and thus may be co-incidental rather than causal in relation to movement strategy evolution (de Jager et al. 2011, Getz et al. 2015, Netz 2017). In general, this points to the interplay between individuals' movement and the landscapes – and begs the question of how rate and predictability of landscape change (*sensu lato* Botero et al. 2015) might affect the evolution of movement types. Spiegel et al. 2017 have demonstrated that this link between movement types (*fast* and *slow*; see parallels with earlier Wolf et al. 2007a, b) and fitness outcomes in landscapes that vary in spatial *predictability* can have consequences at the population level – from social networks to community composition.

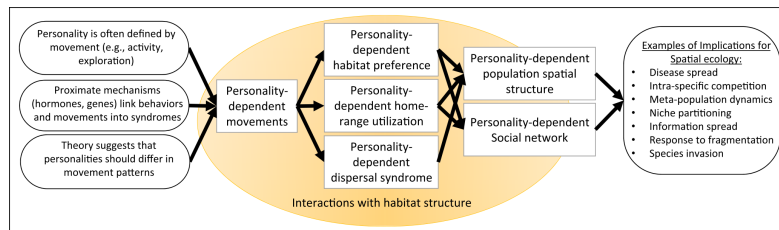


Figure 2: Spiegel et al. (2017) lay out a framework linking personality, movement, and resulting interactions. Personality may be initially measured in terms of movement, but the underlying causes can impact larger-scale processes such as population spatial structure.

## Modelling movement

Many aspects of personality and movement – across scales – can be explored using the waders *Charadrii*, and especially the sandpipers *Scolopacidae* as a model system. Waders are a ubiquitous group of long-lived birds characterised by their littoral foraging on buried macrozoobenthic prey, and their often extreme flyway-channelled migration between generally disjointed



and strongly seasonal global distributions (Boere and Stroud 2006, Gill et al. 2009, Piersma and Bonan 2019). Sandpipers are well known for their huge wintering fission-fusion flocks (Myers 1983, Conklin and Colwell 2008), and as symbols of traditional landscapes (Colwell 2018). Waders (hereafter referring to scolopacids) eking out their precarious existence (Fitzpatrick and Sennner 2018) at the waterline are thus poised to be the new canary in the coalmine: harbingers of global environmental change (Piersma and Lindström 2004, Wikelski and Tertitski 2016) which has swiftly advanced from ‘near’ to ‘here’ (IPCC 2018). Wader movement fulfils many of the requirements one would expect from a system that integrates animal personality and movement studies. First, wader movement has been extensively investigated using a variety of approaches at nearly all spatio-temporal scales: small spatio-temporal scales such as foraging (van Gils et al. 2003, van Gils 2010), large spatio-temporal scales such as migration (Buehler et al. 2006, Piersma 2011), proximate causes for large-scale phenomena (Lank et al. 2003, Ydenberg et al. 2004, Ruthrauff et al. 2013, 2018), and ultimate causes for small-scale phenomena (van Gils et al. 2006, Kraan et al. 2009a). Of the waders, red knots *Calidris canutus* are among the best studied, with a wealth of biological information, from an understanding of physiology and its interaction with exploratory personality (Bijleveld et al. 2014, Mathot et al. 2017), to knowledge of group dynamics across scales (Bijleveld et al. 2010, 2012b, 2015b), to the effect of foragers on their resource landscapes (Bijleveld et al. 2015a).

Many theoretical studies increasingly employ agent-based approaches, which were developed to overcome two flaws in mathematical models (Huston et al. 1988). First, in order to prevent an unreasonably large number of parameters (a disadvantage of ABMs), earlier models had abstracted populations to “golden mean” values that elided individual differences (see previous section) essential to evolutionary and ecological processes. The second issue was the assumption of global interactions, i.e., that all individuals affect all others equally, ignoring central problems of scale (Levin 1992) and local interactions (see Legendre 1993) in ecology. ABMs have since been standardised in terminology (Grimm et al. 2006, 2010), and are widespread in ecology (DeAngelis 2018). In such models, individual organisms are each modelled separately and allowed to make decisions based upon various inputs, akin to real decision making processes. In animal ecology, ABMs are especially relevant in modelling movement (reviewed in DeAngelis and Mooij 2005), and have been used extensively to model avian movement including that of red knots (van Gils 2010, Spiegel et al. 2013, 2017, Getz et al. 2015, 2016 etc). Simple evolutionary algorithms (see Bäck 1996) as implemented in Getz et al. 2015, Netz 2017 that predicate the reproductive output (replicates) of each agent on some measure of fitness, such as net intake, can add evolutionary dynamics to otherwise simple ABMs. This allows the modelling of movement across scales, from small-scale within-patch dynamics, such as competition (Keddy 2001) and the investigation of emergent large-scale evolutionary dynamics, such as community composition (*movement guilds*, Getz et al. 2015), and alternative strategies (Netz 2017). A major advance may be made by having the decisions of agents be the output of a ‘black-box’ process in the form of artificial neural networks (ANNs; Enquist and Ghirlanda 2013; see Netz 2017). Neural network approaches allow for surprising results – such as the evolution of rich movement dynamics and alternative strategies, even when beginning from largely similar populations (Netz 2017).

## Part III.

### About this project

In this section, I outline my approaches to examine the *evolution of movement types* (sensu Wolf and Weissing 2010, Getz et al. 2015) in the context of *environmental predictability and rate of change* (as in Botero et al. 2015), using the *red knot system* as a reference (Bijleveld et al. 2012b, 2014, 2015a, b, Oudman et al. 2018). Wolf and Weissing 2010 lay out the theoretical basis for the expectation that consistent behavioural differences arise in spatially structured landscapes, while Botero et al. 2015 describe how environments in certain regimes of temporal variability and predictability can give rise to similar polymorphisms. Getz et al. 2015 and Netz 2017 show how virtual agents can evolve movement types while structuring initially featureless landscapes. Bijleveld and colleagues (above) provide empirical data on the foraging and movement ecology of red knots that can inform modeling approaches and which may be used to test model predictions.

#### Abstract models

I will begin with an abstract approach and some basic questions. Modelling agent movement as the output of an ANN which takes environmental cues as outputs, I will first investigate how different regimes of landscape patchiness and temporal variability influence the evolution of movement types. Specifically, I will be interested in the following:

1. ***How many movement types are evolved under different regimes of spatial predictability and variability?*** This question is aimed at unifying the Wolf and Weissing (2010) and Botero et al. (2015) approaches at broad evolutionary scales. Recent mechanistic models based on ANNs suggest that genotype-phenotype mapping is not as clear-cut as in Botero and colleagues' work, and that polymorphisms (there identified as diversified hedged bets) may arise under a wider set of conditions in populations of fixed size. I will then examine the behaviour of agents (movement) in response to environment quality (resource landscape), with the idea being to identify the conditions under which different strategies (bet-hedging, plasticity) evolve.
2. ***What is the link between behaviour and labile physiological state?*** Drawing inspiration from recent work in the red knot system that suggests a strong role for behaviour-sociality-physiology feedbacks (Bijleveld et al. 2014; Mathot et al. 2017; discussed in Wolf and Weissing 2010), this question is aimed at investigating whether physiology constrains agents in behavioural parameter space. For example, when movement is made dependent on instantaneous state, it may be constrained by energy reserves, leading to a state-behaviour feedback. Further, intake may face digestive constraints that can strongly affect behaviour (van Gils and Piersma 2004). I will investigate whether behaviour-physiology trade-offs are involved in the evolution of movement types.

179 3. ***How do movement type frequencies develop over ecological and evolutionary time-scales?***

180 Foraging depleting the resource landscape can modify or introduce spatial patterns  
181 over time (de Jager et al. 2011; Getz et al. 2015; Netz 2017). Empirical results suggest  
182 this change can be rapid (Bijleveld et al. 2015). Starting with initially unstructured  
183 landscapes, I will investigate how structure is modified using a relaxed version of (1) in  
184 which agents deplete their landscape at different rates. A natural consequences might  
185 be that foragers specialised to particular regimes of landscape structure could see a  
186 change in their profitability multiple times within their lives. Thus, when (1) includes  
187 the depletion element of (3), agents might be expected to evolve a median (bet-hedged)  
188 phenotype that ensures profitability across landscape structures. This question is then  
189 aimed at investigating both the landscapes and agents:

190 a. ***How does landscape structure change over ecological and evolutionary time?*** In this  
191 scenario, I fall back upon the red knot system as a guide, that foragers are not al-  
192 ways present on the landscape and the resource has time to regenerate. Such sea-  
193 sonal systems are widespread making this a reasonable scenario. I will investigate  
194 the development of landscape patterns (such as the autocorrelation range, or patch  
195 size; see Legendre 1993) when agents are themselves evolving upon such landscapes.

196 b. ***How does the number and phenotype of movement types change over evolutionary***  
197 ***time?*** Agents' consumption rates (set to be identical) could lead to different rates  
198 of landscape change in the scenario outlined above. Foragers would then evolve to  
199 maximise fitness in both space and time. As landscapes traverse the axis of patch  
200 size (autocorrelation range, or predictability) due to agent foraging, the spatial con-  
201 ditions that evolved types in (1) might recur multiple times. This should allow the  
202 investigation of whether there is a change in selection pressures on movement types,  
203 the time-scale at which it occurs, and whether it is mediated by agents' effect on the  
204 landscape.

205 c. ***Do critical transitions occur in the number or profitability of movement types?*** As  
206 agent populations evolve movement types rather than bet-hedged phenotypes, these  
207 types may yet show sufficient flexibility to behaviourally buffer against decreasing  
208 profitability as the landscape shifts to a regime to which they are poorly adapted.  
209 This change may occur within individuals at ecological scales (as resources deplete  
210 or change over a season), and at the population level (as landscapes change over  
211 evolutionary time). Such systems, where the response (here, movement, or fitness)  
212 is initially poorly responsive to the driver (landscape structure, such as patch  
213 size), may then undergo abrupt transitions (Scheffer 2009) to an alternative stable  
214 state. Behavioural changes relating to movement strategy occur in wader systems  
215 (e.g. Oudman et al. 2019), but the process is not fully understood. I will look into  
216 whether changes in such systems can then be characterised as critical transitions.  
217 The same approach can be applied to the landscape, to study whether landscapes  
218 catastrophically shift to another state (as in van de Koppel et al. 1997; Jefferies et al.  
219 2006).

## 220 Wader models and data

221 Following the steps above, I will modify the models to simulate the red knot system. Important  
222 conceptual changes include the addition of regular environmental change in the form of the  
223 tidal cycle. This feature first limits resource landscape availability to agents. Second, it forces  
224 agent movement, further constraining the range within which agent movement types can spe-  
225 cialise. For example, a very efficient movement type in a model elaborated above (1) would be  
226 to remain largely sedentary. This is not an option in tidal systems as most waders cannot swim.  
227 Important practical changes will be the parameterisation of the model following empirical data  
228 or best estimates on resource landscape structure and red knot physiology (body size, energy  
229 requirements, perception range).

230 Finally, I will turn to the empirical red knot tracking data and the benthic sampling data to in-  
231 vestigate whether the models sketched above correspond to reality. The following questions  
232 suggest themselves.

- 233 1. ***Do red knots show movement types that can be identified from a combination of data***  
234 ***sources?*** This question entails cooperation with my co-PhD student. Using scores from  
235 behavioural assays, state variables such as gizzard mass or body mass, and movement  
236 variables such as patch-switching or residence time, I will aim to determine whether  
237 knots evolved in models occupy comparable parameter spaces to real birds.
- 238 2. ***Do red knots show assortative association based on movement type?*** Here, I investigate ex-  
239 pectations from Spiegel et al. (2017), that association and the strength of social networks is  
240 strongly influenced by personality and the clumped-ness of the landscape. This question  
241 is suitable to both an experimental and field tracking approach.

## 242 Part IV.

## 243 Towards movement models

244 In each of these sub-sections, *Modelling landscapes* and *Modelling agents*, I will lay out how I  
245 propose to go about modelling the systems I have described above. I first describe the concept  
246 with some justification (usually drawn from red knot, or other avian systems), and then delve  
247 into the practical considerations of implementation, again seeking to justify my choices. In  
248 each case, I begin with the more abstract model, and then elaborate on a model based on red  
249 knots. It is important to note that while initial, abstract models are based on previous work,  
250 later, more complex models rely on these abstract models. Should the abstract models produce  
251 different dynamics from the ones expected from theory, the implementation and predictions of  
252 later models may have to be adjusted accordingly.

### 253 Modelling landscapes

#### 254 Concept: Spatial predictability

255 Spatial pattern and scale matter in ecology (Levin 1992), and foragers benefit from responding  
256 to spatial structure in resource landscapes in empirical and theoretical studies (Benhamou 1992,  
257 Walsh 1996, Klaassen et al. 2006, van Gils et al. 2006, van Gils 2010, Oudman et al. 2018). Botero  
258 et al. 2015 consider predictability as well as variation in time – however, space-time substitution  
259 (Blois et al. 2013) has found wide use in testing landscape-scale predictions in ecological systems  
260 (eg. Hirota et al. 2011, Staver et al. 2011), and allows the leveraging of extensive empirical  
261 sampling of resource landscapes at small (e.g. Bijleveld et al. 2012a) and large scales (e.g. Huete  
262 et al. 2002).

263 In a spatially structured landscape, autocorrelation is an important measure (Legendre 1993),  
264 and has been widely interpreted as corresponding to patch size (Kraan et al. 2009a, b, van Gils  
265 2010, Bijleveld et al. 2016, Oudman et al. 2018) has understood spatial autocorrelation to repre-  
266 sent the patch size of heterogeneous landscapes. This idea is easily illustrated by creating neu-  
267 tral landscapes with varying autocorrelation ranges – landscapes with a high autocorrelation  
268 range have larger patches, and are more predictable. In the wader-mudflat system, the mecha-  
269 nism underlying patch size does not need to be explicitly modelled to implement patch sizes. It  
270 suffices to understand that macrobenthic abundance is controlled by bottom-up processes over  
271 which agents have little influence.

#### 272 Concept: Temporal predictability and change

273 The assumption of resources being independent of foraging agents is plainly ridiculous (see  
274 e.g. van de Koppel et al. 1997, Jefferies et al. 2006, Bijleveld et al. 2015a). However, the pro-

posed system is also far from agent-influenced resource generation (see e.g. le Roux et al. 2018). This leaves depletion as the main effect of agents on their landscape. Depletion then constitutes one important mechanism of temporal change in model landscapes. Agent-independent mechanisms such as seasonal growth and decline, or within-resource interactions (such as competition and facilitation) are the other major mechanism of temporal change in landscapes.

In initial models, agents will not deplete the landscape. However, this would result in the trivial solution of agents remaining stationary at the first point where resources were above some threshold value. Models without depletion must then include some variation in the resource landscape such that agents are forced to move. This can be achieved by having the landscape change either periodically or stochastically. The first approximates changes such as might be driven by seasonality, while the second is more akin to resource redistribution. The first approach allows near perfect prediction of resource values between times  $t$  and  $t+1$ . In the second case, if the ‘redistribution’ is highly variable, i.e., values at a coordinate at a time  $t$  have a wide range of correlation with values at time  $t+1$ , temporal predictability is reduced (as in Botero et al. 2015). The two extreme cases allow the examination of the interacting effects of spatial and temporal predictability, and identification of the more interesting regime for further investigation.

In a model tailored to waders, the situation is compounded by another source of temporal variation: the tidal cycle. This highly periodic phenomenon both gives and takes away: first, water restricts exploitation of parts of the landscape, but also, second, allows waders to use their pressure-sensitive bills (Piersma et al. 1998) to find prey in the waterlogged substrate. This results in an optimal search area around the waterline where the substrate is exposed yet sufficiently wet to allow knots to probe for food. Coastal systems cause further complications – but also open opportunities – when modelling agents, and these are discussed later.

#### **Practice: Modelling spatio-temporal change in landscapes**

Both resource and tidal landscapes may be implemented in continuous space. While implemented in some models (eg. Spiegel et al. 2016, 2017), continuous space creates a mismatch of resolution between simulations and empirical data, which is an important consideration in this project. Since data from benthic sampling can be converted into predicted intake rate rasters with a maximum resolution of 10 m (see method in Bijleveld et al. 2012a, and examples in Oudman et al. 2018), the resource landscape is best modelled as a two-dimensional square grid of side  $n$  cells, a common approach (Nolet and Mooij 2002, van Gils 2010, Getz et al. 2015, Netz 2017). Grid values can be modelled using flexible tools (Sciaini et al. 2018) as Gaussian random fields (Turner and Gardner 2015, Kery and Royle 2019). Working on the logic of infinite extent (Nolet et al. 2006), the grid boundaries are periodic. Landscapes can thus easily be assigned an autocorrelation regime. Grid cells in this landscape are initialised with certain values of resource between 0.0 and 1.0. This allows the subsequent mapping of empirical values using a variety of functions, such as the sigmoidal (Gershenfeld 1999).

The tidal landscape’s elevation is easily modelled as a distance or edge gradient (Etherington et

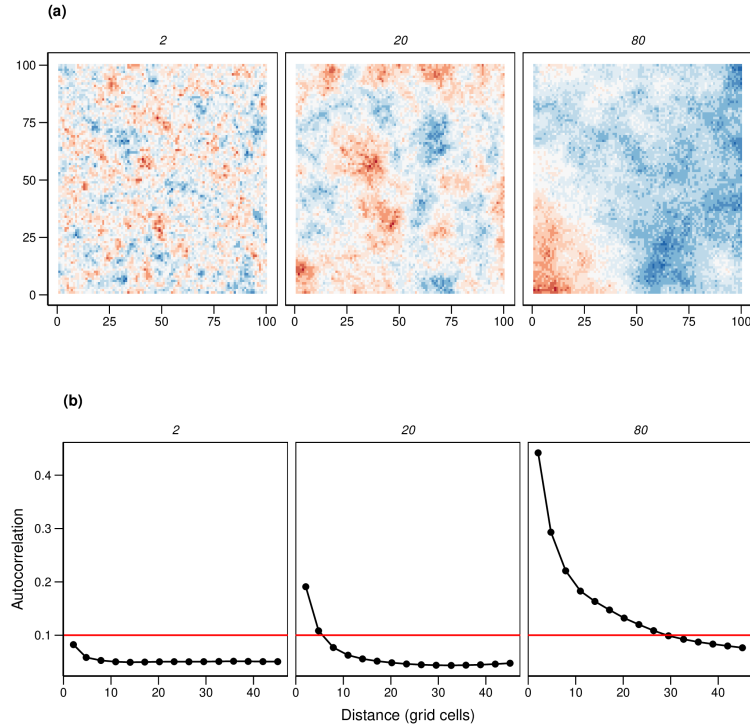


Figure 3: Examples of Gaussian random field neutral landscapes generated in R following methods from Sciaini et al. (2018). **(a)** Landscapes of side 100 cells, with increasing autocorrelation range (numbers above panels). Larger autocorrelation ranges result in smoother transitions between areas of high (blue) and low (red) resources, and thus larger patches. **(b)** Spatial autocorrelation in simulated landscapes; each panel corresponds to the one directly above in **(a)**. Compare with figures in Oudman et al. (2018).

al. 2015). This creates a region of high elevation which is always exposed, approximating islands such as Griend where waders roost. This model will use a circular distance gradient that avoid issues arising from landscape edges. Temporal change in both water level and resource landscapes can initially be considered to be the output of a simple sine function with a wavelength  $R$  (as in Botero et al. 2015): the “relative timescale of environmental change” of each. For water level, the wavelength would be the number of discrete model timesteps contained in one unit of ecological time. Since the tidal cycle (~13 hours off Griend in 2017; *unpublished data*) is a prominent feature, it is intuitive to also consider this a unit of ecological time, with a single non-breeding season comprising some 6 – 8 months (~450 tidal cycles). Each season would then be a unit of evolutionary time. In the case of the resource landscape, the wavelength can be set to vary across a range to mimic either seasonal (renewal each season) or long-term (climatic cycles) dynamics, corresponding very well to Botero et al. 2015.

## 326 Modelling agents

### 327 Concept: Agent Based Models

328 I will implement ABMs (see Section 2.3) first for abstract foragers, and second for foragers simi-  
329 lar to waders. While waders are an ideal system in which to study foraging, they are specialised  
330 upon a small subset of resources and ecological conditions that will constrain more realistic  
331 models. For a general forager, it is important to be able to gain some key information: its posi-  
332 tion, the profitability of its position, and its potential future positions (*why* and *where* to move;  
333 Nathan et al. 2008). An agent will move when its current location cannot sustain it, possibly due  
334 to some metabolic requirement (Barraquand and Benhamou 2008). There is a strong interplay  
335 between *where* to move and *how* to move when agents are capable of more than one movement  
336 mode, such as in birds which can switch from cursorial to volant. While the exact mechanism  
337 may be abstracted, movement carries a cost, and this cost must be taken into account when de-  
338 ciding when and where to move (Charnov 1976). Movement decisions can be made as the result  
339 of explicitly written functions (e.g. Getz et al. 2015), but this entails and often elides implicit  
340 assumptions about the functional response of agents to their environment. This environment  
341 may include other agents, allowing for facilitation by local enhancement (Beauchamp 2013).

### 342 Concept: Agent-resource and agent-agent interactions

343 In the models sketched above I began with the assumption that while especially large  
344 or numerous foragers (~ecosystem engineers) are capable of transforming their re-  
345 source landscapes (Laundré et al. 2001, Jefferies et al. 2006, le Roux et al. 2018),  
346 this cannot be expected for all consumer-resource systems. However, there is evi-  
347 dence from observational studies at small spatial scales (~0.067 km<sup>2</sup>) that medium-sized  
348 foragers can significantly deplete their resources (Guillemette et al. 1996, Jefferies et al. 2006),  
349 and Markedly smaller waders too can deplete resources over small spatio-temporal scales  
350 (Székely and Bamberger 1992, van Gils et al. 2003, Bijleveld et al. 2015a). Thus, in more  
351 realistic models, I will allow foragers to deplete their landscapes. This depletion will replace  
352 the sinusoidal temporal variation I proposed for initial, abstract models (see Section 4.1.3), and  
353 will more realistically approximate seasonal dynamics where resource replenishment occurs  
354 in a single growing period, and further declines are largely due to harvesting.

355 Depletion introduces the prospect of exploitative competition (Keddy 2001), where agents affect  
356 each other by consuming shared resources. Its inclusion in the simplest models has stark eco-  
357 evolutionary consequences – for example, Getz et al. (2015) showed that larger population sizes  
358 (and thus higher competition) resulted in more movement types and at a more rapid rate of  
359 evolution. I propose to take this into account by reducing the intake rate that agents achieve  
360 on a grid cell proportional to the number of agents on the cell. Interference competition is  
361 widely seen in waders (Goss-Custard 1980), yet is also more challenging to include in discrete  
362 time models (Vahl 2006). I will leave this aspect of wader ecology out of the model (but see next  
363 sub-section).



#### 364 **Concept: Modelling interference competition**

365 I intend to supervise a master's student with an interest in evolutionary game theory, and  
366 modelling skills. This master's project will extend the work of Vahl (2006), and take into  
367 account the following: first, that mechanisms can strongly influence the dynamics of games  
368 (van den Berg and Weissing 2015), second, that competition is often state dependent (van  
369 Gils and Piersma 2004), and third, that both direct and indirect competition (Vahl et al. 2005,  
370 Bijleveld et al. 2012b) can have consequences for agent space-use (Vahl et al. 2007). I envision  
371 the following modules for this project: individual based models following Vahl's ideas, with  
372 pairwise interactions determining some contest outcome that translates to fitness. These will  
373 be implemented in an evolutionary system, where successful agents replicate, either with fixed  
374 or flexible population size. Second, some state dependence of behaviour to examine behaviour  
375 – physiology trade-offs. Third, to have the agent decisions as the output of neural networks.  
376 Fourth, implementation in a limited spatial system, such as a two dimensional  $3 \times 3$  grid, or a  
377 single dimensional vector. In this final, more realistic system, movement would be an option,  
378 allowing interesting dynamics between direct competition, state-dependence of behaviour,  
379 and spatial distribution in a game theoretical framework.

#### 380 **Practice: Agent Based Models using Artificial Neural Networks**

381 Agents in ABMs possess attributes, including knowledge of their coordinate position on the grid  
382 ( $x, y$ ) and some proxy of internal state (energy reserves; e.g. van Gils 2010). Other attributes  
383 may comprise the overall phenotype of the agent. For example, Getz et al. (2015, 2016)  
384 draw three parameters that correspond broadly to giving-up value  $\bar{U}$ , competitiveness  $\bar{C}$ , and  
385 sociability  $\bar{S}$  from suitable distributions, and assign them to agents. These values are implastic  
386 through the agent's life, and while a useful starting point, assumes behavioural consistency.  
387 The ANN approach allows for far richer dynamics, where agents assess their environment  
388 (described above) and make a single decision about what move to make in the next time-step.  
389 This environment may include landscape values and/or other agents (see Netz 2017). These  
390 cues are the activations of the agent's ANN nodes, while state variables can be mapped to node  
391 weights and biases. Agent movement is often limited to the Moore neighbourhood of size 1,  
392 i.e., from agent grid position to the eight cells around it in each timestep (Getz et al. 2015, Netz  
393 2017). Movements of unit distance in unit time assume constant speed; clearly unfounded  
394 since real animals such as knots can achieve at least two broad movement speeds by flying or  
395 walking (Bijleveld et al. *unpublished data*). The ANN output sketched above – next grid position –  
396 allows agents to choose their movement distance at each time step. At an ecological scale, this  
397 first allows the investigation of individual consistency in step length, and then an examination  
398 of whether movement types have characteristic step lengths, eg. that are some whole number  
399 multiple of the autocorrelation range. Movement carries a travel cost, which is subtracted from  
400 energy reserves at each time-step.

401 In more complex models, cues of where best to forage need not be equally available to  
402 foraging agents. Knots can sense only very local macrobenthos availability using their

403 pressure sensitive bills (Piersma et al. 1998). At intermediate and local scales, knots  
 404 may use public information from other foragers (Bijleveld et al. 2015b), while it is to be  
 405 assumed that across scales, knots are able to avoid deep water. This creates a cue gradi-  
 406 ent: at very small ranges, agents have much more reliable information than at larger ones,  
 407 where local enhancement due to conspecific presence may play a greater role (Beauchamp  
 408 2013). Thus agents in such models may evolve movement types that trade the cost of  
 409 poor information for the cost of exploitative competition, and vice-versa, all while balanc-  
 410 ing the cost of travel with the intake from the landscape. Evolutionary models require  
 411 that traits are inherited, implying reproduction, and also birth and death. Agent fitness is  
 412 best modelled as some function, possibly sigmoidal, of net intake, i.e., agents do have an  
 413 upper limit to the offspring produced; for example, many sandpipers produce a clutch  
 414 of four eggs (Piersma and Bonan 2019), and this is a realistic upper limit. Agents must  
 415 therefore also have some mechanism approximating death; this can be modelled as en-  
 416 ergy reserves reaching zero, after which the agent dies. Agents must reproduce at some  
 417 time – in systems worldwide, most species have a fixed breeding season, and this can be  
 418 modelled as agents that survive until the next ecological time-step producing offspring. The  
 419 value of energy reserves at which agents decide to reproduce may also be allowed to evolve,  
 420 possibly evolving interesting life-history strategies.

## 421 **Confronting models with data**

422 Models are always wrong, but they do yield insights into real systems. Empirical data on the  
 423 red knot system is collected both from the agents (MacCurdy et al. 2015 in Bijleveld 2015; e.g.  
 424 Bijleveld et al. 2016, Oudman et al. 2018) and their resource landscape (Bijleveld et al. 2012a).  
 425 These data include morphometric measures, as well as movement measures which may be ob-  
 426 tained using a number of tools now available for the processing of animal tracking data (most  
 427 recent review by Joo et al. 2019). Coupled with behavioural scores from aviary experiments  
 428 (currently ongoing at NIOZ; see e.g. Bijleveld et al. 2012b, 2015b), these can be used to cluster  
 429 individuals. These clusters can then be compared with movement types evolved in simulations.  
 430 I aim to use simulations to predict which types should be expected given the resource landscape  
 431 structure experienced in the Wadden Sea by *islandica* red knots, and then to examine how well  
 432 these predictions hold up in the face of data.

433 Individual associations of red knots are not expected to be non-random, consistent with the  
 434 pattern for other waders (Myers 1983, Conklin and Colwell 2008). However, that expectation  
 435 might yet hold for movement types, with assortative association within or between types in dif-  
 436 ferent environmental regimes (Spiegel et al. 2017). The strength and nature of associations  
 437 could be predicted from simulations, and then tested using extensive tracking data.

## Part V.

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