

Many Ways to Tie a Knot

An Introductory Essay and PhD Plan 2018 – 2022

Pratik R. Gupte

Contents

1 Summary	4
2 Introduction	5
Animal movement	5
Movement as personality	6
Modelling movement	7
3 About this project	9
Abstract models	9
Wader models and data	10
4 Towards movement models	12
Modelling landscapes	12
Concept: Spatial predictability	12
Concept: Temporal predictability and change	12
Practice: Modelling spatio-temporal change in landscapes	13
Modelling agents	14
Concept: Agent Based Models	14
Concept: Agent-resource and agent-agent interactions	14
Concept: Modelling interference competition	15
Practice: Agent Based Models using Artificial Neural Networks	15
5 Confronting models with data	17
References	18

Introductory Essay

© **Pratik R Gupte** Modelling Adaptive Response Mechanisms Group, Groningen Institute for Evolutionary Life Sciences, University of Groningen

Bijleveld Lab, Department of Coastal Systems, Royal Netherlands Institute for Sea Research

Contact information Groningen Institute for Evolutionary Life Sciences University of Groningen
Nijenborgh 7-5172.0583 9747 AG Groningen Netherlands p.r.gupte@rug.nl

Supervisors

FJ Weissing, AI Bijleveld, AGG Groothuis, T Piersma

Promoters

FJ Weissing, AGG Groothuis

Funding

1 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. Section four, A PhD plan 2018 – 2022 gives a brief overview of how I propose to invest my time towards those same goals.

2 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. Scantlebury et al. (2014); Williams et al. (2004)).

Despite advances in empirical methods, animal movement studies are still subject to limitations of scale. Among these are emergent group-size effects (Tunstrøm et al. (2013)), which are difficult to quantify empirically notwithstanding recent advances (Dhanjal-Adams et al. (2018); Handegard et al. (2012); Kays et al. (2015); Strandburg-Peshkin et al. (2015)); a distinct problem when animal grouping is near-universal (Krause and Ruxton (2002)). The impracticality of research across scales of organisation (eg. physiology to population) has similarly confined most movement studies to answering at most one MEP question at a time (but see Curtin et al. (2018); Fryxell et al. (2008); Strandburg-Peshkin et al. (2015)). This is linked to the choice of study system, which among vertebrates has been restricted by the technical difficulty in hewing to the 3% body-mass rule (Naef-Daenzer et al. (2001)). Finally, animal movement has been captured by the movement ecol-

ogy paradigm because of the difficulty in studying movement at evolutionary timescales. Here, simulation models can help to shine “the light of ecology” on evolutionary biology (Grant and Grant (2008)), by uncovering the importance of individual interactions for emergent phenomena (eg. Hildenbrandt et al. (2010); Tunstrøm et al. (2013)), the surprising extrinsic drivers of movement mode (Guttal et al. (2012)), the evolutionary effects of higher trophic levels (Ioannou et al. (2012)), and the evolution of movement rules (family=Jager et al. (2011); Netz (2017)).

Movement as personality

The work cited above may be safely claimed to make at least one of two assumptions; the first is the “tyranny of the golden mean” (Bennet et al 1987 in Martin et al 1987). The second is the assumption of optimality (Fretwell and Lucas (1970)) entailing infinite behavioural plasticity. Neither of these assumptions is very well founded. While the first is methodologically convenient, theory from Darwin (1859) onwards has recognised it as untrue; models find that differences among individuals can have population level consequences (eg. Pruitt and Riechert (2011)). The second assumption is squarely challenged by the study of consistent individual differences in behaviour. The field of animal personality and behavioural syndromes (Sih et al. (2004a), Sih et al. (2004b)) and its consequences (Dingemanse and Réale (2005)) seeks to quantify between and within individual consistency in behavioural responses “through time or across situations”. Variation along two or more axes of personality (Réale et al. (2007)) may be correlated into a ‘behavioural type’ (examples in Bell et al. (2009); Sih and Bell (2008)); for example, ‘boldness’ and ‘aggression’ form two of the major axes of personality, and are often quantified together as a syndrome (Carter et al. (2013)).

Behavioural ecology has only slowly come to terms with the idea that such individual differences within populations could be advantageous (Wilson (1998)). Individual differences have been explained in terms of mechanisms engaged during development (Groothuis and Trillmich (2011); Wolf and Weissing (2010)), trade-offs in life-history (Wolf et al. (2007a), Wolf et al. (2007b)), and the feedback loops created between individual state and behaviour (Wolf and Weissing (2010)) as prominent proximate causes. Evolutionary explanations of these differences and especially their consistency have remained elusive because the default expectation has been that plasticity is more adaptive (Wilson (1998)). Wolf and Weissing (2010) have since shown that consistent behavioural types may yet achieve comparable fitness outcomes if selection is frequency-dependent (Maynard Smith (1982)), and rarer types have a selective advantage. Spatio-temporal variation, a ubiquitous feature of environments (Levin (1992)), may have a major role to play when it hosts a population 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), Wolf and Weissing (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), Wolf and Weissing (2012)), and it is unsurprising that populations might have evolved behavioural polymorphisms for movement, or movement types (Getz et al. (2015); Netz (2017); Wolf and Weissing (2010)). Indeed, movement types are inherent predictions of previous theoretical work that did not necessarily consider movement as its central theme (eg. Lima and Zollner (1996); Watson and Miller (1971)). 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 (Clobert et al. (2009); (???); Duckworth and Badyaev (2007); 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 (Getz et al. (2015); family=Jager et al. (2011); 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), Wolf et al. (2007b)) and fitness outcomes in landscapes that vary in spatial predictability can have consequences at the population level – from social networks to community composition.

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 (Conklin and Colwell (2008); Myers (1983)), and as symbols of traditional landscapes (Colwell (2018)). Waders (hereafter referring to scolopacids) eking out their precarious existence (Fitzpatrick and Senner (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 (family=Gils (2010); family=Gils et al. (2003)), large spatio-temporal scales such as migration (Buehler et al. (2006); Piersma (2011)), proximate causes for large-scale phenomena (Lank et al. (2003); Ruthrauff et al. (2013), Ruthrauff et al. (2018); Ydenberg et al. (2004)), and ultimate causes for small-scale phenomena (family=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), Bijleveld et al. (2015b), Bijleveld et al. (2012b)), 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), Grimm et al. (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 (Getz et al. (2015), Getz et al. (2016); family=Gils (2010); Spiegel et al. (2013), Spiegel et al. (2017) 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)).

3 About this project

144

In this section, I outline my approaches to examine the evolution of movement types (sensu Getz et al. (2015); Wolf and Weissing (2010)) 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. (2014), Bijleveld et al. (2015a), Bijleveld et al. (2015b), Bijleveld et al. (2012a); 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.

145
146
147
148
149
150
151
152
153
154
155

Abstract models

156

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:

157
158
159
160

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

161
162
163
164
165
166
167
168
169
170
171
172
173
174
175
176
177
178
179

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

- a. How does landscape structure change over ecological and evolutionary time? In this scenario, I fall back upon the red knot system as a guide, that foragers are not always present on the landscape and the resource has time to regenerate. Such seasonal systems are widespread making this a reasonable scenario. I will investigate the development of landscape patterns (such as the autocorrelation range, or patch size; see Legendre 1993) when agents are themselves evolving upon such landscapes.
- b. How does the number and phenotype of movement types change over evolutionary time? Agents' consumption rates (set to be identical) could lead to different rates of landscape change in the scenario outlined above. Foragers would then evolve to maximise fitness in both space and time. As landscapes traverse the axis of patch size (autocorrelation range, or predictability) due to agent foraging, the spatial conditions that evolved types in (1) might recur multiple times. This should allow the investigation of whether there is a change in selection pressures on movement types, the time-scale at which it occurs, and whether it is mediated by agents' effect on the landscape.
- c. Do critical transitions occur in the number or profitability of movement types? As agent populations evolve movement types rather than bet-hedged phenotypes, these types may yet show sufficient flexibility to behaviourally buffer against decreasing profitability as the landscape shifts to a regime to which they are poorly adapted. This change may occur within individuals at ecological scales (as resources deplete or change over a season), and at the population level (as landscapes change over evolutionary time). Such systems, where the response (here, movement, or fitness) is initially poorly responsive to the driver (landscape structure, such as patch size), may then undergo abrupt transitions (Scheffer 2009) to an alternative stable state. Behavioural changes relating to movement strategy occur in wader systems (e.g. Oudman et al 2019), but the process is not fully understood. I will look into whether changes in such systems can then be characterised as critical transitions. The same approach can be applied to the landscape, to study whether landscapes catastrophically shift to another state (as in van de Koppel et al 1997; Jefferies et al 2006).

Wader models and data

Following the steps above, I will modify the models to simulate the red knot system. Important conceptual changes include the addition of regular environmental change in the form of the tidal cycle. This feature first limits resource landscape availability to agents. Second, it forces agent movement, further constraining the range within which agent movement types can specialise. For example, a very efficient movement type in a model elaborated above (1) would be to remain largely sedentary. This is not an option in tidal systems as most waders cannot swim. Important

practical changes will be the parameterisation of the model following empirical data or best estimates on resource landscape structure and red knot physiology (body size, energy requirements, perception range).	223 224 225
Finally, I will turn to the empirical red knot tracking data and the benthic sampling data to investigate whether the models sketched above correspond to reality. The following questions suggest themselves.	226 227 228
1. Do red knots show movement types that can be identified from a combination of data sources? This question entails cooperation with my co-PhD student. Using scores from behavioural assays, state variables such as gizzard mass or body mass, and movement variables such as patch-switching or residence time, I will aim to determine whether knots evolved in models occupy comparable parameter spaces to real birds.	229 230 231 232 233
2. Do red knots show assortative association based on movement type? Here, I investigate expectations from Spiegel et al (2017), that association and the strength of social networks is strongly influenced by personality and the clumped-ness of the landscape. This question is suitable to both an experimental and field tracking approach.	234 235 236 237

4 Towards movement models

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

Modelling landscapes

Concept: Spatial predictability

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

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

Concept: Temporal predictability and change

The assumption of resources being independent of foraging agents is plainly ridiculous (see e.g. Bijleveld et al. (2015a); Jefferies et al. (2006); family=Koppel et al. (1997)). However, the proposed system is also far from agent-influenced resource generation (see e.g. family=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 an avoidable 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 (Getz et al. (2015); family=Gills (2010); Netz (2017); Nolet and Mooij (2002)). Grid values can be modelled using flexible tools (Sciaini et al. (2018)) as Gaussian random fields (Kery and Royle (2019); Turner and Gardner (2015)). 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)).

insert figure here

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

Insert figure here

Modelling agents

Concept: Agent Based Models

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

Concept: Agent-resource and agent-agent interactions

In the models sketched above I began with the assumption that while especially large or numerous foragers (~ecosystem engineers) are capable of transforming their resource landscapes (Jefferies et al. (2006); Laundré et al. (2001); family=Roux et al. (2018)), this cannot be expected for all consumer-resource systems. However, there is evidence from observational studies at small spatial scales (~0.067 km²) that medium-sized foragers can significantly deplete their resources (Guillemette et al. (1996); Jefferies et al. (2006)), and Markedly smaller waders too can deplete resources over small spatio-temporal scales (Bijleveld et al. (2015a); family=Gils et al. (2003); Székely and Bamberger (1992)). Thus, in more realistic models, I will allow foragers to deplete their landscapes. This depletion will replace the sinusoidal temporal variation I proposed for initial, abstract models (see Section 4.1.3), and will more realistically approximate seasonal dynamics where resource replenishment occurs in a single growing period, and further declines are largely due to harvesting.

Depletion introduces the prospect of exploitative competition (Keddy (2001)), where agents affect each other by consuming shared resources. Its inclusion in the simplest models has stark evolutionary consequences – for example, Getz et al (2015) showed that larger population sizes

(and thus higher competition) resulted in more movement types and at a more rapid rate of evolution. I propose to take this into account by reducing the intake rate that agents achieve on a grid cell proportional to the number of agents on the cell. Interference competition is widely seen in waders (Goss-Custard (1980)), yet is also more challenging to include in discrete time models (Vahl (2006)). I will leave this aspect of wader ecology out of the model (but see next sub-section).

Concept: Modelling interference competition

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

Practice: Agent Based Models using Artificial Neural Networks

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

In more complex models, cues of where best to forage need not be equally available to foraging

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

5 Confronting models with data

414

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

415
416
417
418
419
420
421
422
423
424
425

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

426
427
428
429
430

References

- Austin D, Bowen WD, McMillan JI (2004) Intraspecific variation in movement patterns: Modeling individual behaviour in a large marine predator. *Oikos* 105:15–30. doi: 10.1111/j.0030-1299.1999.12730.x
- Bäck T (1996) *Evolutionary Algorithms in Theory and Practice: Evolution Strategies, Evolutionary Programming, Genetic Algorithms*. Oxford University Press
- Barraquand F, Benhamou S (2008) Animal Movements in Heterogeneous Landscapes: Identifying Profitable Places and Homogeneous Movement Bouts. *Ecology* 89:3336–3348. doi: 10.1890/08-0162.1
- Bartumeus F, Levin SA (2008) Fractal reorientation clocks: Linking animal behavior to statistical patterns of search. *Proceedings of the National Academy of Sciences of the United States of America* 105:19072–7. doi: 10.1073/pnas.0801926105
- Beauchamp G (2013) *Social Predation: How Group Living Benefits Predators and Prey*. Elsevier
- Bell AM, Hankison SJ, Laskowski KL (2009) The repeatability of behaviour: A meta-analysis. *Animal Behaviour* 77:771–783. doi: 10.1016/J.ANBEHAV.2008.12.022
- Benhamou S (1992) Efficiency of area-concentrated searching behaviour in a continuous patchy environment. *Journal of Theoretical Biology* 159:67–81. doi: 10.1016/S0022-5193(05)80768-4
- Bijleveld AI (2015) *Untying the knot: Mechanistically understanding the interactions between social foragers and their prey*. University of Groningen
- Bijleveld AI, Egas M, Gils JAV, Piersma T (2010) Beyond the information centre hypothesis: Communal roosting for information on food, predators, travel companions and mates? *Oikos* 119:277–285. doi: 10.1111/j.1600-0706.2009.17892.x
- Bijleveld AI, family=Gils p given=Jan A., family=Meer p der given=Jaap et al (2012a) Designing a benthic monitoring programme with multiple conflicting objectives. *Methods in Ecology and Evolution* 3:526–536. doi: 10.1111/j.2041-210X.2012.00192.x
- Bijleveld AI, family=Gils p given=Jan A., Jouta J, Piersma T (2015a) Benefits of foraging in small groups: An experimental study on public information use in red knots *Calidris Canutus*. *Behavioural Processes* 117:74–81. doi: 10.1016/j.beproc.2014.09.003
- Bijleveld AI, Folmer EO, Piersma T (2012b) Experimental evidence for cryptic interference among socially foraging shorebirds. *Behav Ecol* 23:806–814. doi: 10.1093/beheco/ars034
- Bijleveld AI, MacCurdy RB, Chan Y-C et al (2016) Understanding spatial distributions: Negative density-dependence in prey causes predators to trade-off prey quantity with quality. *Proceedings*

of the Royal Society B: Biological Sciences 283:20151557. doi: 10.1098/rspb.2015.1557	463
Bijleveld AI, Massourakis, Georgina, van der Marel, Annemarie et al (2014) Personality drives physiological adjustments and is not related to survival. <i>Proceedings of the Royal Society B: Biological Sciences</i> 281:20133135. doi: 10.1098/rspb.2013.3135	464 465 466
Bijleveld AI, Twietmeyer S, Piechocki J et al (2015b) Natural selection by pulsed predation: Survival of the thickest. <i>Ecology</i> 96:1943–1956. doi: 10.1890/14-1845.1	467 468
Blois JL, Williams JW, Fitzpatrick MC et al (2013) Space can substitute for time in predicting climate-change effects on biodiversity. <i>PNAS</i> 110:9374–9379. doi: 10.1073/pnas.1220228110	469 470
Boere GC, Stroud D (2006) The flyway concept: What it is and what it isn't. In: <i>Waterbirds Around the World: A Global Overview of the Conservation, Management and Research of the World's Waterbird Flyways</i> . Scottish Natural Heritage, Edinburgh, UK, pp 40–47	471 472 473
Botero CA, Weissing FJ, Wright J, Rubenstein DR (2015) Evolutionary tipping points in the capacity to adapt to environmental change. <i>PNAS</i> 112:184–189. doi: 10.1073/pnas.1408589111	474 475
Buehler DM, Baker AJ, Piersma T (2006) Reconstructing palaeoflyways of the late Pleistocene and early Holocene Red Knot <i>Calidris canutus</i> . 15	476 477
Carter AJ, Feeney WE, Marshall HH et al (2013) Animal personality: What are behavioural ecologists measuring? <i>Biological Reviews</i> 88:465–475. doi: 10.1111/brv.12007	478 479
Charnov E (1976) <i>Optimal foraging: The marginal value theorem</i>	480
Clobert J, Galliard J-FL, Cote J et al (2009) Informed dispersal, heterogeneity in animal dispersal syndromes and the dynamics of spatially structured populations. <i>Ecology Letters</i> 12:197–209. doi: 10.1111/j.1461-0248.2008.01267.x	481 482 483
Colwell M (2018) <i>Curlew moon</i> , 1st edn. Harper Collins	484
Conklin JR, Colwell MA (2008) Individual associations in a wintering shorebird population: Do Dunlin have friends? <i>Journal of Field Ornithology</i> 79:32–40. doi: 10.1111/j.1557-9263.2008.00143.x	485 486
Cooke SJ, Hinch SG, Wikelski M et al (2004) Biotelemetry: A mechanistic approach to ecology. <i>Trends in Ecology & Evolution</i> 19:334–343. doi: 10.1016/j.tree.2004.04.003	487 488
Curtin NA, Bartlam-Brooks HLA, Hubel TY et al (2018) Remarkable muscles, remarkable locomotion in desert-dwelling wildebeest. <i>Nature</i> 563:393–396. doi: 10.1038/s41586-018-0602-4	489 490
Darwin C (1859) <i>On the Origin of Species by means of natural selection</i> . John Murray, London	491
Darwin C, Wallace AR (1858) On the Tendency of Species to form Varieties; and on the Perpetuation of Varieties and Species by Natural Means of Selection. <i>Journal of the Proceedings of the Linnean Society of London Zoology</i> 3:45–62. doi: 10.1111/j.1096-3642.1858.tb02500.x	492 493 494
DeAngelis DL (2018) <i>Individual-based models and approaches in ecology: Populations, communities and ecosystems</i> . CRC Press	495 496
DeAngelis DL, Mooij WM (2005) Individual-based modeling of ecological and evolutionary processes. <i>Annual Review of Ecology, Evolution, and Systematics</i> 36:147–168. doi: 10.1146/an-	497 498

nurev.ecolsys.36.102003.152644

Dhanjal-Adams KL, Bauer S, Emmenegger T et al (2018) Spatiotemporal Group Dynamics in a Long-Distance Migratory Bird. *Current Biology* 28:2824–2830.e3. doi: 10.1016/j.cub.2018.06.054

Dingemanse NJ, Réale D (2005) Natural selection and animal personality. *Behaviour* 142:1159–1184. doi: 10.1163/156853905774539445

Duckworth RA, Badyaev AV (2007) Coupling of dispersal and aggression facilitates the rapid range expansion of a passerine bird. *Proceedings of the National Academy of Sciences* 104:15017–15022

Duckworth RA, Sockman KW (2012) Proximate mechanisms of behavioural inflexibility: Implications for the evolution of personality traits. *Functional Ecology* 26:559–566. doi: 10.1111/j.1365-2435.2012.01966.x

Enquist M, Ghirlanda S (2013) Neural networks and animal behavior. Princeton University Press

Etherington TR, Holland EP, O'Sullivan D (2015) NLMpy: A python software package for the creation of neutral landscape models within a general numerical framework. *Methods in Ecology and Evolution* 6:164–168. doi: 10.1111/2041-210X.12308

family=Berg p den given=Pieter, Weissing FJ (2015) Evolutionary Game Theory and Personality. In: *Evolutionary Perspectives on Social Psychology*. Springer, Cham, pp 451–463

family=Gils p given=Jan A. (2010) State-dependent Bayesian foraging on spatially autocorrelated food distributions. *Oikos* 119:237–244. doi: 10.1111/j.1600-0706.2009.17497.x

family=Gils p given=Jan A., Piersma T (2004) Digestively constrained predators evade the cost of interference competition. *Journal of Animal Ecology* 73:386–398. doi: 10.1111/j.0021-8790.2004.00812.x

family=Gils p given=Jan A., Schenk IW, Bos O, Piersma T (2003) Incompletely Informed Shorebirds That Face a Digestive Constraint Maximize Net Energy Gain When Exploiting Patches. *The American Naturalist* 161:777–793. doi: 10.1086/374205

family=Gils p given=Jan A., Spaans B, Dekinga A, Piersma T (2006) Foraging in a tidally structured environment by red knots (*Calidris Canutus*): Ideal, but not free. *Ecology* 87:1189–1202. doi: 10.1890/0012-9658(2006)87[1189:FIATSE]2.0.CO;2

family=Jager p given=Monique, Weissing FJ, Herman PMJ et al (2011) Lévy Walks Evolve Through Interaction Between Movement and Environmental Complexity. *Science* 332:1551–1553. doi: 10.1126/science.1201187

family=Koppel p de given=Johan, Rietkerk M, Weissing FJ (1997) Catastrophic vegetation shifts and soil degradation in terrestrial grazing systems. *Trends in Ecology & Evolution* 12:352–356. doi: 10.1016/S0169-5347(97)01133-6

family=Roux p given=Elizabeth, Kerley GIH, Crooms J (2018) Megaherbivores Modify Trophic Cascades Triggered by Fear of Predation in an African Savanna Ecosystem. *Current Biology* 28:2493–2499.e3. doi: 10.1016/j.cub.2018.05.088

Fitzpatrick JW, Senner NR (2018) Shorebirds, the World's Greatest Travelers, Face Extinction. *The*

New York Times: Opinion	536
Fretwell SD, Lucas HL (1970) On territorial behavior and other factors influencing habitat distribution in birds. <i>Acta Biotheoretica</i> 19:16–36	537 538
Fryxell JM, Hazell M, Börger L et al (2008) Multiple movement modes by large herbivores at multiple spatiotemporal scales. <i>Proceedings of the National Academy of Sciences of the United States of America</i> 105:19114–9. doi: 10.1073/pnas.0801737105	539 540 541
Gershenfeld NA (1999) <i>The nature of mathematical modeling</i> . Cambridge University Press	542
Getz WM, Salter R, Lyons AJ, Sippl-Swezey N (2015) Panmictic and Clonal Evolution on a Single Patchy Resource Produces Polymorphic Foraging Guilds. <i>PLOS ONE</i> 10:e0133732–e0133732. doi: 10.1371/journal.pone.0133732	543 544 545
Getz WM, Salter R, Seidel DP, family=Hooft p given=Pim (2016) Sympatric speciation in structure-less environments. <i>BMC Evolutionary Biology</i> 16:50–50. doi: 10.1186/s12862-016-0617-0	546 547
Gill RE, Lee TT, David C. D et al (2009) Extreme endurance flights by landbirds crossing the Pacific Ocean: Ecological corridor rather than barrier? <i>Proceedings of the Royal Society B: Biological Sciences</i> 276:447–457. doi: 10.1098/rspb.2008.1142	548 549 550
Goss-Custard JD (1980) Competition for food and interference among waders. <i>Ardea</i> 55:31–53. doi: 10.5253/arde.v68.p31	551 552
Grant PR, Grant BR (2008) <i>How and why species multiply: The radiation of darwin's finches</i> . Princeton University Press	553 554
Grimm V, Berger U, Bastiansen F et al (2006) A standard protocol for describing individual-based and agent-based models. <i>Ecological Modelling</i> 198:115–126. doi: 10.1016/j.ecolmodel.2006.04.023	555 556
Grimm V, Berger U, DeAngelis DL et al (2010) The ODD protocol: A review and first update. <i>Ecological Modelling</i> 221:2760–2768. doi: 10.1016/J.ECOLMODEL.2010.08.019	557 558
Groothuis TGG, Trillmich F (2011) Unfolding personalities: The importance of studying ontogeny. <i>Developmental Psychobiology</i> 53:641–655. doi: 10.1002/dev.20574	559 560
Guillemette M, Himmelman JH, Reed A (1996) Availability and consumption of food by common eiders wintering in the Gulf of St. Lawrence: Evidence of prey depletion. <i>Can J Zool</i> 74:32–38. doi: 10.1139/z96-005	561 562 563
Guttal V, Romanczuk P, Simpson SJ et al (2012) Cannibalism can drive the evolution of behavioural phase polyphenism in locusts. <i>Ecology Letters</i> 15:1158–1166. doi: 10.1111/j.1461-0248.2012.01840.x	564 565 566
Hamilton WD (1971) Geometry for the selfish herd. <i>Journal of theoretical Biology</i> 31:295–311	567
Handegard NO, Boswell KM, Ioannou CC et al (2012) The Dynamics of Coordinated Group Hunting and Collective Information Transfer among Schooling Prey. <i>Current Biology</i> 22:1213–1217. doi: 10.1016/j.cub.2012.04.050	568 569 570
Hildenbrandt H, Carere C, Hemelrijk C (2010) Self-organized aerial displays of thousands of star-	571

lings: A model. *Behavioral Ecology* 21:1349–1359. doi: 10.1093/beheco/arq149

Hirota M, Holmgren M, Nes EHV, Scheffer M (2011) Global Resilience of Tropical Forest and Savanna to Critical Transitions. *Science* 334:232–235. doi: 10.1126/science.1210657

Holyoak M, Casagrandi R, Nathan R et al (2008) Trends and missing parts in the study of movement ecology. *Proceedings of the National Academy of Sciences of the United States of America* 105:19060–5. doi: 10.1073/pnas.0800483105

Huete A, Didan K, Miura H et al (2002) Overview of the radiometric and biophysical performance of the MODIS vegetation indices. *Remote Sens Environ* 83:195–213

Hussey NE, Kessel ST, Aarestrup K et al (2015) Aquatic animal telemetry: A panoramic window into the underwater world. *Science* 348:1255642–1255642. doi: 10.1126/science.1255642

Huston M, DeAngelis D, Post W (1988) New Computer Models Unify Ecological Theory. *BioScience* 38:682–691. doi: 10.2307/1310870

Ioannou CC, Guttal V, Couzin ID (2012) Predatory fish select for coordinated collective motion in virtual prey. *Science* 337:1212–1215

IPCC (2018) Summary for Policymakers. In: Global warming of 1.5°C. An IPCC Special Report on the impacts of global warming of 1.5°C above pre-industrial levels and related global greenhouse gas emission pathways, in the context of strengthening the global response to the threat of climate change, sustainable development, and efforts to eradicate poverty. World Meteorological Organisation, Geneva

Jefferies RL, Jano AP, Abraham KF (2006) A biotic agent promotes large-scale catastrophic change in the coastal marshes of Hudson Bay. *Journal of Ecology* 94:234–242. doi: 10.1111/j.1365-2745.2005.01086.x

Joo R, Boone ME, Clay TA et al (2019) Navigating through the R packages for movement

Kays R, Crofoot MC, Jetz W, Wikelski M (2015) Terrestrial animal tracking as an eye on life and planet. *Science* 348:aaa2478. doi: 10.1126/science.aaa2478

Keddy PA (2001) *Competition*, 2nd edn. Springer Netherlands

Kery M, Royle JA (2019) *Applied hierarchical modeling in ecology: Analysis of distribution, abundance and species richness in R and BUGS: Dynamic and advanced models*. Academic Press

Klaassen RHG, Nolet BA, Bankert D (2006) Movement of Foraging Tundra Swans Explained by Spatial Pattern in Cryptic Food Densities. *Ecology* 87:2244–2254. doi: 10.1890/0012-9658(2006)87[2244:MOFTSE]2.0.CO;2

Kraan C, family=Meer p der given=Jaap, Dekinga A, Piersma T (2009a) Patchiness of macrobenthic invertebrates in homogenized intertidal habitats: Hidden spatial structure at a landscape scale. *Marine Ecology Progress Series* 383:211–224. doi: 10.3354/meps07994

Kraan C, Gils JAV, Spaans B et al (2009b) Landscape-scale experiment demonstrates that Wadden Sea intertidal flats are used to capacity by molluscivore migrant shorebirds. *Journal of Animal*

Ecology 78:1259–1268. doi: 10.1111/j.1365-2656.2009.01564.x	608
Krause J, Ruxton GD (2002) <i>Living in groups</i> . Oxford University Press	609
Lank DB, Butler RW, Ireland J, Ydenberg RC (2003) Effects of predation danger on migration strategies of sandpipers. <i>Oikos</i> 103:303–319. doi: 10.1034/j.1600-0706.2003.12314.x	610 611
Laundré JW, Hernández L, Altendorf KB (2001) Wolves, elk, and bison: Reestablishing the “landscape of fear” in Yellowstone National Park, U.S.A. <i>Can J Zool</i> 79:1401–1409. doi: 10.1139/z01-094	612 613
Leclerc M, Vander Wal E, Zedrosser A et al (2016) Quantifying consistent individual differences in habitat selection. <i>Oecologia</i> 180:697–705. doi: 10.1007/s00442-015-3500-6	614 615
Legendre P (1993) Spatial Autocorrelation: Trouble or New Paradigm? <i>Ecology</i> 74:1659–1673. doi: 10.2307/1939924	616 617
Levin SA (1992) The Problem of Pattern and Scale in Ecology: The Robert H. MacArthur Award Lecture. <i>Ecology</i> 73:1943–1967. doi: 10.2307/1941447	618 619
Lima SL, Zollner PA (1996) Anti-predatory vigilance and the limits to collective detection: Visual and spatial separation between foragers. <i>Behav Ecol Sociobiol</i> 38:355–363. doi: 10.1007/s002650050252	620 621 622
MacArthur RH, Wilson EO (2001) <i>The Theory of Island Biogeography</i> . Princeton University Press	623
MacCurdy R, Bijleveld A, Gabrielson R et al (2015) Automatic, intensive wildlife radiotracking. In: <i>Untying the knot</i> . p 17	624 625
Mathot KJ, Dekinga A, Piersma T (2017) An experimental test of stateBehaviour feedbacks: Gizzard mass and foraging behaviour in red knots. <i>Functional Ecology</i> 31:1111–1121. doi: 10.1111/1365-2435.12827	626 627 628
Maynard Smith J (1982) <i>Evolution and the theory of games</i> . Cambridge University Press	629
Myers JP (1983) Space, time and the pattern of individual associations in a group-living species: Sanderlings have no friends. <i>Behav Ecol Sociobiol</i> 12:129–134. doi: 10.1007/BF00343203	630 631
Naef-Daenzer B, Widmer F, Nuber M (2001) A test for effects of radio-tagging on survival and movements of small birds. <i>Avian Science</i> 1:15–23	632 633
Nathan R (2008) An emerging movement ecology paradigm. <i>Proc Natl Acad Sci</i> 105:19050–19051. doi: 10.1073/pnas.0808918105	634 635
Nathan R, Getz WM, Revilla E et al (2008) A movement ecology paradigm for unifying organismal movement research. <i>PNAS</i> 105:19052–19059. doi: 10.1073/pnas.0800375105	636 637
Netz C (2017) <i>A neural-network model for predator-prey coevolution</i> . Master, Faculty of Science and Engineering	638 639
Nolet BA, Klaassen RHG, Mooij WM (2006) The use of a flexible patch leaving rule under exploitative competition: A field test with swans. <i>Oikos</i> 112:342–352. doi: 10.1111/j.0030-1299.2006.13460.x	640 641
Nolet BA, Mooij WM (2002) Search paths of swans foraging on spatially autocorrelated tubers. <i>Jour-</i>	642

- nal of Animal Ecology 71:451–462. doi: 10.1046/j.1365-2656.2002.00610.x
- Oudman T, Piersma T, Ahmedou Salem MV et al (2018) Resource landscapes explain contrasting patterns of aggregation and site fidelity by red knots at two wintering sites. *Movement Ecology* 6:24–24. doi: 10.1186/s40462-018-0142-4
- Piersma T (2011) Flyway evolution is too fast to be explained by the modern synthesis: Proposals for an “extended” evolutionary research agenda. *J Ornithol* 152:151–159. doi: 10.1007/s10336-011-0716-z
- Piersma T, Bonan A (2019) Sandpipers, Snipes, Phalaropes (Scolopacidae). In: *Handbook of the Birds of the World Alive*. Lynx Edicions, Barcelona
- Piersma T, family=Aelst p given=Renée, Kurk K et al (1998) A new pressure sensory mechanism for prey detection in birds: The use of principles of seabed dynamics? *Proceedings of the Royal Society of London Series B: Biological Sciences* 265:1377–1383. doi: 10.1098/rspb.1998.0445
- Piersma T, Lindström Å (2004) Migrating shorebirds as integrative sentinels of global environmental change. *Ibis* 146:61–69. doi: 10.1111/j.1474-919X.2004.00329.x
- Pruitt JN, Riechert SE (2011) How within-group behavioural variation and task efficiency enhance fitness in a social group. *Proceedings of the Royal Society B: Biological Sciences* 278:1209–1215. doi: 10.1098/rspb.2010.1700
- Réale D, Reader SM, Sol D et al (2007) Integrating animal temperament within ecology and evolution. *Biological Reviews* 82:291–318. doi: 10.1111/j.1469-185X.2007.00010.x
- Ruthrauff DR, Dekinga A, Gill RE, Piersma T (2018) Energetic solutions of Rock Sandpipers to harsh winter conditions rely on prey quality. *Ibis* 160:397–412. doi: 10.1111/ibi.12534
- Ruthrauff DR, GILL RE, TIBBITTS TL (2013) Coping with the Cold: An Ecological Context for the Abundance and Distribution of Rock Sandpipers during Winter in Upper Cook Inlet, Alaska. *Arctic* 66:269–278
- Scantlebury DM, Mills MGL, Wilson RP et al (2014) Flexible energetics of cheetah hunting strategies provide resistance against kleptoparasitism. *Science* 346:79–81. doi: 10.1126/science.1256424
- Sciaini M, Fritsch M, Scherer C, Simpkins CE (2018) NLMR and landscapetools: An integrated environment for simulating and modifying neutral landscape models in R. *Methods in Ecology and Evolution* 0: doi: 10.1111/2041-210X.13076
- Sih A, Bell A, Johnson J (2004a) Behavioral syndromes: An ecological and evolutionary overview. *Trends in Ecology & Evolution* 19:372–378. doi: 10.1016/j.tree.2004.04.009
- Sih A, Bell AM (2008) Insights for behavioral ecology from behavioral syndromes. In: *Advances in the Study of Behavior*. Academic Press, pp 227–281
- Sih A, Bell AM, Johnson JC, Ziemba RE (2004b) Behavioral Syndromes: An Integrative Overview. *The Quarterly Review of Biology* 79:241–277. doi: 10.1086/422893
- Sih A, Cote J, Evans M et al (2012) Ecological implications of behavioural syndromes. *Ecology Letters* 15:278–289. doi: 10.1111/j.1461-0248.2011.01731.x
- Spiegel O, Getz WM, Nathan R (2013) Factors influencing foraging search efficiency: Why do

scarce lappet-faced vultures outperform ubiquitous white-backed vultures? The American naturalist 181:E102–15. doi: 10.1086/670009	681 682
Spiegel O, Leu ST, Bull CM, Sih A (2017) What's your move? Movement as a link between personality and spatial dynamics in animal populations. Ecology Letters 20:3–18. doi: 10.1111/ele.12708	683 684
Staver AC, Archibald S, Levin SA (2011) The Global Extent and Determinants of Savanna and Forest as Alternative Biome States. Science 334:230–232. doi: 10.1126/science.1210465	685 686
Strandburg-Peshkin A, Farine DR, Couzin ID, Crofoot MC (2015) GROUP DECISIONS. Shared decision-making drives collective movement in wild baboons. Science (New York, NY) 348:1358–61. doi: 10.1126/science.aaa5099	687 688 689
Sutherland WJ (1996) From individual behaviour to population ecology. Oxford University Press	690
Székely T, Bamberger Z (1992) Predation of Waders (Charadrii) on Prey Populations: An Exclosure Experiment. Journal of Animal Ecology 61:447–456. doi: 10.2307/5335	691 692
Tunstrøm K, Katz Y, Ioannou CC et al (2013) Collective states, multistability and transitional behavior in schooling fish. PLoS Comput Biol 9:e1002915–e1002915	693 694
Turner MG, Gardner RH (2015) Causes of Landscape Pattern. In: Turner MG, Gardner RH (eds) Landscape Ecology in Theory and Practice: Pattern and Process. Springer New York, New York, NY, pp 33–62	695 696 697
Vahl WK (2006) Interference competition among foraging waders. s.n.	698
Vahl WK, Lok T, family=Meer p der given=Jaap et al (2005) Spatial clumping of food and social dominance affect interference competition among ruddy turnstones. Behav Ecol 16:834–844. doi: 10.1093/beheco/ari067	699 700 701
Vahl WK, Van Der Meer J, Meijer K et al (2007) Interference competition, the spatial distribution of food and free-living foragers. Animal Behaviour 74:1493–1503. doi: 10.1016/j.anbehav.2007.03.006	702 703
Walsh PD (1996) Area-restricted Search and the Scale Dependence of Path Quality Discrimination. Journal of Theoretical Biology 183:351–361. doi: 10.1006/jtbi.1996.0227	704 705
Watson A, Miller GR (1971) Territory Size and Aggression in a Fluctuating Red Grouse Population. Journal of Animal Ecology 40:367–383. doi: 10.2307/3251	706 707
Wikelski M, Tertitski G (2016) Living sentinels for climate change effects. Science 352:775–776. doi: 10.1126/science.aaf6544	708 709
Williams TM, Fuiman LA, Horning M, Davis RW (2004) The cost of foraging by a marine predator, the Weddell seal Leptonychotes weddellii: Pricing by the stroke. Journal of Experimental Biology 207:973–982. doi: 10.1242/jeb.00822	710 711 712
Wilson DS (1998) Adaptive individual differences within single populations. Philosophical Transactions of the Royal Society of London Series B: Biological Sciences 353:199–205. doi: 10.1098/rstb.1998.0202	713 714 715
Wolf M, family=Doorn p given=G. Sander, Leimar O, Weissing FJ (2007a) Wolf et al. reply. Nature	716

717 450:E5–E6. doi: 10.1038/nature06327

718 Wolf M, family=Doorn p given=G. Sander, Leimar O, Weissing FJ (2007b) Life-history trade-offs
 719 favour the evolution of animal personalities. *Nature* 447:581–584. doi: 10.1038/nature05835

720 Wolf M, Weissing FJ (2010) An explanatory framework for adaptive personality differences.
 721 *Philosophical Transactions of the Royal Society B: Biological Sciences* 365:3959–3968. doi:
 722 10.1098/rstb.2010.0215

723 Wolf M, Weissing FJ (2012) Animal personalities: Consequences for ecology and evolution. *Trends*
 724 *in Ecology & Evolution* 27:452–461. doi: 10.1016/j.tree.2012.05.001

725 Ydenberg RC, Butler RW, Lank DB et al (2004) Western sandpipers have altered migration tactics as
 726 peregrine falcon populations have recovered. *Proceedings of the Royal Society of London Series*
 727 *B: Biological Sciences* 271:1263–1269. doi: 10.1098/rspb.2004.2713