

ABSTRACT

Title of Document: ANIMAL DISTRIBUTIONS AND
MOVEMENT BEHAVIORS IN RELATION
TO RESOURCE DYNAMICS

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Animal movements, whether spatially constrained or spread across broad spatial scales, are often motivated by a need for resources. This thesis seeks to explore the role spatial and temporal resource dynamics may play in animal movements and population distributions.

The **first chapter** synthesizes existing research of animal movements and builds a *conceptual framework* that integrates individual-level movement behaviors. It distinguishes among (1) non-oriented movements in response to proximate stimuli, (2) oriented movements utilizing perceptual cues of distant targets, and (3) memory mechanisms that assume prior knowledge of a target's location. I outline how species' use of these mechanisms should depend on resource dynamics and lead to population-level patterns, such as sedentary ranges, migration between disjunct and predictable seasonal resource areas, or nomadism when resource distributions are unpredictable in both space and time.

The **second chapter** examines resource dynamics in an *empirical setting*, which, especially in ecosystems where changes may happen rapidly across broad spatial scales, is challenging because field measurements may be logistically infeasible. I use satellite imagery of vegetation productivity to track habitat dynamics for Mongolian gazelles in the eastern steppes of Mongolia. I show that spatiotemporal variation of gazelle habitats is extremely high, which may force gazelles to range over vast areas in search of food. This has important conservation implications because single protected areas may not provide sufficient gazelle habitats at all times and landscape level management plans are needed.

In the **third chapter** I develop a *theoretical simulation model*, that implements and combines the three different classes of movement behaviors (non-oriented, oriented, memory) and explores their efficiency under different scenarios of resource dynamics. Adapting techniques from artificial evolution and intelligence, I show how individuals evolve to rely heavily on memory if their landscape dynamics are predictable. In contrast, non-oriented movement evolves predominately in situations where landscape dynamics are unpredictable. Oriented movement proves important at smaller scales, when movement targets are distributed within perceptual ranges.

Future studies may transfer this theoretical model into empirical settings and use actual dynamic habitat models like that developed in chapter two, to reveal the underlying movement behaviors of real animals.

ANIMAL DISTRIBUTIONS AND MOVEMENT BEHAVIORS IN RELATION TO
RESOURCE DYNAMICS

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Introduction

Animal movements have long intrigued scientists and laypersons, and active animal movements play an important role in many subdisciplines of ecology and population biology. For example, studies on disease spread, metapopulation dynamics, or reserve design all depend critically on movement behavior of individuals (Patterson 2008). Not surprisingly, scientists have used many different approaches, ranging from manipulative experiments to mathematical or statistical models, to investigate diverse movement phenomena including searching behavior for food, homing navigation to a nest site, predator avoidance, defense of a territory, or dispersal to find a mate (Turchin 1998, Gagliardo et al. 1999, Morales et al. 2005, Moorcroft et al. 2006).

The question arises whether it is possible to synthesize these efforts and organize movements within a cohesive conceptual framework. Such a synthesis may reveal whether fundamentally different types of movements exist, and how species rely on those movement types relative to characteristics of movement targets or environmental conditions. Chapter one attempts such a synthesis. It focuses chiefly on food resources as a driver of movements and provides an overview of the different disciplines that have studied animal search and navigation. In a second step, this chapter focuses on the level of individuals and classifies all active movement behaviors into fundamental behavioral categories. For example, how is movement to a known target different compared to a search for an unknown location of food? A third part of this chapter adopts a population perspective and examines the different outcomes of movement behaviors among individuals. This section asks the question:

How do spatial and temporal dynamics of resources cause some species to be sedentary range residents, –whereas other species move regularly and predictably to and from seasonal ranges thereby exhibiting migratory movements? In partitioning these two types of movement patterns, this work also explores under what type of resource dynamics we might expect large-scale, long-range movements that are fundamentally unpredictable both temporally and spatially, which I define as nomadism. In sum, chapter one examines the relation of individual-level movement mechanisms, their effectiveness in relation to resource dynamics, and their outcomes in terms of population distributions. The chapter concludes with an outlook on how these concepts could be applied in future research of animal movements in relation to resources.

One challenge in examining the effect of resource dynamics on animal movements and distributions lies in empirically monitoring resource dynamics. This is especially true in ecosystems where resource locations change over the short term across broad scales making it impossible to monitor such changes in the field. One solution to capture such dynamics is the use of satellite imagery with a high temporal resolution. In chapter two I investigate resource dynamics for Mongolian gazelles in the eastern steppes of Mongolia, a grassland ecosystem that has been described by George Schaller as one of the largest remaining intact grazing systems in the world (Schaller 1998). The Mongolian steppes contain huge stretches of largely unfragmented grasslands, and very few nomadic pastoralists live in the steppes. There is almost no private land, and for hundreds of kilometers there are no paved roads, fences or other barriers that might hinder animal movement. In these steppes,

Mongolian gazelles are the most abundant wild large herbivore, with at least 800,000 – 900,000 animals in the central part of the steppe. Movements of Mongolian gazelles occur year round over large distances. However, unlike better known regular long-distance migrations of wildebeest or caribou, gazelle movements appear to be nomadic, lacking both regularity and predictability over large distances.

Although most existing habitat models are static (e.g., Hanski 1999; Higgins *et al.* 2000; Wahlberg, Klemetti & Hanski 2002), I seek to develop a technique that suits grassland ecosystems where conditions change rapidly across broad scales. I use Modis satellite imagery of vegetation productivity that is available at 16-days intervals to generate habitat models that predict the location of high quality gazelle habitat as a function of time. I examine how such dynamic habitat models could be used to estimate habitat overlap across seasons or years and how the unpredictability and spatiotemporal heterogeneity of habitats might be responsible for the far ranging movements of gazelles.

Finally, in a third chapter, I investigate how one could go about combining the fundamental different movement behaviors outlined in chapter one into a cohesive quantitative model. Modeling of movement has made many advances in recent years, fueled by ever increasing amounts of data from rapidly developing relocation devices such as GPS receivers (e.g., Fauchald and Tveraa 2003, Jonsen *et al.* 2005, Morales *et al.* 2005). However, few studies actually try to combine different types of movement in single models, even though real animals certainly depend on a multitude of different movement behaviors (Bailey *et al.* 1996). How does one compare such seemingly different behaviors like movements based on memory of a previously

visited location versus visual perception of an observable target? Because these different behaviors must ultimately integrate into a single quantitative movement response, I adopt techniques from artificial evolution and artificial intelligence to build neural networks that are able to process different types of information. This approach allows artificially evolving organisms to integrate information specific to certain movement behaviors (such as visual information or memory related information) into a single movement response. I train these networks with a genetic algorithm to avoid the problematic step of many traditional movement models wherein movement rules are defined a priori by the modeler. Using this new technique, I examine how individuals can evolve to use different types of information to solve search and navigation problems in relation to a variety of underlying scenarios of resource distributions. In particular, I investigate how the efficiency of different movement behaviors varies depending on whether resource locations are predictable or unpredictable.

Under the auspices of a recently funded NSF grant, I will be pursuing a variety of future studies. One approach may combine the theoretical model developed in chapter three with the empirical dynamic resource model of chapter two to investigate how real gazelles may rely on different movement behaviors in search of food. My colleagues are currently collecting GPS relocations of Mongolian gazelles that I intend to use as an optimization target for movement paths of model individuals. Analogous to chapter three, model individuals in this future work will be trained to search habitat resources; however, the individuals will move on the empirical resource landscapes derived from habitat models as in chapter two.

Chapter 1: Search and navigation in dynamic environments from individual behaviors to population distributions

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Abstract

Animal movement receives widespread attention within ecology and behavior. However, much research is restricted within isolated sub-disciplines focusing on single phenomena such as navigation (e.g., homing behavior), search strategies (e.g., Levy flights) or theoretical considerations of optimal population dispersion (e.g., ideal free distribution). To help synthesize existing research, we outline a unifying conceptual framework that integrates individual-level behaviors and population-level spatial distributions with respect to spatio-temporal resource dynamics. We distinguish among (1) non-oriented movements based on diffusion and kinesis in response to proximate stimuli, (2) oriented movements utilizing perceptual cues of distant targets, and (3) memory mechanisms that assume prior knowledge of a target's location. Species' use of these mechanisms depends on life-history traits and resource dynamics, which together shape population-level patterns. Resources with little spatial variability should facilitate sedentary ranges, whereas resources with

predictable seasonal variation in spatial distributions should generate migratory patterns. A third pattern, 'nomadism', should emerge when resource distributions are unpredictable in both space and time. We summarize recent advances in analyses of animal trajectories and outline three major components on which future studies should focus: (1) integration across alternative movement mechanisms involving links between state variables and specific mechanisms, (2) consideration of dynamics in resource landscapes or environments that include resource gradients in predictability, variability, scale, and abundance and finally (3) quantitative methods to distinguish among population distributions. We suggest that combining techniques such as evolutionary programming and pattern oriented modeling will help to build strong links between underlying movement mechanisms and broad-scale population distributions.

Introduction

Animal movements, such as searching behavior for food, homing navigation to a nest site, or dispersal to find a mate, are important contributors to a species' autecology and geographic distribution. Movements are key elements of the ecology of diverse species and occur across a wide range of spatial and temporal scales (see summaries in Estes 1991, Alerstam et al. 2003). Many studies have investigated orientation mechanisms, drivers of movements, and resulting patterns of population distributions (c.f. Bell 1991, Turchin 1998, Alerstam 2006). However, ecologists also recognize the need to organize these studies into a cohesive framework to better understand and model animal movements. For example, a recent special feature in *Science* suggested 'movement ecology' as new subdiscipline within which these

efforts can be summarized (Holden 2006); however, the actual organization structure for movement ecology was left open. Here we contribute to a synthesis of movement ecology by outlining an integrative, conceptual framework encompassing many of the various movement types that animals, usually exhibit.

We suggest that traditional approaches to the study of animal movements can be organized in 3 categories:

- a) Studies of how animals *search* when they lack or have limited information about potential targets. These studies usually assume random and unpredictable resource environments. Some examples include theoretical models designed to identify optimal search strategies under different conditions (e.g., optimized random searches [Bartumeus et al. 2005], optimal ‘tortuosity’ for central place foraging [Bovet and Benhamou 1991], or ‘foray searches’ in fragmented landscapes [Conradt et al. 2003]). Other studies seek to reveal the strategy at work by fitting empirical data to alternative hypothesized movement strategies (e.g., fitting ‘Levy flights’ to movements of sea birds [Viswanathan et al. 1999], or modeling movement of ungulates as mixtures of random walks [Morales et al. 2004]).
- b) Studies investigating animals’ *navigational* skills relative to known targets. In this category, resources are predictable, and animals use pre-existing information to locate those resources. In broad terms, the pre-existing information represents memories, with the caveat that those memories may be either genetically inherited (e.g., monarch butterflies *Danaus plexippus*, Brower 1996) or previously learned by individuals (e.g., honey bees *Apis*

mellifera, von Frisch 1967). Studies in this category are chiefly empirical and focus on revealing the underlying means animals use to navigate to their targets. Often the navigational skills are remarkable; examples include the waggle dance of bees (von Frisch 1967, Riley et al. 2005), long distance orientation of migrating birds (e.g., Alerstam 2006), and homing capabilities of pigeons *Columba livia* (e.g., Gagliardo et al. 1999, Biro et al. 2007) or marine turtles (e.g., Bowen et al. 2004).

- c) Studies that consider the optimal spatial distribution of animals in relation to conspecifics and resources as a driver of movement behaviors. Unlike the above two categories, this body of research adopts ***population-level perspectives*** that emerge from individual-level decisions. Classic examples are the ideal free distribution (IFD, Fretwell and Lucas 1969) and the marginal value theorem (Charnov 1976), which predict that animals will leave a patch when their fitness drops below the average fitness in all patches, leading to a landscape in which the density of individuals is everywhere proportional to resource density. Also in this category are studies of the scaling relationships between body size and optimal home range sizes (e.g., Haskell et al. 2002).

Categories a) and c) often share a common assumption that animal fitness is related to efficiency of foraging behavior and that specific measures, such as energy intake, can be directly linked to fitness (i.e., optimal foraging, Pyke 1984).

Consequently, several strong links exist between these two categories. Examples include investigations of how an adaptive search behavior can lead to ideal population

distributions and attempts to identify which factors (e.g., different competitive abilities, incomplete knowledge, movement costs, conspecific attraction, site fidelity) explain observed departures from ideal distributions (Farnsworth and Beecham 1999, Gautestad and Mysterud 2005, Hancock and Milner-Gulland 2006).

On the other hand, a significant disconnect exists between search-related (group a) and navigational (group b) studies. To see this, consider that two recent syntheses analyzing animal movements and animal navigation have almost no content in common (Turchin 1998, Alerstam 2006). For example, Turchin's (1998) book on movement analysis summarizes diffusion based random walks and rule-based searching models but does not mention navigational issues described in Alerstam (2006) such as how migration routes are affected by orientation mechanisms (e.g., migration trajectories in relation to sunset azimuths). Despite the weakly developed links between these fundamental areas of research, it is likely that a variety of different search and navigation mechanisms work simultaneously, but at different scales, to determine animals' movements and spatial distributions (see Bailey et al. 1996 for a review in mammalian herbivores or Fritz et al. 2003 for a seabird example). Search and navigation may also be used by animals consecutively for different purposes. For example, seabirds may go on foraging trips searching for prey such as krill or fish that exhibit great spatial variability but later return to a specific nest site, using homing and navigation techniques (e.g. albatrosses, Bonadonna et al. 2005). We believe that progress can be made towards a synthesis of these disparate categories of research on animal movements. This synthesis will require systematically identifying the underlying mechanisms of different movement

strategies and providing a conceptual framework that integrates those mechanisms with landscape dynamics and emergent population patterns.

To build toward such a synthesis, we organize our paper as follows. First, we identify three individual-level mechanisms that animals may employ to search and navigate their resource landscapes. We next outline three common population-level patterns that emerge from individuals' movements. In a third section, we consider alternative resource distributions as critical determinants of the efficiency of individuals' movement mechanisms and population patterns. Also in the third section, we specifically investigate the consequences of the temporal predictability and spatial heterogeneity of resources within a given landscape. In a final, fourth, section, we provide modeling ideas related to our conceptual framework. We focus on bottom up approaches assuming that animals' movement decisions are governed by state variables of individuals such as physiological condition or perceptual information. Some of these state variables can be linked to specific individual-level movement mechanisms, and we outline the potential of evolutionary programming to combine these qualitatively different types of information. In presenting this synthetic framework, we focus on resource distributions as a main driver for movements. However, our concepts are sufficiently flexible to include life-history traits (e.g., diet type [Boyle and Conway 2007] or sex [Ruckstuhl and Neuhaus 2002]) and other factors such as predator avoidance, conspecific interaction, and mate finding (e.g., Fauvergue, Hopper and Antolin 1995, Moorcroft, Lewis and Crabtree 1999, 2006, Morrell and Kokko 2005).

Individual level movement mechanisms

We suggest that all active animal movements (versus passive movements such as dispersal of many freshwater invertebrates etc., Bilton et al. 2001) can be assigned to one of three fundamentally different classes: **non-oriented mechanisms**, **oriented mechanisms**, and **memory-based mechanisms**. We emphasize, however, that no single mechanism in isolation is likely to provide a comprehensive framework for the complex patterns of animal movements observed in nature and that different mechanisms likely act simultaneously at different spatial scales (Bailey et al. 1996).

Class 1: Non-oriented mechanisms

Non-oriented mechanisms involve simple movements, such as diffusion and kinesis that result in a movement decision with *random direction*. With non-oriented mechanisms, sensory stimuli (e.g., resource availability, habitat type) *originating from an animal's current location* cause an alteration in an individual's movement parameters, such as speed, the distribution of turning angles, or the frequency of movement (Benhamou and Bovet 1989). Non-oriented mechanisms can be represented mathematically as correlated random walks (Turchin 1998). For example, habitats that provide an individual with a higher energy intake rate can produce lower velocity and more frequent, less correlated turns leading to an encamped walking pattern. In contrast, lower quality habitats may result in "explorative walks" with higher velocity and correlated turns (Kareiva and Odell 1987). Non-oriented mechanisms have been studied extensively in insect dispersal (Turchin 1998).

Class 2: Oriented mechanisms

Oriented mechanisms rely on perceptual cues, which unlike stimuli in Class 1, stem from a location beyond the animal's current position and result in movement in a predictable direction. Oriented mechanisms utilize sensory cues (e.g. visual, olfactory, acoustic) and various forms of taxis in which movements are defined by the organism's perception of a resource or target location. A few empirical studies have explored perceptual ranges of individuals of different taxa, such as insects (e.g., Schooley and Wiens 2003), small mammals (e.g., Zollner and Lima 1999), pigs (Crony et al. 2003) or birds (Biro et al. 2004). In addition, some models investigate scaling relationships between body size and perceptual ranges (Mech and Zollner 2002) or study the context-dependence of perceptual ranges (Olden et al. 2004). Overall, however, relatively little empirical research has sought to quantify organisms' perceptual ranges. Consequently, it often remains unknown whether perceptual ranges of individuals operate at spatial and temporal scales comparable to the scales over which resource availability changes. For example, in open grassland systems, we do not know whether foraging ungulates can identify and move towards rain on the horizon.

Class 3: Memory mechanisms

In this class of mechanisms, previous information about the location of the movement target is available. This previous information may derive from the recollection of an individual's own history (e.g., large herbivores, Bailey et al. 1996), communication from conspecifics (e.g., bees, von Frisch 1967), or as a genetic

inheritance from its ancestors (e.g., monarch butterflies, Brower 1996). Research suggests that individuals using memory-based mechanisms may draw upon two fundamentally different techniques, path integration or compass navigation and cognitive maps (i.e. pilotage via known landmarks; Gagliardo et al. 1999, Vickerstaff and Di Paolo 2005, Biro et al. 2007). These techniques, which may be used simultaneously, are best known from studies of birds and insects. For birds, combinations of celestial and olfactory cues, geomagnetic coordinates, magnetic compasses and landmarks facilitate global navigation and homing (Alerstam 2006, Wiltschko and Wiltschko 2006, Åkesson and Hedenström 2007). Other examples are the waggle dance of bees that allows bees to navigate to food sources via communication with conspecifics (e.g., von Frisch 1967). Other taxa exhibit similar memory-based movements, including magnetoreception in turtles and magnetic compasses for path integration in moles (see references in Wiltschko and Wiltschko 2006). For large mammalian herbivores, research has focused on spatial learning of resource locations (Bailey et al. 1996).

To understand why an individual moves the way it does, ecologists need a systematic approach that compares and integrates across these three classes of mechanisms. Unfortunately, very few studies have attempted to compare alternative movement models to one another. Recent modeling efforts seek to integrate memory (e.g., Grünbaum 2000), social information on conspecifics (e.g., Hancock and Milner-Gulland 2006), or predator avoidance (e.g., Morales et al. 2005) in models of movement decisions, but to our knowledge no movement models have integrated non-oriented, oriented and spatial memory mechanisms within a 2-dimensional

context. Certainly none have done so in connection with empirical data collected on the movement of a specific organism.

Population level distributions

Here, we build on the approach that Roshier and Reid (2003) developed for birds, which allows for the quantification of spatial patterns by considering the spatial distribution of individuals relative to conspecifics. In this framework, three major population-level distribution strategies emerge. These are sedentary ranges, migration, and nomadism.

Distribution 1: Sedentary ranges

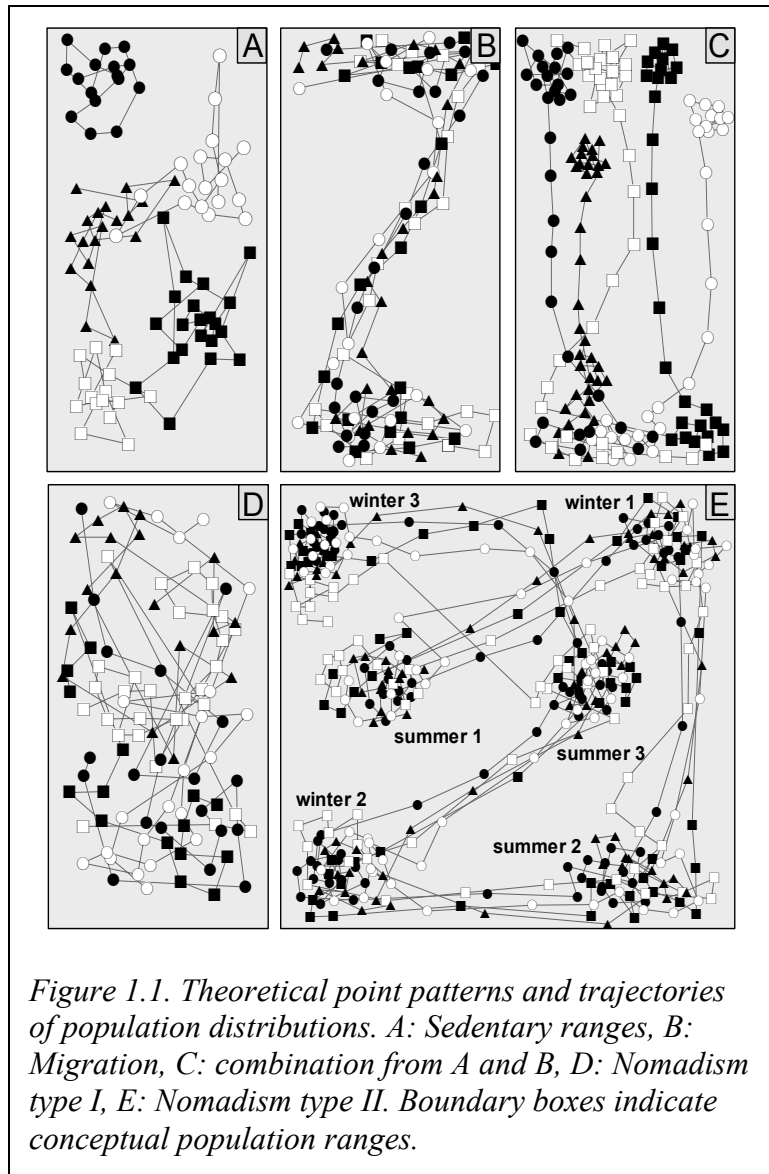
Sedentary ranges comprise resident strategies such as home ranges or territories, and are characterized by distributions in which an individual over its lifetime occupies a relatively small area compared to the population range (Roshier and Reid 2003). Long-distance movements in sedentary animals are usually limited to events of natal dispersal. Depending on the species, single individuals or small groups may occupy a sedentary range. A population of range residents exhibits a spatial distribution wherein individual ranges (or those of small groups) are dispersed from each other (Fig. 1.1A). Resident ranges are usually found when resources are sufficiently abundant throughout the year across the entire population range. Alternatively, resident ranges emerge if animals are dormant and suspend activity in unfavorable seasons (e.g., many bear species). Several studies have explored

environmental determinants leading to different types of range residency (from home ranges to territorialism, reviewed in Mahler and Lott 2000).

Distribution 2: Migration

Migration is

generally defined as a regular, long-distance pattern of movement, and is typically observed in systems with regular, seasonal fluctuations in environmental conditions (Sinclair 1983, Dingle and Drake 2007). Migrations are usually periodic in nature: movement occurs consistently to and from spatially disjunct seasonal ranges (Fig. 1.1B; Roshier and Reid 2003).



Migration is a common population-level strategy for animals and occurs in diverse taxa (reviewed in Alerstam et al. 2003 and Dingle and Drake 2007). Ramenofsky and

Wingfield (2007) make clear that an important distinction exists between migration in iteroparous animals (i.e., species that breed multiple times) and semelparous animals (i.e., species that breed once). In iteroparous species, migratory movements usually repeat in adult life history stages (with the possible exception of natal dispersal). For example, individual whales, birds, or caribou migrate to and from breeding grounds multiple times during their lives. In contrast, semelparous animals may migrate during ontogeny but do not repeat their movements (e.g., anadromous Pacific Salmon *Oncorhynchus* spp.; see Ramenofsky and Wingfield [2007] for a detailed review of migratory mechanisms). Among semelparous animals, insects are unique in that a single migration event can involve multiple generations (e.g., Monarch butterflies stretch their annual migration across North America over several generations [Brower 1996]).

Distribution 3: Nomadism

Nomadism occurs when animals are neither resident nor migratory, and instead move across the landscape in routes that do not repeat across years. Such wandering movements occur when resources fluctuate irregularly on a multi-year timeframe over large geographic areas, leading to a) spatial patterns that vary widely among individuals and b) a lack of predictability in where individuals will be from one year to the next.

The term nomadism unfortunately suffers from a lack of or conflicting definitions in the movement literature (e.g., Estes 1991, Fahse et al. 1998, Bennetts and Kitchens 2000, Roshier and Reid 2003, Fryxell et al. 2004, Dingle and Drake

2007). Here, we define nomadism as a category of movement patterns on par with sedentary ranges and migration. Nomadism occurs at broad spatial scales, but does not follow the prescribed regular temporal and geographic patterns that characterize migration. These movements lack the inter-year predictability that characterizes both sedentary ranges and migration. In contrast, we suggest that nomadism is characterized by unpredictable movements that vary among individuals for any given year (Type I Nomadism; Fig. 1.1D) or among years for any given individual (Type II Nomadism; Fig. 1.1E). Compared to sedentary ranges and migration, nomadism has received extraordinarily little research by ecologists, even though elements of unpredictability are a common feature of movements by many species.

We recognize that these three categories are not always mutually exclusive. For example, many birds occupy territories between migration events (Fig. 1.1C) and employ a combination of movement strategies that yield resident ranges and migration at different times of the year. Seabirds, such as albatrosses, constitute another exception in that they occupy territories within colonies but show nomadic movements while on foraging trips. In addition, some animal populations simultaneously express different strategies, such as when only a fraction of the population follows regular long distance movements (reviewed in Jahn et al. 2004).

Certainly there are also other frameworks for studying the spatial distribution of populations than just the three part classification we propose. As mentioned above, an obvious one involves ideal free distributions (e.g., Sutherland 1983, Hancock and Milner- Gulland 2006, Haugen et al. 2006). The IFD framework is frequently used for testing hypotheses about underlying mechanisms that influence organisms' spatial

distributions or activity patterns. For example, researchers have used the IFD framework to study the effects of interference competition or movement costs in studies of oystercatchers and knots (van der Meer and Ens 1997, van Gils et al. 2006). Likewise, behavioral studies about social organization and spacing among individuals, e.g., grouping behavior due to predation (e.g., Fryxell et al 2007), are ultimately studies about population distributions. Such intra- and interspecific factors may all be at work within each of the three classes of population distributions presented here. For example, variability of density of red knots across intertidal patches may be partly explained by IFD (van Gils et al. 2006), and at the same time, on a broader scale, the movements of these birds can be classified as migratory. We emphasize that the three categories we propose focus on broad scale and long term dynamics, i.e. spatially these categories are based on the landscape ranges of entire populations and functionally these categories are built on effects due to large-scale resource dynamics. Consequently, the three classes we discuss integrate across longer time and consider movement between varying resource landscapes. For example, our use of the term migration is restricted to scenarios involving multiple seasons and years. Although we don't have the space here for a more complete development of the concept, we suggest that the term "ideal free pathway" may be a good descriptor for the conceptual framework that links multiple spatial distributions of individuals over time.

Resource distributions and synthesis

A conceptual framework that links different combinations of individual-level movement mechanisms with patterns of resource dynamics is a key to understanding alternative population-level spatial distributions. Resource environments interact with individual behaviors to influence population-level movement and distribution patterns. Typically, theoreticians explore such linkages by implementing movement models in alternative neutral landscapes (see review in With and King 1997). In these models, change in habitat or resource abundance often only occurs in different realizations of a randomly generated landscape or is due to resource depletion by the consumers themselves. Such approaches ignore temporal environmental variation as a driver of resource abundance and availability. This is an important limitation because the consensus is that large-scale movement patterns such as migration are the result of seasonally changing resource abundance (e.g., Fryxell et al. 2004). Some studies do recognize the importance of temporal predictability to species movements. For example, Fryxell et al. (2005) demonstrated that for Thomson's gazelle (*Gazella thomsoni*) in the Serengeti Plains, adaptive movements that cause individuals to follow stochastic rainfall events (and thus take advantage of ephemeral food sources) are necessary for population viability. Overall, however, a clear need exists for systematic investigations that explore the performance of alternative movement mechanisms in landscapes with temporal heterogeneity.

Another gap exists between the neutral resource landscapes favored by many theoreticians and the resource distributions evident in empirical landscapes. Though little explored, using empirical landscapes may be advantageous in some modeling

studies because model outcomes can be compared with empirical data on organisms' actual distributions via linked GIS and remote sensing databases. This approach allows for predictions about animal movements and distributions in real landscapes, and thus makes results available for conservation and population management (Wiegand et al. 2004, Morales et al. 2005).

We assume that landscape structure is a major driver determining the efficiency of different individual-level movement mechanisms and resulting population-level distributional patterns. We focus on the general case of gradients in resource distributions, which includes but is not limited to a patchy structure divided into habitat and matrix (e.g., Bowler and Benton 2005). We suggest that resource gradients can principally change across four axes: 1) resource abundance 2) spatial configuration of resources (e.g. degree of spatial heterogeneity of resource distributions), 3) temporal variability of resource locations, and 4) temporal predictability of resources. It is important to differentiate between temporal variability and temporal predictability of resources. If resources are distributed differently in summer and winter, but those distributional changes occur every year, the resources would be variable but predictable. In contrast, if resource availability changed over time but the spatial patterns were not consistent, the resources would be variable and unpredictable.

We further suggest that the four gradients follow a hierarchical order. For example, spatial configuration (gradient 2) matters only if some resources are present (gradient 1). Likewise, temporal variability (gradient 3) depends on resources being heterogeneously distributed in space (gradient 2). Lastly, predictability of resources

(gradient 4) is only relevant with resource variability (gradient 3) as a pre-requisite. Note also, that within a particular landscape, the strengths of the four gradients may themselves vary over time. Conceptualizing resource variation in terms of gradients in total amount, spatial configuration, and degrees of variability and predictability is especially advantageous because such quantification facilitates modeling of resource dynamics.

Different combinations of these gradients should affect the relative efficacy of different individual-level mechanisms and should result in alternative population-level distributions.

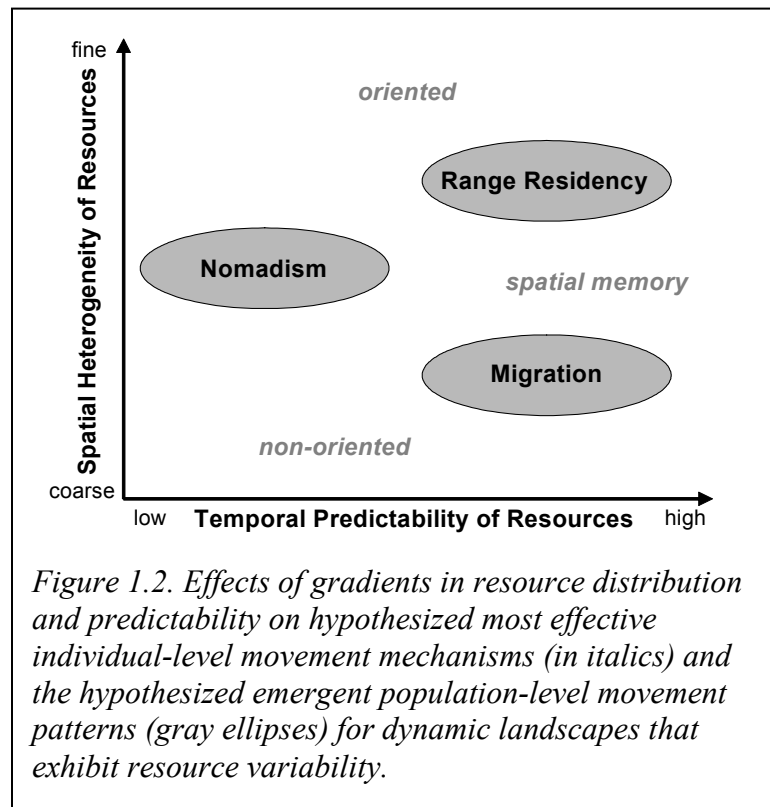
First, for landscapes with little resource variability, memory should generally play an important role. An individual's previous moves are important sources of information for decisions about future movement as the previous moves provide information about where resources might be expected. Home ranges cannot be understood with simple diffusion or low order Markovian random walk models (Turchin 1998) but need to consider the individual history of an organism (e.g., Gautestad and Mysterud 2005). However, not only resources alone but also social factors may help configure resident ranges (e.g. intra-specific scent marks may constrain home ranges: Moorcroft, Lewis and Crabtree 1999, 2006). Discrimination between known neighbors and strangers may be an important mechanism for conflict avoidance and is believed to favor the establishment of territoriality. For example, in some songbird species, individuals can discriminate not just con-specifics but individual neighbors (Lovell and Lein 2004). Social factors may also play a role in cases where populations are resident even though resources are temporally variable

and unpredictable provided the resources are sufficiently abundant and fine-grained to ensure long term survival within a consistent range (Fig. 1.2). Movement mechanisms at work in this scenario should be twofold: memory to recognize neighbors and boundaries of territories plus oriented foraging moves to obtain resources within an organism's perceptual range. Non-oriented movement will be a less beneficial strategy under these

conditions: altering turning angles based on food intake will not increase an animal's chances of relocating into good habitat when resources are rather homogenously distributed.

Second, for

landscapes that vary at increasingly longer temporal and broader spatial scales, average (spatiotemporal) distances between high resource areas will increase, and animals will be required to travel increasingly larger (spatiotemporal) distances between resource patches. Under these conditions, distributional patterns such as resident ranges will break up and transform to migration provided there is sufficient repetition to the seasonal changes. Landscapes exhibiting regular and predictable



temporal dynamics should enhance the relative success of movement strategies requiring memory (e.g., it would be beneficial for organisms to remember where and when conditions would be favorable for reproduction and wintering).

Third, if changes between seasons become unpredictable, our framework predicts that migration or sedentary ranges would switch to nomadism as individuals sought resources whose availability was not dependable. In this case, the efficiency of memory would decrease as resources became more unpredictable and the environment changed on scales vastly larger than an individual's perceptual range. Under these conditions, non-oriented movements may constitute the most effective strategy as they would allow an animal to locate resources beyond its perceptual range and successful movements would not depend on the predictability of resources (Fig. 1.2). On the population level, we suggest that two different types of nomadic patterns can emerge (see Fig. 1.1D and 1.1E). In Type I nomadism, individuals move between and within years in ways that cannot be predicted and will differ among individuals. We expect this movement strategy will appear in landscapes featuring multiple rich resource areas. In Type II nomadism, we envision the case that, at any one time, only very few resource patches exist and that the spatial location of those patches is unpredictable in time. If animals search for these patches they will eventually aggregate in the same locations/patches even if their search paths towards these patches are independent. Consequently, on larger spatial scales individuals' movements may be correlated with each other as in migration but, unlike migration, individual paths will not repeat across years. While both migration and sedentary

strategies could transform to Nomadism I (and vice versa), it seems plausible that Nomadism II is particularly linked to migration.

Modeling concepts

Recent approaches

Any attempt to gain a mechanistic understanding of animal movement faces the challenge that it is generally not feasible to measure the entire suite of relevant low-level parameters (and their interactions) that are hypothesized to determine an animal's movement decisions under field conditions. For some mechanisms, experimental manipulations may allow one to alter a 'normal' movement behavior to demonstrate the relevance of a particular behavior. For example, experimental control of food intake may identify a non-oriented movement mechanism (e.g., 'preytaxis' Kareiva and Odell 1987) and measurements of perceptual ranges in small mammals may demonstrate an oriented mechanism (e.g., Zollner and Lima 1999). Likewise, clock-shifting experiments that generate internal conflicts between sun-compass and landmark information may help uncover spatial memory mechanisms, such as whether memorized landmarks or compass navigation are at work, (Biro et al. 2007). While such experiments do elucidate the importance of certain behaviors in specific cases, for many organisms such techniques are unlikely to be practical or transferable to field settings. This is certainly true when movement decisions may be context-specific, may depend on the interaction of several mechanisms, and/or may depend on interactions with conspecifics.

A more powerful approach to understand empirical movements may entail statistical analyses of relocation data, which recently has become an increasingly viable option, particularly for large mammals. For example, coupled GPS-ARGOS systems use satellite-linked collars to provide relocation data that can be acquired independent of field observers. Such data are now precise to within a few meters, meaning that the movement trajectories of individual animals can be captured in great detail. The high spatiotemporal resolution of relocation data emerging from modern tracking technologies has facilitated research on movements at multiple scales and has spawned a new body of literature concerning quantitative analysis of movement paths (e.g., Fauchald and Tveraa 2003, Jonsen et al. 2005, Morales et al. 2004, 2005). These approaches identify and parameterize statistics such as estimates of first passage time or shape parameters for distributions of velocity or turning angles that characterize movements in a context-specific fashion. Among many approaches tried, hierarchical state space models based on animal movements have been particularly revealing (e.g., Jonsen et al. 2005, Morales et al. 2004). Coupled with field-based relocation data, these models can be used to identify alternative movement states (e.g., feeding or relocating) or environmental covariates that trigger switches between movement states (Morales et al. 2004).

While these probabilistic models do not necessarily allow one to reveal and disentangle the mechanistic underpinnings of movement directly, the statistics they provide could serve as assessment criteria for simulation models that do implement and combine different movement mechanisms. Multiple assessment criteria can provide a framework that allows the parameterization of high dimensional models

where not all lower level parameters (e.g., estimates for the spatial extent of perceptual ranges or the temporal duration of detailed memory) can be known from empirical data (Reynolds and Ford 1999). The idea is that a bottom-up individual-based model that reproduces not just one, but multiple characteristic movement statistics as emergent patterns, is likely to be a structurally realistic representation of the processes underlying a species movement. This is termed ‘pattern oriented modeling’ (Wiegand et al. 2003, 2004, Grimm et al. 2005, Grimm and Railsback 2005) and several studies have parameterized high dimensional individual-based models of movement or animal dispersal in this fashion (Morales et al. 2005, Revilla et al. 2004, Aumann et al. 2006). However, what is missing to date are individual based models that systematically implement the underlying movement mechanisms (oriented, non-oriented and spatial memory) with regard to variability in resources and population patterns.

Future directions

Here we provide a final overview of three essential components that will be critical to future studies of movement that seek to integrate individual-level mechanisms, resource variability, and population-level movement patterns. We synthesize ideas from the recent literature with our own suggestions. First, it will be necessary to combine the qualitatively different underlying individual-level movement mechanisms (oriented, non-oriented and spatial memory) into a single quantitative framework. Second, models are needed that allow for the manipulation and study of resource gradients in abundance, spatial heterogeneity, temporal

variability, and predictability. Third, we make suggestions how model outcomes as well as empirical animal tracking data could be measured at the emergent population level (sedentary ranges, migration, nomadism) to take advantage of pattern oriented modeling techniques (Fig. 1.3). We now discuss each of these three modeling components in turn.

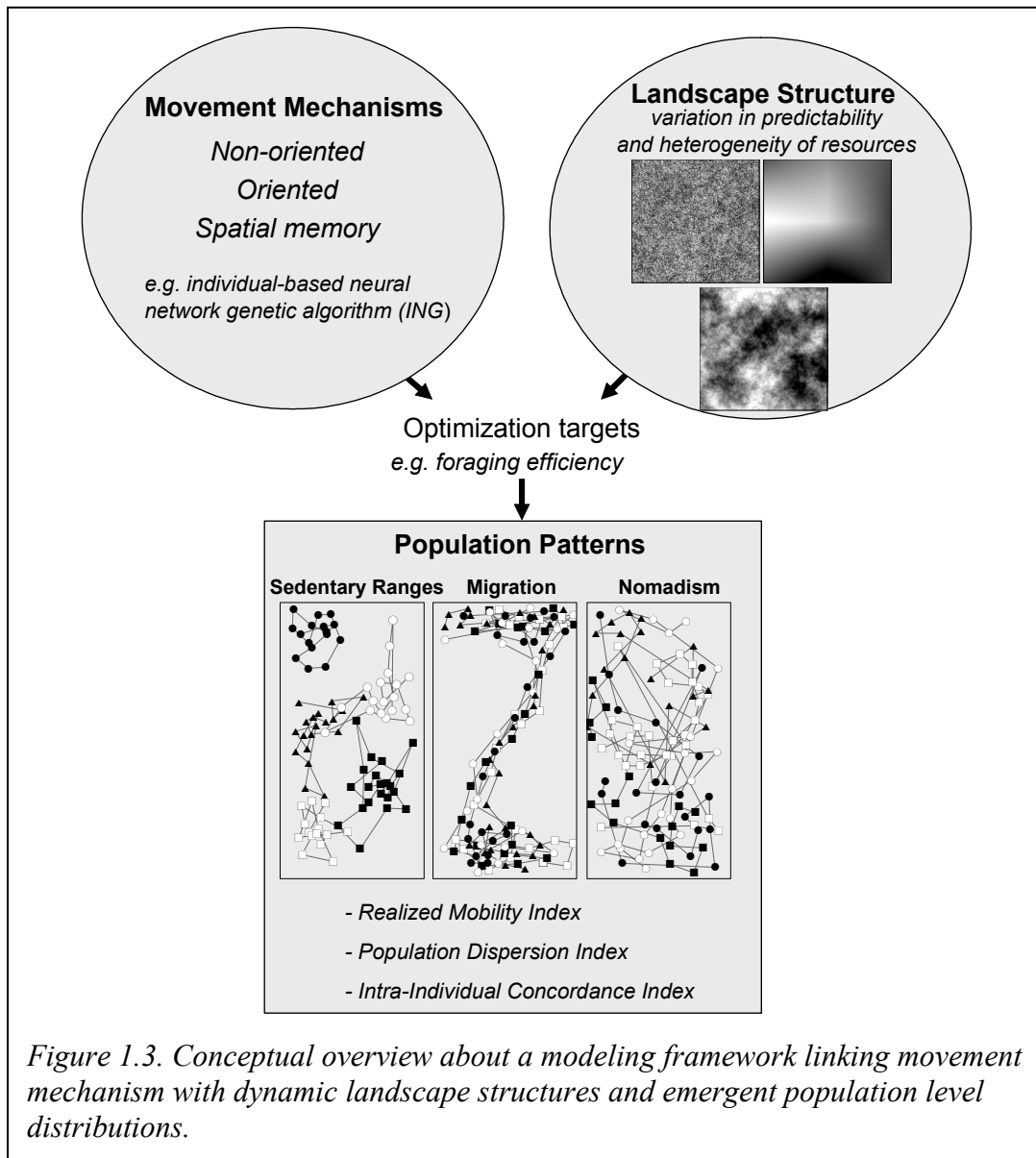
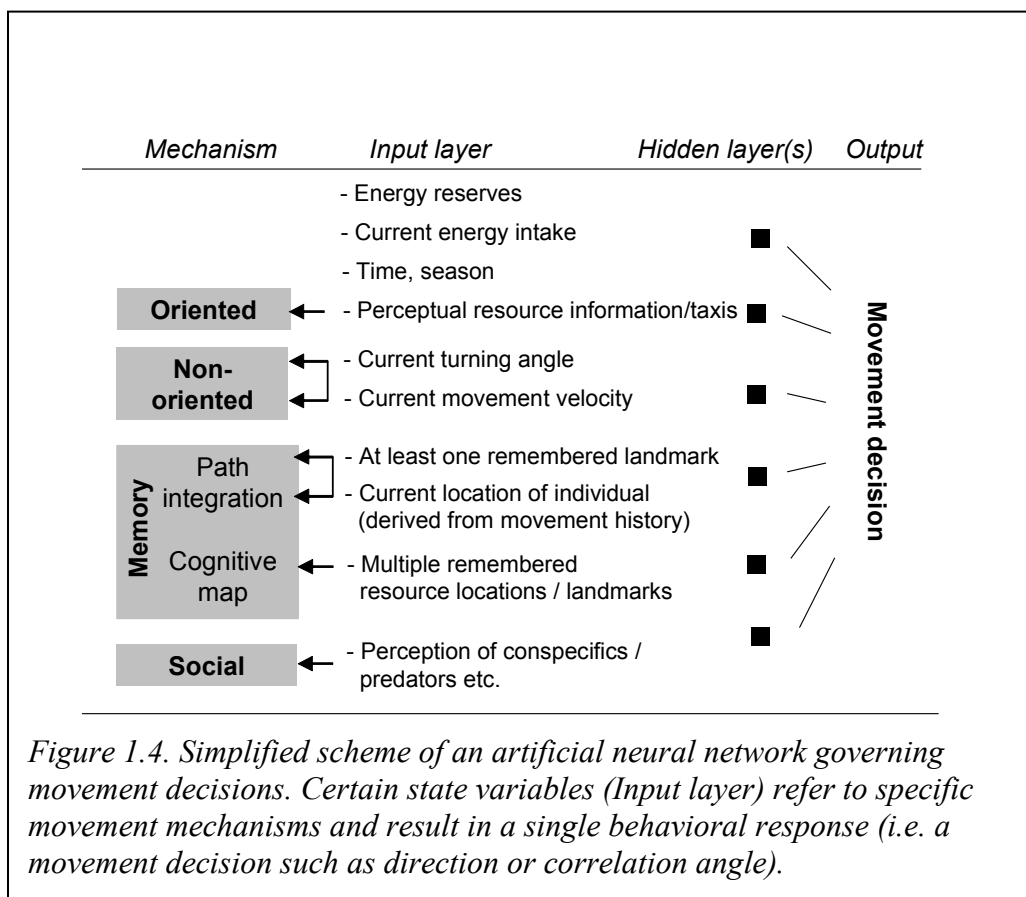


Figure 1.3. Conceptual overview about a modeling framework linking movement mechanism with dynamic landscape structures and emergent population level distributions.

Combining movement mechanisms

A particular challenge in modeling animal movement is that each of the mechanisms (oriented, non-oriented and memory) represents a qualitatively different method by which an animal can search or navigate, yet the effects of each mechanism need to be linked into a single response—namely, a new location for an individual in space and time. Here we suggest one way of dealing with this complex issue. Our key

idea is that each of the three types of individual-level movement mechanisms relies on type-specific input parameters. For example, stimuli such as the current movement angle and velocity are specific to non-oriented mechanisms. Likewise, specified perceptual ranges are unique to oriented movement mechanisms, and memory mechanisms require constraints on how much temporal and spatial information an individual can ‘remember’.



Excellent examples of how movement can be modeled by updating velocity and direction based on a suite of dynamic states have been achieved using artificial intelligence approaches to navigate autonomous driving robots (Thrun et al. 2006 and

references therein). Meanwhile in ecology, evolutionary programming techniques such as genetic algorithms (GA) and artificial neural networks (ANN), have been used to model complex animal movements (Morales et al. 2005, Bennet and Tang 2006, Boone et al. 2006, Hancock and Milner-Gulland 2006). Combining GAs and ANNs in individual-based models yields so-called individual-based neural network genetic algorithms (ING models), which were first used in ecology to study one-dimensional movements in fish (Huse et al. 1999, Strand et al. 2002). The ING technique is generally advantageous because it integrates qualitatively different input information but is not contingent on ecologists' abilities to discern or define the rules that govern animal behavioral decisions. This is an especially important consideration in that behavioral rules in the real world may not be transparent, simple, or context-independent, making them difficult to identify from empirical datasets (Morales et al. 2005). However, these techniques have not yet been used to systematically explore alternative movement mechanisms. We suggest that certain variables in the input layer of an ANN may be mechanism-specific (Fig. 1.4), and by adding or removing mechanism-specific stimuli from an ANN, it might be possible to test the effects of those variables (and their interactions) with regard to a fitness criterion such as foraging success under different landscape scenarios.

Dynamic Resources

Modeling variability in resource distributions is just as critical for a synthetic understanding of animal movement as is modeling of the movements themselves. For theoretical investigations, several established methods exist by which artificial

landscapes may be generated (e.g., as spectral representations; Keitt 2000, Csillag and Kabos 2002). To produce temporal landscape dynamics, a series of such landscapes may be used to simulate seasonal change within years. To represent periodicity across years, landscape series may be repeated in sequence, with varying degrees of ‘error’ introduced to generate temporal unpredictability. In this way temporal heterogeneity could be introduced within years (simulating seasonal changes in resource availability) as well as between years (varying predictability of resource landscapes). A more challenging task relates to measuring and modeling of empirical resource landscapes that capture, in detail, how the availability of resources changes over space and time. With ground methods, such data are almost impossible to acquire at high temporal resolutions and across broad spatial scales. Nevertheless, for some ecosystems such as grasslands, remote sensing techniques have provided a partial solution to this problem via indices of vegetation productivity that capture dynamics of landscapes (e.g., Boone et al. 2006, Pettorelli et al. 2005, Mueller et al. 2007). These indices of vegetation dynamics constitute an important advance because remote sensing techniques have traditionally focused on static, rather than dynamic, habitat or habitat suitability maps.

Quantifying Population-level Distributional Patterns

The third critical component in a comprehensive modeling framework for animal movement would be to evaluate and quantify emergent dispersion patterns at the population level (e.g., sedentary ranges, migration, nomadism). Several metrics are possible that can be applied equally well to empirical distributions and the

outcomes of simulation models, and each can be used to gain insight into the connections between individual level movements and population level distributions (Table 1.1).

For example, one might calculate a modified ‘realized mobility index’ (Roshier and Reid 2003) as the ratio of an individual’s yearly range to the entire population’s yearly range. In addition, we suggest that if telemetry data are available for several individuals of a single population, methods of multivariate point pattern analysis (reviewed in Fortin and Dale 2005) may be applied to the relocation data to quantify the spatial relationships of locations between different individuals or between different time periods within the same individuals. More specifically, a ‘population dispersion index’, could determine independence, clustering or dispersion of relocation patterns among individuals. If inter-individual relocation patterns of a population are dispersed, it would indicate sedentary ranges whereas clustering would indicate migration or type II nomadism. A third possible metric is an ‘intra-individual concordance index’ that could measure independence, clustering or dispersion of point patterns within individuals and between years for a given season. If relocations from the same season and different years are spatially clustered it would indicate that an individual has a high fidelity to the same area every year, whereas a dispersed or independent distribution would indicate nomadism. Taken together, these three indices should allow one to distinguish among the three emergent population-level distributional patterns (Table 1.1).

Table 1.1: Indices quantifying and distinguishing population level distributional patterns.

	Migration	Sedentary ranges	Nomadism I	Nomadism II
Realized Mobility Index (RMI, quantifies the ratio individual range vs. population range)	<i>Large</i>	<i>Small</i>	<i>Large</i>	<i>Large</i>
Population Dispersion Index (PDI, quantifies spatial relation among individuals)	<i>Clustered</i>	<i>Dispersed</i>	<i>Independent</i>	<i>Clustered</i>
Intra-Individual Concordance Index (ICI, quantifies spatial relation of relocations for specific individuals among years)	<i>Clustered</i>	<i>Clustered</i>	<i>Dispersed</i>	<i>Dispersed</i>

Conclusions

We suggest that combinations of individual-level state variables can be used to represent specific movement mechanisms, and that those mechanisms can be implemented and integrated in individual based models. Integrating different types of movement ranging from search to navigation with dynamic landscapes that vary in predictability and heterogeneity may provide a better understanding of emergent, population-level spatial patterns such as sedentary ranges, migration, and nomadism.

That said, we feel that another strength of the approaches we outlined may lie in their capability to serve as a tool for ecological forecasting. Population dynamics of many species—and specifically long-distance migrants—rely critically on their movement behaviors. To understand better how human activities affect animal movements in real landscapes, we suggest that structurally realistic movement models operating on empirically derived landscapes may provide a valuable tool for resource

planning. Such an approach would allow ecologists to predict how individuals' movements and species' spatiotemporal population dynamics could respond to landscape changes.

Chapter 2: In search of forage: Predicting dynamic habitats of Mongolian gazelles using satellite based estimates of vegetation productivity

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Summary

1. Temporal variability in habitat suitability has important conservation and ecological implications. In grasslands, changes in resource availability can occur at broad spatial scales and enlarge area requirements of ungulate populations which increases their vulnerability to habitat loss and fragmentation. Understanding and predicting these dynamics, though critical, has received little attention so far.
2. We investigated habitat dynamics for Mongolian gazelles (*Procapra gutturosa*) in the eastern steppes of Mongolia. We quantified the distribution of gazelles at four different time periods and tracked primary productivity using Normalized Difference Vegetation Index (NDVI) data from satellite imagery.

3. A second order logistic model showed that NDVI was an efficient predictor of gazelle presence. We tested the predictive power of the model with independent data of a gazelle telemetry study and 85% of all relocations were found within the predicted area.
4. Gazelles preferred an intermediate range of vegetation productivity presumably facing quality quantity trade-offs where areas with low NDVI are limited by low ingestion rates, and areas with high NDVI are limited by the low digestibility of mature forage.
5. Spatiotemporal variation of gazelle habitat areas was high. Only 15% of the study area was consistently gazelle habitat throughout all survey periods, indicating that gazelles need to range over vast areas in search of food. Only 1% of the gazelle habitats were consistently located inside protected areas.
6. *Synthesis and applications.* Habitat variability in grasslands often leads to area requirements of ungulates that prevent effective conservation within single protected areas. They require landscape level management plans, but dynamic habitat predictions to inform such plans are difficult to implement and often missing. We showed that satellite estimates of vegetation productivity can be used successfully to generate dynamic habitat models in landscapes with highly variable resources and demonstrated that intermediate NDVI values were critical to predict occurrence of Mongolian gazelles.

Introduction

Mongolian gazelles (*Procapra gutturosa* Pallas) are the dominant wild large herbivore in Mongolia's eastern steppe, one of the largest remaining grasslands in the temperate zone (Schaller 1998b; Olson *et al.* 2005a). While these gregarious animals still roam Mongolian grasslands in large numbers (at least 800,000 – 900,000 animals in the study region; Olson *et al.* 2005a), the species has experienced a major reduction in range during the past century, and is further threatened by continued habitat loss, fragmentation, and excessive hunting (Lhagvasuren & Milner-Gulland 1997; Reading *et al.* 1998). Although individuals or small groups are found across a wider geographic range, higher concentrations of this gazelle species are now limited to the eastern steppe (Lhagvasuren & Milner-Gulland 1997; Wang *et al.* 1997; Reading *et al.* 1998; Sneath 1998).

Movements of Mongolian gazelles occur year round over large distances with only short interruptions throughout calving time (Lhagvasuren & Milner-Gulland 1997; Schaller 1998b; Olson *et al.* 2005b; Ito *et al.* 2006). They appear to be nomadic and lack regularity (Olson *et al.* unpublished data), yet their paths and patterns are little understood (Ito *et al.* 2006). Quantifying the spatiotemporal heterogeneity of gazelle habitat use will be helpful in better understanding the species' area needs and developing much needed integrative and landscape-level conservation strategies.

Modeling habitat use in grasslands is particularly challenging as these ecosystems are characterized by a continuously varying landscape (Fernandez-Gimenez & Allen-Diaz 1999; Fryxell *et al.* 2005). Most existing habitat models are static and only recently have habitat modeling studies started to focus on dynamic

landscapes (Hanski 1999; Higgins *et al.* 2000; Wahlberg, Klemetti & Hanski 2002). In addition, many of these models either focus on metapopulation theory (Keymer *et al.* 2000; DeWoody, Feng & Swihart 2005; Xu *et al.* 2006) or on modeling habitats in ecosystems that are dynamic over longer time frames (e.g. forests: Akcakaya *et al.* 2004; Verheyen *et al.* 2004; Wintle *et al.* 2005). Short-term and broad-scale changes that are common in grasslands are difficult to model, as data on environmental covariates are usually difficult to acquire at similar temporal and spatial scales (Fryxell, Wilmshurst & Sinclair 2004). However, satellite-borne sensors allow measurement of vegetation productivity, a key variable indicating resource availability for grassland ungulates, across broad spatial scales and at relatively high temporal intervals (Reed *et al.* 1994; Huete *et al.* 2002). Normalized Difference Vegetation Index (NDVI) is a satellite-based vegetation estimator that has consistently shown close correlations with vegetation productivity in a diverse range of ecosystems (reviewed in Pettoirelli *et al.* 2005) and, specifically in grasslands, with total biomass as well (Kawamura *et al.* 2003, 2005).

Numerous studies already demonstrate that NDVI is a useful tool to predict habitats for ungulates in grasslands. It has been used successfully to test the relationship between ungulate diversity and plant productivity across the African continent (Baird 2001) and to evaluate ungulate habitat use in the Kalahari (Verlinden & Masogo 1997), rangeland stocking rates in Argentina (Oesterheld, DiBella & Kerdiles 1998), wildebeest (*Connochaetes taurinus*) population declines and movements in Kenya (Serneels & Lambin 2001; Musiega & Kazadi 2004), distribution of impala (*Aepyceros melampus*) in Botswana (Van Bommel *et al.* 2006)

and also to characterize habitat use of Mongolian gazelles (Leimgruber *et al.* 2001; Ito *et al.* 2005, 2006). However, none of these studies use detailed and broad scale distribution data of a species to identify preferred ranges of NDVI and make predictions on habitat occupancy, when availability changes.

We used NDVI satellite imagery to predict gazelle occurrence data from four extensive surveys across the eastern steppes. Specifically we sought to reveal whether gazelles select for a specific range of productivity. Instead of assuming a monotonic relationship between NDVI and resource availability we tested predictions with regard to forage maturation: While areas with too little vegetation may not provide sufficient ingestion rates, most grasses decline considerably in nutritional quality as they grow (Van Soest 1994). Mature forage may provide high vegetation productivity yet little resources to gazelles as digestion rates are reduced (Fryxell 1991; Murray & Illius 1996; Wilmshurst *et al.* 1999; Wilmshurst, Fryxell & Bergman 2000, Bergman *et al.* 2001). As the landscape in the eastern steppe features almost no trees and few shrubs, it is likely that in general high NDVI values are associated with higher, more mature and therefore less nutritious grasses, which has been shown elsewhere (Payero *et al.* 2004, Kawamura *et al.* 2005a ,b). An intermediate range of NDVI allowing for sufficient forage quantity as well as quality may provide most resources to gazelles and might be a useful tool to delineate habitats and reveal area needs of Mongolian gazelles.

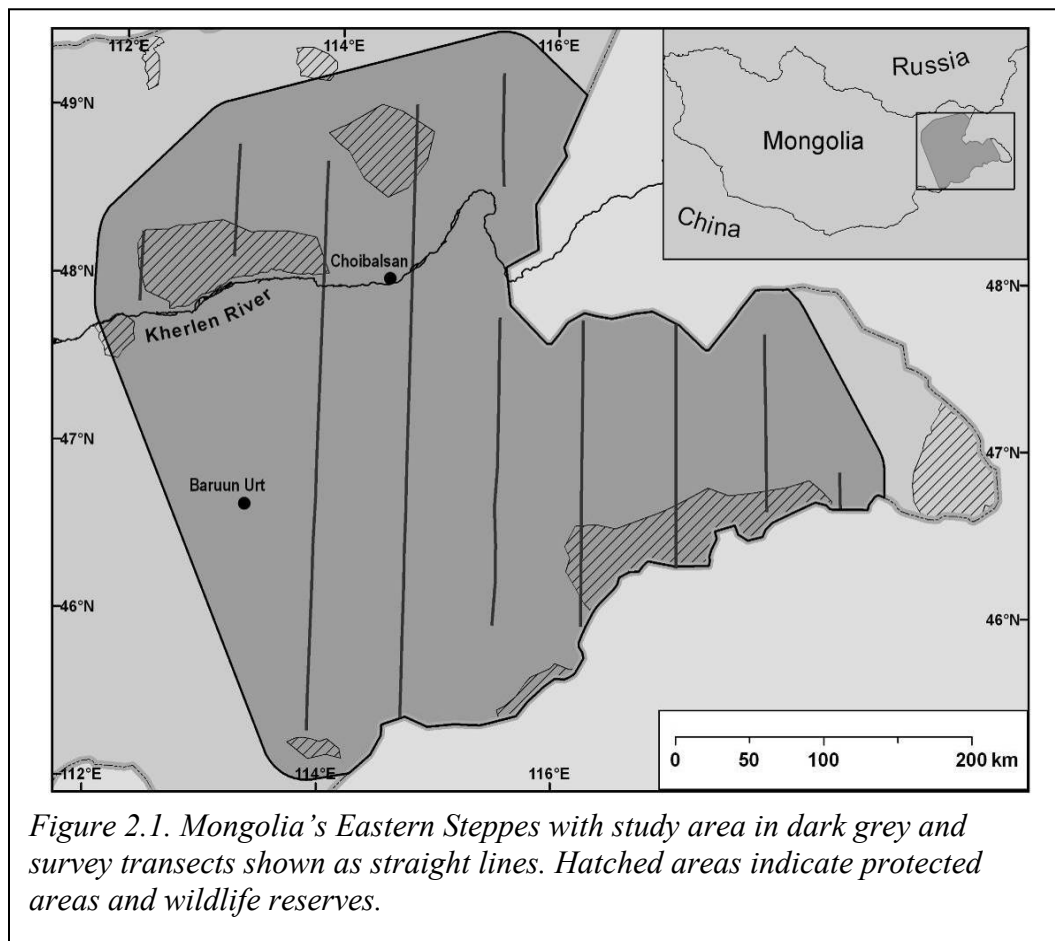
Methods

Study area

Mongolia's eastern steppe is one of the world's largest remaining intact grasslands and harbours the greatest concentration of wild ungulates in Asia (Schaller 1998b). Neighbouring grasslands to the south in Inner Mongolia, China are severely overgrazed and degraded (Jiang *et al.* 2003) and have fewer wild ungulates (Wang *et al.* 1997). The eastern steppe is characterized by gently rolling hills, broad flat plains (altitude 600-1,100 m a.s.l.) and sparsely scattered small ponds and springs. The region's major river, the Kherlen, bisects the steppe from west to east. The climate is continental with long cold winters (January mean = -26°C) and short warm summers (July mean = 19°C). Warm season precipitation mainly occurs during July and August and overall precipitation is generally between 200-300 mm/year (Gunin *et al.* 2000). Onset of green-up during the 1980's occurred from late May to early June (Lee *et al.* 2002; Yu *et al.* 2003). Dominant soil types are characterized as sandy loamy chestnut soils with localized sites of highly salinized soil (Gunin *et al.* 2000). The steppe is homogeneous in both its topography and vegetation. Vegetation is mostly dominated by grasses such as *Stipa* spp. and *Leymus* spp. as well as forbs *Artemisia* spp. and *Allium* spp.; a few shrubs *Caragana* spp. are present and trees are rare, occurring in isolated pockets (Gunin *et al.* 2000; Tong *et al.* 2004). A narrow band of woody vegetation consisting of mostly willow (*Salix* spp.) exists along the floodplain of the Kherlen. Semi-nomadic pastoralists live throughout the region at some of the lowest densities in the country (0.7/km²; Milner-Gulland & Lhagvasuren 1998).

Gazelle survey and radio tracking

We used gazelle locations in a 150,000 km² area during four surveys conducted by Olson *et al.* (2005a), adding data from north of the Kherlen River (Fig. 2.1). The survey protocol followed guidelines recommended in Buckland *et al.* (2001). Transect locations were spaced at 60 km intervals running north – south and driving speeds were kept between 25-35 km/h (Olson *et al.* 2005a; Fig. 2.1). Transect



locations remained the same for all surveys and ranged between 50 and 350 km in length and 6-7 transects/survey. The total distance covered for these surveys was 5,169 km (Table 2.1). Gazelle group locations were recorded using Global

Positioning Systems (GPS) (Olson *et al.* 2005a). Spring surveys (2000, 2002) were conducted during late May to mid June and autumn surveys (2001, 2002) were conducted from late August to early October (Table 2.1). For model validation, we used locations obtained from radio-collared calves in 2001 (Olson *et al.* 2005b). Calving aggregations can be detected in late June (Olson *et al.* 2005b). By walking through the calving region we were able to detect newborn hiding calves which were captured and fitted with an expanding VHF-radio transmitter (Olson *et al.* 2005b). Movements of marked calves were monitored from the ground by vehicles over the course of the year. When a marked gazelle was detected, Olson *et al.* (2005b) visually confirmed the group location and recorded the position with a GPS.

Table 2.1. Dates and distances of gazelle surveys and matching periods for NDVI composites.

Year	Season	Gazelle survey			NDVI composite	
			start	end	start	end
2000	Spring	1286 km	05-15	06-02	05-25	06-09
2001	Autumn	1252 km	09-27	10-10	09-30	10-15
2002	Spring	1591 km	05-19	06-08	05-25	06-09
2002	Autumn	1454 km	08-26	09-06	08-29	09-13
2001	Summer	telemetry	07-15	07-30	07-12	07-27

Remote sensing, GIS, and model development

To develop a habitat model based on vegetation productivity we used NDVI data acquired by the Moderate Resolution Imaging Spectroradiometer (MODIS) onboard the TERRA satellite. For each of the survey periods we obtained a 16-day NDVI composite in 500 m resolution from NASA's Earth Observing System Gateway (<http://edcimswww.cr.usgs.gov/pub/imswelcome/>); for details see Huete *et*

al. 2002) and re-projected the data to Transverse Mercator (UTM Zone 50N; Table 2.1). We matched gazelle and satellite data by subdividing each transect line into 1 x 5 km blocks and determined the mean NDVI as well as gazelle presence or absence for each block. The 1 km width of these blocks approximated the effective strip width for detection of gazelles (Buckland *et al.* 2001; Olson *et al.* 2005a) and, given the high mobility of gazelles, finer scales than 5 km seemed to be inappropriate. Mongolian gazelles move an average of about 9 km per day (Olson *et al.* unpublished data), and even at the coarse 5 km scale an asymmetric sample distribution of presence and absence data is most likely caused by many false negatives (Tyre *et al.* 2003). To eliminate sample asymmetry (i.e. more absent than present data) and balance statistical analysis we randomly sub-sampled the absence blocks to equal the number of presence samples in each survey. We equalized phenological differences in total vegetation productivity by linearly normalizing the NDVI data for each survey using minimum-maximum scaling.

We used maximum likelihood and the Akaike Information Criterion (AIC) for model selection and penalized quasi likelihood (PQL, lme4 library in R; Bates 2005; R Development Core Team 2006) to implement second order autologistic generalized linear mixed models predicting gazelle presence/absence based on NDVI (Manly *et al.* 2002; Boyce & McDonald 1999; Boyce *et al.* 2003; Bates 2005). To test predictions regarding forage maturation related quantity-quality trade-offs, we used the first and second order polynomial of the scaled NDVI variable. The first order term tested for low probability of gazelle occurrence at low productivity areas (quantity limitation of forage). A significant negative coefficient of the second order

polynomial would predict low probability of occurrence at high productivity areas (quality limitation of mature forage). However, not just the relative range of NDVI may be important but also interactions with absolute resource amount i.e. the variation in phenology between surveys. We considered that by including the median of the non-scaled NDVI data from each survey into the model and testing for interaction effects with the relative (minimum-maximum scaled) NDVI data. Between season differences in vegetation quality may occur and we incorporated seasons (autumn versus spring) as fixed factor in the analysis. Additionally, we explicitly modeled spatial autocorrelation (Augustin, Mugglestone, & Buckland 1996) by including the number (zero, one, or two) of neighboring blocks (i.e. the next 5 km block to the north and to the south) where gazelles did occur as an autocovariate. Based on AIC, we excluded effects which did not significantly improve the model in any factor combination. As observations were grouped in four different surveys, those were included as a random effect in the final minimum adequate model. As a predictive tool to classify new NDVI scenes in gazelle presence and absence areas without prior information about gazelle occurrence in adjacent areas, we calculated a reduced model excluding the auto-regressive term.

While probabilities are generally more informative and were used for model testing, we believe thresholds are a helpful tool in conservation management and for simple and applied assessments as intended in this study. Comparison of predicted values and actual prevalence (Vaughan & Ormerod 2005) suggested 0.5 probability-thresholds as an appropriate measure to classify NDVI scenes into predicted gazelle presence/absence areas and explore omission as well as commission errors.

We tested the reduced model with an independent data set from the telemetry study. We selected all relocations of gazelle groups (≥ 2 animals) in the second half of July 2001 (67 group relocations of 33 radio-tagged animals) and acquired a MODIS NDVI 16-day composite for the according time lag (Table 2.1). At this time of the year, calves already follow the generally mixed herds and are representative for both male and female habitat selection. The NDVI data were processed following the same procedures applied during model development. By applying our model to this NDVI scene, we calculated a surface predicting the probability of gazelle occurrence throughout the eastern steppe. From this surface we calculated the mean of all pixel values where actual relocations occurred. To test whether this mean was significantly higher than expected by chance we simulated 1000 random toroidal shifts (Fortin & Dale 2005) of the relocation pattern within a boundary box (i.e. a minimum rectangle of $\sim 18,000 \text{ km}^2$ encompassing all relocations). For each shift we extracted the pixel values of the prediction surface and calculated their mean. We determined the significance of our model by counting how many of the simulated patterns had a higher average probability of occurrence than the mean calculated from actual gazelle relocations. We also created a minimum convex polygon (excluding areas in China) derived from all gazelle telemetry observations obtained during the duration of the entire telemetry study from June 2001 to January 2002 (telemetry area, Fig. 2.4). We used 0.5 probability thresholds to classify the surface into predicted gazelle presence versus absence areas. We qualitatively compared the proportion of available habitats to selected habitats. However, we did not test these findings due to clumping and non-independence of the relocation data.

Results

Vegetation productivity approximated by NDVI was an important factor shaping gazelle habitat use. The auto-logistic model relating gazelle presence/absence with NDVI showed that gazelles preferred an intermediate range of vegetation productivity; despite a strong positive spatial autocorrelation of gazelle locations at a 5 km scale, NDVI was relevant to discriminate between gazelle presence and absence areas (Table 2.2).

*Table 2.2. Logistic mixed models predicting gazelle occurrence with NDVI across four field surveys. Null deviance: 884.46 on 637df; significance code: '****' 0.001. A. full model including spatial autocovariance (AutoCov); residual deviance: 666.14, AIC: 674, estimated scale: 1.02. B. reduced model; residual deviance: 849.77, AIC: 858, estimated scale: 1.00.*

Random effect	Coefficient	Variance	Std. Dev.		
	Survey	5e-10	2.24e-05		
Fixed effects	Coefficient	Estimate	Std. Error	Z value	
	Deviance				
A	(Intercept)	-2.55	0.42	-6.11***	1.59
	NDVI	6.64	1.88	3.53***	7.44
	NDVI ²	-6.58	2.00	-3.29***	25.65
	AutoCov	1.71	0.15	11.60***	183.63
B	(Intercept)	-1.91	0.36	-5.27***	1.59
	NDVI	8.77	1.66	5.29***	7.44
	NDVI ²	-8.33	1.75	-4.76***	25.65

The coefficients for both NDVI predictors, the first and second order polynomial, were highly significant (the first being positive and the second negative, Table 2.2). Variation in biomass between surveys (median of absolute NDVI at each survey), season (spring versus autumn surveys) and interactions terms did not significantly improve the model and were removed based on AIC. The model that included

vegetation productivity and spatial autocorrelation as predictors explained 25% of the overall deviance (Table 2.2A). This model also classified 76% of both presence and absence blocks correctly assuming 0.5 probability thresholds.

We employed a model using solely NDVI as a predictor excluding the autoregressive term to predict gazelle habitats independent of any ancillary knowledge on gazelle occurrences (Table 2.2B). While the overall fit of the model decreased, both estimates of coefficients of the NDVI predictors remained significant (Table 2.2B). The reduced model was still very efficient in classifying the gazelle presence data and the omission error did not increase; 77% of gazelle presence blocks

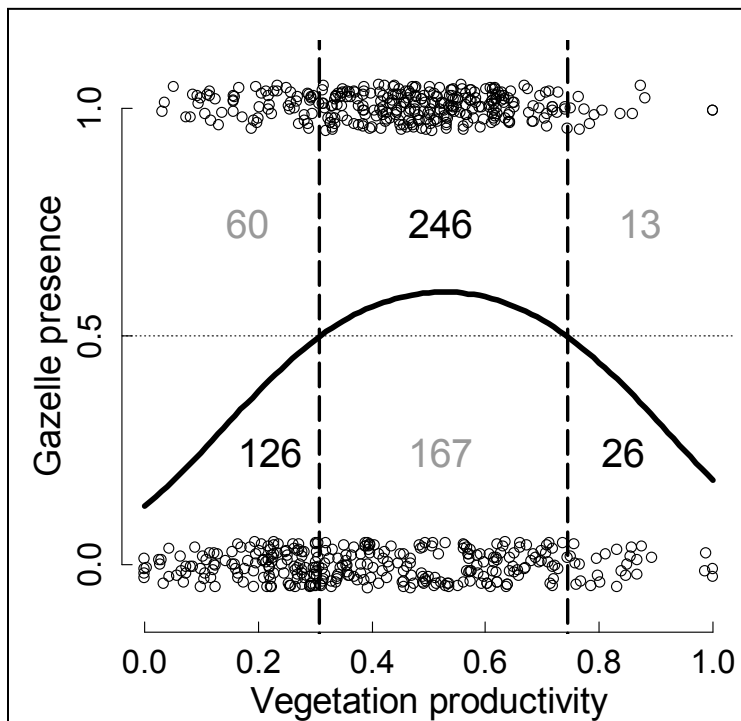


Figure 2.2. Probability of gazelle presence predicted based on relative vegetation productivity. Solid line: logistic model; dashed vertical lines: 0.5 probability thresholds for gazelle presence; jittered dots: sample values; black numbers: correctly classified samples based on thresholds; grey numbers: misclassifications.

were correctly classified (246 of 319), 4% (13) of the presence blocks had according to the model a too high productivity, and 19% (60) too low productivity (Fig. 2.2). However, the commission error increased and, with 48% accuracy (152 of 319), the model was not effective in classifying gazelle absence.

Thresholds indicating a probability of gazelle occurrence ≥ 0.5 for this model were at 0.31 and 0.74 of the range of the minimum-maximum scaled NDVI values (Fig. 2.2).

We used these thresholds to delineate gazelle habitats in the four NDVI data sets of the survey periods. While the average NDVI between surveys varied considerably with lowest biomass in autumn 2001 and most productivity in autumn 2002, in each survey about 50-65% of the study area was delineated as gazelle habitat (Fig. 2.3). Consistently across seasons most areas were predicted to be unoccupied by gazelle because vegetation productivity was too low rather than too high (Fig. 2.3). We found a pronounced spatiotemporal heterogeneity of NDVI, as well as of observed gazelle habitats between surveys. Only 7% of the study area was never classified as gazelle habitat, and only 15% had a probability of gazelle occurrence above 0.5 across all four seasons (compared to 11% overlap to be expected at a total random distribution and 49% with maximum overlap). Merely 1% of the study area was located within protected areas and gazelle habitat throughout all four surveys. The average overlap of habitats between seasons (46%) was similar to the average overlap within seasons (43%).

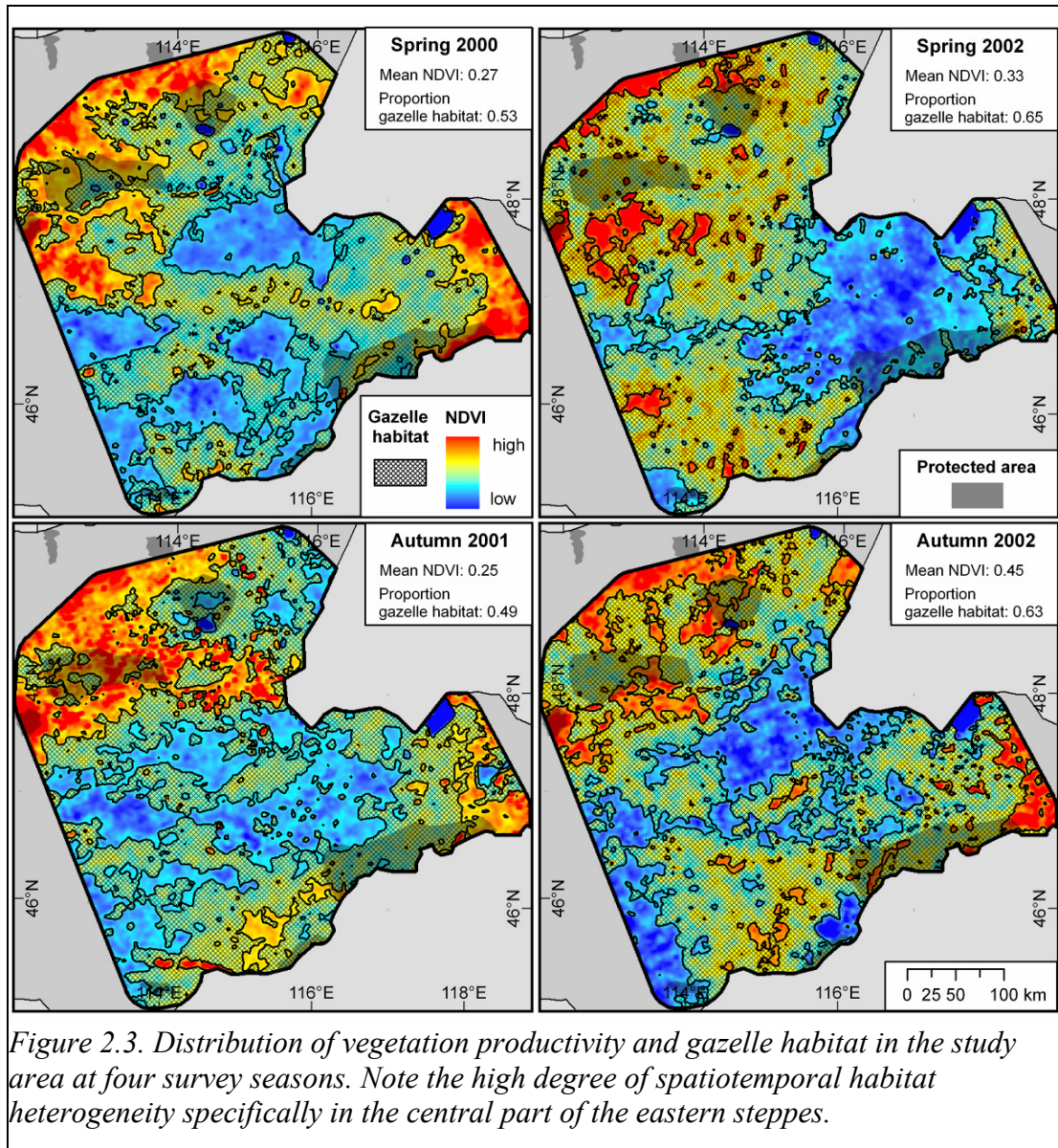


Figure 2.3. Distribution of vegetation productivity and gazelle habitat in the study area at four survey seasons. Note the high degree of spatiotemporal habitat heterogeneity specifically in the central part of the eastern steppes.

We further tested the predictive power of the model using gazelle telemetry locations and NDVI data from a 16-day period in July 2001. Random shifts of these locations across a prediction surface calculated from the NDVI had in only 5 out of 1000 ($p = 0.005$) permutations a higher average than the average of the actual gazelle locations. The area these gazelles used throughout the entire year comprised a minimum convex polygon of about 45,000 km² (Fig. 2.4; telemetry area). For the second half of July 2001 the model predicted that 56% (~26,000 km²) of the

telemetry area was preferred gazelle habitat and 85% of all groups were found within the predicted area (Fig. 2.4). The remaining 10 gazelle groups were located in low productivity areas but always in close proximity to predicted habitat (maximum distance = 7 km; Fig. 2.4).

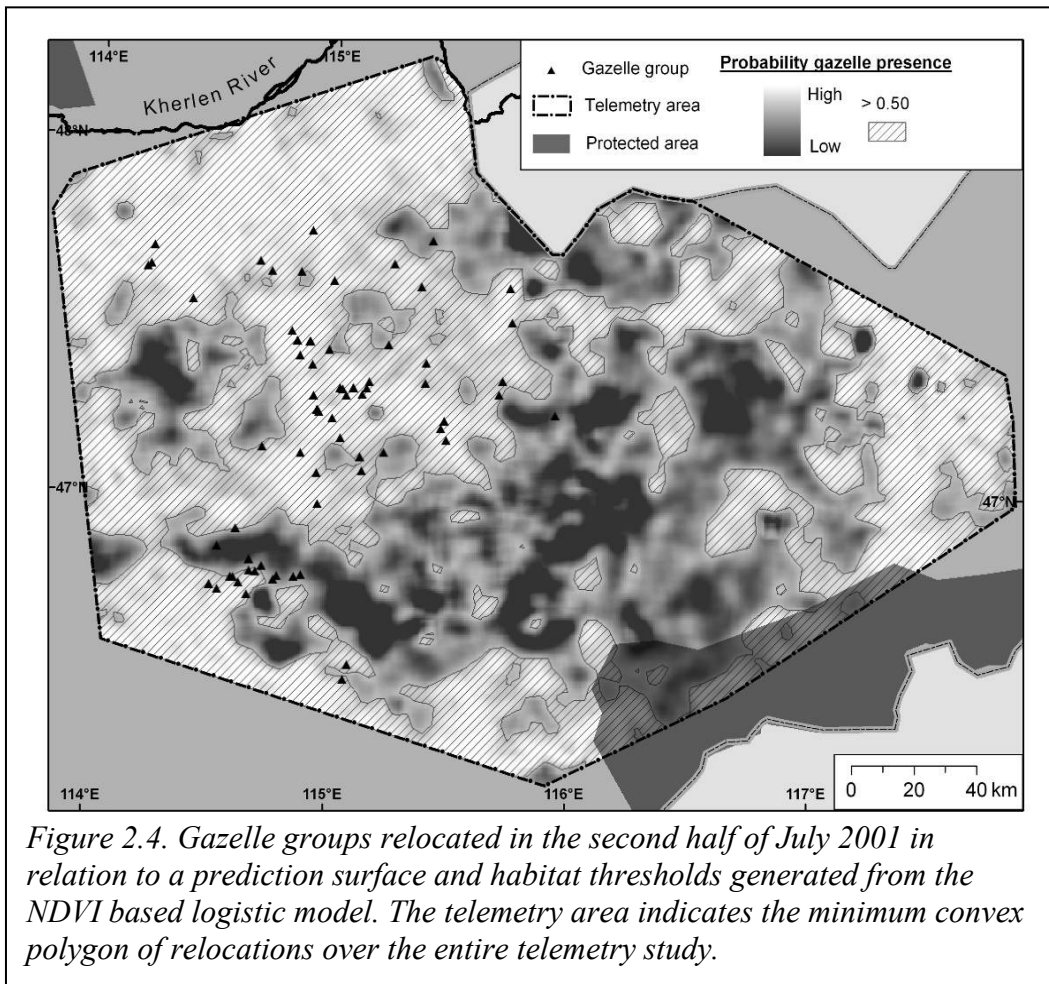


Figure 2.4. Gazelle groups relocated in the second half of July 2001 in relation to a prediction surface and habitat thresholds generated from the NDVI based logistic model. The telemetry area indicates the minimum convex polygon of relocations over the entire telemetry study.

Discussion

Gazelle habitat selection and NDVI

We assessed habitat selection of Mongolian gazelle with regard to vegetation productivity and found a significant relationship between NDVI and gazelle

occurrence. Omission errors for both models (with and without spatial autocorrelation) were generally low and only few gazelle presence locations (24% and 23% respectively) occurred outside the predicted areas. Consistently, 85% of gazelle relocations from the telemetry study were found within the predicted range. Gazelles preferred an intermediate range of NDVI values independent of variation in total biomass between surveys or survey season.

While areas with low vegetation productivity may simply not offer sufficient forage quantity, resources in high productivity areas are expected to be limited by altered plant stoichiometry (i.e. changes in C:N:P ratios) and an overall decrease in forage quality (Moe *et al.* 2005). As grasses mature they accumulate structural tissues and their fiber content increases, reducing their digestibility (McNaughton 1984, 1985). Previous studies have related vegetation nutritional content, vegetation quantity and growth state with the foraging ecology of different herbivores (Murray & Brown 1993; Murray & Illius 2000; Wilmshurst *et al.* 1999). Additionally satellite-based biomass estimates may not only capture quantity but also indirectly measure vegetation quality. Kawamura *et al.* (2005a) established a negative relationship between relative protein content and the Enhanced Vegetation Index (EVI) for Inner Mongolia, an area close to our study site. Previous studies relating gazelle presence with NDVI were based on less extensive data on gazelle distributions and focused solely on forage quantity in explaining gazelle occurrence (Leimgruber *et al.* 2001; Ito *et al.* 2005, 2006). The present study demonstrates that consideration of forage quality-quantity trade offs may be important for broad-scale satellite-based habitat models for wild ungulates in temperate grasslands, and suggests that future

investigations how satellite estimates of vegetation may be related to plant stoichiometry might be worthwhile. Specifically interesting in that respect would be to compare our method to the approach of Boone, Thirgood & Hopcraft (2006). They calculated the difference of two NDVI scenes and focused on new vegetation growth as one habitat-quality measure for wildebeest in the Serengeti.

NDVI alone, however, was not useful in discriminating gazelle absence. Many areas that were classified as suitable for gazelles had none, a result of excluding spatial autocorrelation in the model. For a constantly moving species it may simply be that not all suitable habitat is used at any one moment. False negatives are a critical problem in predicting mobile species habitats (Tyre *et al.* 2003). Longer term or repeated observations may be necessary to gain higher confidence about gazelle absence, but they would be logistically difficult to conduct. Additionally, not only elimination of false negatives but other covariates than vegetation productivity may be instrumental to refine the current model. Three additional factors which potentially influence gazelle habitat selection seem to be particular worth considering. First, variation in plant species composition may go along with differences in nutritional quality (Hooper & Vitousek 1998; Reich *et al.* 2001) while productivity rates are similar. Information about species composition and their spatiotemporal dynamics may thus aid efforts to predict gazelle presence. Second, anthropogenic influences, despite the area's sparse human population, may be important, and spatial variation in density of herders may be an informative covariate. Finally, insect harassment has been shown to significantly affect caribou (*Rangifer tarandus*; Walsh *et al.* 1992; Toupin, Huot & Manseau 1996; Weladji, Holand, & Almøy 2003).

Mosquitoes and biting flies are temporarily abundant at high densities in parts of the eastern steppes. Detailed data on any of these covariates were not available to apply to the gazelle survey data used in this study and would require additional extensive and repeated field surveys. Obtaining these data would be particularly important to disentangle which of these covariates may be confounded with NDVI, i.e., the degree to which species composition, insect density and/or human density are interrelated with NDVI. We also know little about habitat selection throughout winter; nutritional quality of forage in winter generally decreases and the physiology of the rumen in Mongolian gazelles adapts by shifting towards a grazer oriented digestive strategy (Jiang *et al.* 2002a, b, 2003). Consequently, gazelle habitat selection potentially could switch towards a preference of higher biomass areas in winter.

Habitat variability

Throughout the four surveys we observed a high degree of spatiotemporal heterogeneity of gazelle habitat. While in each season 50-65% of the area was classified as gazelle habitat, the total overlap was only 15%. This is very close to what would be expected if habitats had no temporal or spatial autocorrelation and would be randomly distributed (11%) and relatively far from the minimum variation at total overlap (49%). Heterogeneity seems to be specifically prominent in the central part of our study area (Fig. 2.3). These shifts in resource availability not only demonstrate the species area needs, which are dynamic and may shift between years; it also may illustrate why movement of gazelles appear so irregular and nomadic. Under a regular and seasonal migration regime we would have expected that the habitat overlap within season and between years would be greater than the habitat

overlap between seasons. This was not the case as the average between season overlap was slightly higher (46%) compared to the within season overlap (43%). Habitat heterogeneity may be the critical factor explaining far ranging and irregular movement behavior enlarging Mongolian gazelles' area needs as has been demonstrated previously for Thompson gazelles (*Gazella thomsoni*, Fryxell *et al.* 2005).

Yet, little is known about the mechanisms that drive the spatiotemporal variability in plant communities and/or quantity we detected based on NDVI - satellite imagery. There is, however, evidence for pronounced variation in plant phenology and reversible, non-equilibrium dynamics of plant communities (Briske, Fuhlendorf, & Smeins 2003, 2005) when measured on a temporal scale. Comparison of climatic patterns with date of onset of green-up suggests that climatic variation may be a major factor driving changes and interannual variation in plant phenology (Lee *et al.* 2002, Inner Mongolia). Fernandez-Gimenez & Allen-Diaz (1999) demonstrated for a steppe area in central Mongolia that variation in biomass, species cover and functional group cover (forb versus grass) were all dependent on both grazing intensity and climatic variability. Identifying to what degree grazing intensities of Mongolian gazelles are sufficient to allow them to shape their own habitat (Hobbs & Swift 1988), as do livestock in Mongolia (Fernandez-Gimenez & Allen-Diaz 1999; Kawamura *et al.* 2005a) or wild ungulates in other grasslands (e.g. Serengeti, McNaughton 1984, 1985, Murray & Illius 2000), is critical to understanding the grazing ecology of the eastern steppes.

Conservation implications and future applications

Long-distance movement behavior of grassland ungulates, such as Mongolian gazelles, increases their vulnerability to habitat loss and fragmentation (Murray & Illius 1996; Berger 2004). Ungulates often need to move across large areas to follow shifts in resource availability (Sinclair 1983; McNaughton 1985; Fryxell, Greever & Sinclair 1988; Murray 1995). Existing protected areas systems usually cover only a fraction of these areas (e.g. wildebeest, McNaughton 1985; Sinclair & Arcese 1995; Thirgood *et al.* 2004; pronghorn *Antilocapra americana*, Berger 2004; caribou, Nellemann & Cameron 1998; saiga *Saiga tatarica*, Bekenov, Grackhev & Milner-Gulland 1998; and chiru *Pantholops hodgsoni*, Schaller 1998a), leaving these species exposed to increasing threats of development and poaching.

Mongolian gazelles and their habitat are under increasing threats from intense hunting, transportation infrastructure development, and oil extraction activities (Pentilla 1994; Reading *et al.* 1998; Asian Development Bank 2002). In 1995, Mongolia's Ministry of Nature and Environment established a series of protected areas and nature reserves to conserve Mongolian gazelles, covering approximately 18,800 km², but this represents less than 5% of the gazelle's estimated 475,000 km² range (Finch 1996). In this study we show that throughout four surveys, only 1% of the study area was consistently classified as gazelle habitat and located within protected areas. The ranges of Mongolian gazelle are simply too large and variable to be completely included within a single protected area and excluding humans from these ranges would negatively affect traditional pastoralist societies and is unrealistic. The long-term conservation of Mongolian gazelles requires the development of

landscape-level conservation strategies for the region (Leimgruber *et al.* 2001; Jiang *et al.* 2003; Zahler *et al.* 2004). Landscape level approaches which facilitate traditional rangeland use retain intact grasslands and simultaneously promote protection of migrating wild ungulates are required (Coppolillo 2000). The impacts of deviating from policies promoting open rangelands can be observed in many places. Examples are the changing land use patterns in the Kenyan side of the Serengeti-Mara ecosystem resulting in declines of wildlife populations (Serneels & Lambin 2001), the construction of irrigation canals and intensive sedentary livestock grazing in Kazakhstan and Kalmykia resulting in disruption of saiga migrations (Milner-Gulland 1994), and the fencing in Inner Mongolia, China leading to severe land degradation (Williams 1996).

Our approach using satellite based estimates of vegetation productivity to predict wildlife habitat requirements can directly inform such landscape level strategies. Wherever an integrative and large scale conservation framework for grassland ungulates is needed, dynamic models based on high temporal resolution satellite data can predict habitat patterns for critical periods in their life history (e.g. for Mongolian gazelles calving in late June). Interannual variability of these habitats can also be assessed. Predicted habitat use may then be combined with human land use needs to create a dynamic management framework that defines conservation actions. It would contain measures that are specific in time and space (e.g. hunting restrictions, limits on vehicle access or other disturbance, livestock grazing restrictions, fence removal) and mitigate between conflicting interests of rangeland use and wildlife needs.

Future research applications and needs include ground truthing to empirically corroborate the relationship between NDVI and forage quantity and digestibility, delineating and estimating inter-annual variability of calving grounds, and the assessment of long-term spatial and temporal patterns in grassland productivity and gazelle habitats in the eastern steppes.

Chapter 3: Integrating individual search and navigation behaviors in mechanistic movement models

Co-authored with: *W.F. Fagan* and *V. Grimm*

Abstract

To understand complex movement behaviors, researchers have tried many approaches ranging from manipulative experiments investigating navigation behavior to statistical decomposition of movement paths. Although the importance of different movement behaviors has been widely recognized, systematic modeling frameworks to integrate these behaviors in one single model remain elusive.

Toward such a unification, we differentiate among three fundamentally different classes of mechanistic movement behaviors and distinguish (1) non-oriented movements based on random movement in response to proximate stimuli, (2) oriented movements utilizing perceptual cues from distant targets, and (3) memory mechanisms that assume prior knowledge of a target's location. We propose that each of these movement behaviors is linked to certain cognitive abilities and sensory stimuli which in turn can be represented by state variables in models. Adapting techniques from studies on artificial evolution and intelligence, we built a theoretical simulation model wherein individuals, using information provided by state variables,

evolve movement behaviors adaptively in response to the landscapes on which they search and navigate.

To develop this model, we implemented an individual-based neural network genetic algorithm (ING) in which information that forms the input to individual's movement decisions are specific to each of the three classes of movement behaviors. In this system, state variables with perceptual information represent oriented movements, state variables with information about turn angles and resource uptake represent non-oriented movements, and state variables providing information on an animal's spatiotemporal position are linked to memory. By altering these state variables for the model input, we tested their contributions to movement under different landscape scenarios. In particular, we contrasted movement behaviors that emerge in landscapes where movement targets (i.e. resources) were predictably distributed at the same location versus scenarios where resources were unpredictable. We demonstrated that individuals evolved to rely more heavily on state variables related to memory if their landscape dynamics were predictable. In contrast, non-oriented movement evolved predominately in situations where landscape dynamics were unpredictable. Oriented movement proved important at smaller scales, when movement targets were distributed within perceptual ranges.

Although this study introduces a theoretical framework, we suggest that the ideas discussed here may be readily adapted to fit simulations to empirical movement paths. Reproducing empirical movement paths using state variables related to specific movement behaviors may help reveal how real animals employ underlying behavioral mechanisms in particular empirical settings.

Introduction

Animal movements are central to population ecology because many spatial processes (e.g., disease spread, metapopulation dynamics) and applications (e.g., reserve design) critically depend on the movement behavior of individuals (Patterson et al. 2008). The importance of movement ecology has recently received much recognition (e.g., Holden 2006) and advancements have been made in several areas. For example, progress has been made in manipulative experiments, in which researchers expose individual animals to artificially changed environments to test for the existence of specific hypothesized navigation mechanisms. In one key study, a clock-shifting experiment with pigeons generated internal conflicts between sun-compass and landmark information and revealed how both memorized landmarks and compass navigation inform homing navigation of pigeons (Biro et al. 2007). Progress has also been made in statistical models that discern movement states from properties of movement paths. For example, state space models of movement paths of elk can distinguish among alternative movement states such as encamped foraging walks versus exploratory walks and identify environmental covariates that trigger changes between states (Morales et al. 2005).

Despite these advances, a key challenge remains: How can qualitatively different mechanistic movement behaviors be integrated into individual models? For example, how can a single model integrate search behaviors, such as would be necessary to locate an unknown food source, with homing behavior necessary to relocate a nest site? Many animals exhibit such combinations of behaviors, including species that practice central place foraging or home range maintenance (Bovet and

Benhamou 1991, Gautestad and Mysterud 2005, Fagan et al. 2007, Wang and Grimm 2007, Boerger et al. 2008). Albatrosses, which routinely search for previously unknown locations of prey and also must exhibit homing behavior to a breeding colony, constitute a particularly clear case where a single species exhibits strongly contrasting movement behaviors. While search behaviors may be driven by a combination of optimality of search moves and sensing ranges (Bell 1991, Viswanathan et al. 1999, Edwards et al. 2007), homing behaviors may be based on memory and depend on environmental idiosyncrasies and the individual itself (Bonadonna et al. 2005.).

Mueller and Fagan (2008) classify active animal movements into three major categories. The first class contains non-oriented mechanisms that involve movements with random directions. Here, the animal reacts to a sensory stimulus that originates from an animal's current location by altering its velocity or turning angle (Kareiva and Odell 1987, Benhamou and Bovet 1989). One such local stimulus could be resource uptake: high resource uptake can produce lower velocity and more frequent, less correlated turns leading to an encamped walking pattern ("area restricted search"). In contrast, lower quality habitats may result in "explorative walks" with higher velocity and correlated turns (Kareiva and Odell 1987, Morales et al. 2004). Mathematically, non-oriented movements have been frequently described as correlated random walks (Turchin 1998).

The second class of animal movements involves oriented mechanisms. These mechanisms rely on perceptual cues that, unlike stimuli for non-oriented mechanisms, originate from distant locations and result in movements in predictable directions

(i.e., towards or away from the direction of a stimulus). Oriented mechanisms are usually limited by the perceptual ranges of their sensory cues (e.g. visual, olfactory, acoustic; Zollner and Lima 1999b, Croney et al. 2003, Schooley and Wiens 2003).

The third class describes memory mechanisms, where previous information about the location of the movement target is important. In general this information may derive from different sources: the recollection of an individual's own history, communication from conspecifics, or as a genetic inheritance from its ancestors (Benhamou 1994, Bowen et al. 2004, Winter and Stich 2005, Mueller and Fagan 2008 and references therein). These three classes of movement mechanisms likely act simultaneously at different spatial scales (Bailey et al. 1996). To understand why an individual moves the way it does, ecologists need a systematic approach that integrates across them.

Recent approaches have tried to combine such qualitatively different processes into models. For example, models about home range behavior, wherein animals restrict their movements to smaller areas than would be expected from observed levels of mobility (Boerger et al. 2008), have combined non-oriented and memory movements via self-attracting random walk models (Tan et al. 2001). Other models have combined non-oriented movement with perceptual ranges (e.g., Nams et al. 2006) to detected oriented behavior. However, so far no systematic synthesis of all three movement types has been proposed. To make progress toward such a unification, we adopted a Lagrangian (individual-based) approach and assumed resource availability as a major driver of movement decisions. We built on a recently proposed technique in evolutionary programming and artificial intelligence called

individual-based neural network genetic algorithms (INGs, Huse et al. 1999, Strand et al. 2002) to demonstrate, in a theoretical context, how qualitatively different movement behaviors can be combined into individual models. Importantly, we also demonstrate one way to assess and quantify the relative importance of these alternative movement behaviors within a given scenario of resource dynamics (e.g., landscapes with predictably available versus unpredictable resources).

Modeling background

In ING models for movement, an individual employs at each movement step an artificial neural network (ANN, Hopfield 1982) for a behavioral decision. The ANN uses context-specific state variables as an input layer and converts them into a single movement response. To do this, individuals carry specific weights (i.e., their ‘genetic code’ in the model) that are used to transform the state variables and the interconnections in the network. A genetic algorithm (GA, Goldberg 1989) evolutionarily trains those weights by differentially selecting, reproducing, and modifying those individuals in a population which, at the end of their lifecycle, made the better moves with regard to a fitness measure such as resource uptake. In this way, state variables are transformed to produce near-optimal movement decisions (for model details see methods section below). This method is advantageous because it is not contingent on predetermined behavioral rules. Finding or defining such rules for optimal movement behavior is often difficult, especially when many factors are important to movement decisions, when those factors are interconnected and context-specific, or when those factors are time-dependent (Morales et al. 2005). In ING models, movement decisions are an emergent behavior limited by the input

information of the state variables and optimized relative to its fitness measure. In ecology this technique has been used to model one dimensional fish behavior (Huse et al. 1999, Strand et al. 2002), and more recently, to model two dimensional elk movements (Morales et al. 2005). However these models were intended to reproduce an empirical pattern, rather than to investigate different types of movement behavior, which is the goal of this paper.

Here we present a new approach as we built an ING model where the input information for the ANN was characteristic as it represented cognitive information and sensory stimuli that were specific for single movement mechanisms. For example, information about previous movement angles represented non-oriented mechanisms. Similarly, spatial information on movement targets within perceptual ranges represented oriented mechanisms and spatiotemporal information of an animal's position were unique to spatial memory mechanisms. By adding or removing these mechanism-specific state variables from an ANN that governs movement, we tested the effects of those variables (i.e., mechanisms) with regard to a fitness criterion such as foraging success under different landscape scenarios.

We varied landscape scenarios in that resource patches could be either predictably distributed at always the same location, or the location of resource patches was unpredictable. We expected animals to evolve movement behaviors according to these differences in resource landscapes: For predictable resource landscapes we hypothesized that state variables related to spatial memory would have much greater importance whereas non-oriented behavior should be more important and used more often in landscapes with unpredictable resource patches. Finally we

expected oriented movement to be the key mechanism of exploiting resources within patches at scales where they did occur within perceptual ranges.

Methods

Model

The following model description follows the ODD (Overview, Design concepts, and Details) protocol of Grimm et al. (2006), that was developed to standardize model descriptions for individual-based models in ecology.

Purpose: The purpose of our model was to evolutionarily train model organisms to use and combine different types of information representing different movement behaviors (i.e., memory, oriented, and non-oriented movements). The model allowed testing the efficiency of these behaviors and their combinations in different resource landscapes.

State variables and scales: The model consisted of individuals and landscapes. Landscapes were 64 * 64 cell grids with reflective boundaries. Each grid cell of a landscape either held a resource (i.e. its value was one) or was empty (i.e. its value was 0). Resources were distributed in two quadratic 8*8 patches. Landscapes principally varied in one key way: The resource patches were either distributed in a predictable fashion and their location did not change over the course of a simulation or they were unpredictable and their location was random (for further details see initialization below).

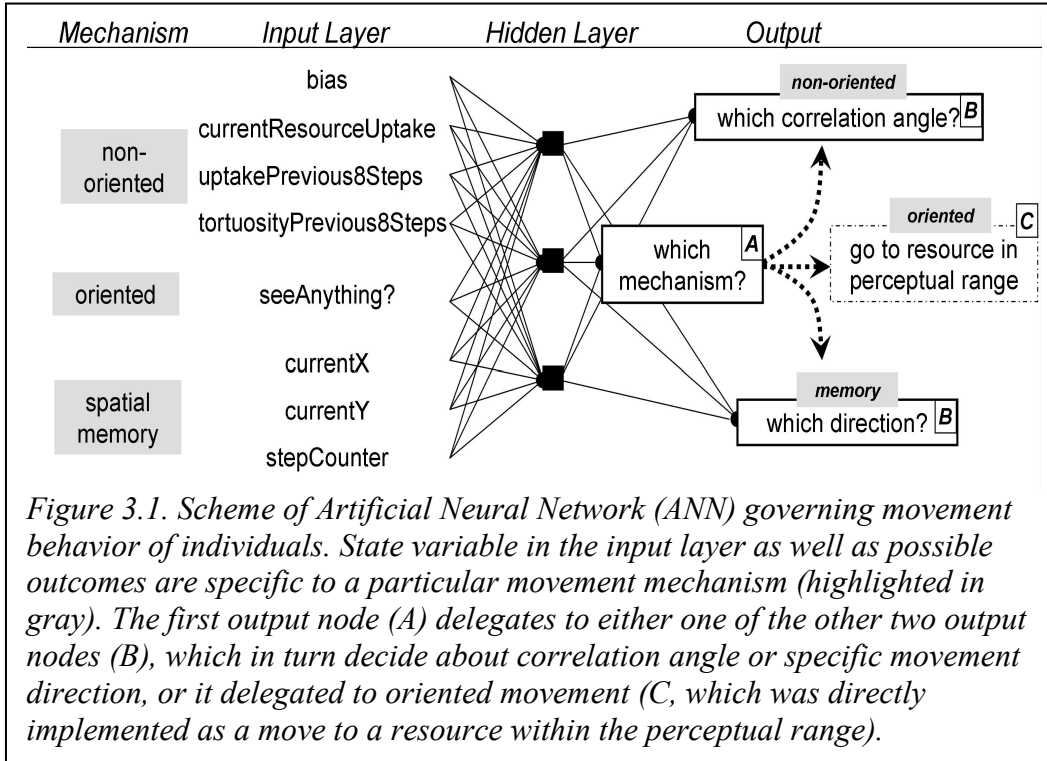
Individuals were characterized by their location, seven variables with cognitive information or sensory stimuli related to movement mechanisms, a string of

variables that held the individual's genetic code, and a variable counting the individual's resource uptake.

An individual's location was specified by the landscape cell it occupied. Among the mechanism-related variables, three variables pertained to memory-related movements. They held information about the current x and y coordinates of the individual, as well as a time/step counter. Information for non-oriented movement was represented by three variables that described the tortuosity of the previous eight movement steps (see section submodels for further detail), resource uptake within the last eight steps, and resource uptake of only the very last movement step. Information relevant for oriented moves was described by one variable that held information about whether a cell that contained resources was within the perceptual range. The perceptual range of an individual was limited to the eight neighboring cells of an individual's current location.

The individual's genetic code consisted of weights that were used within its ANN to transform the values of the information provided by the movement mechanism related state variables into a movement decision. The ANN was a fully connected feed forward network that had eight nodes (seven for the mechanism-related variables described above and one bias unit) in the input layer, three nodes in a single hidden layer, and three nodes in the output layer (boxes with solid outline in Fig. 3.1). Consequently each individual held 33 [$(7 \text{ nodes of input layer} + 1 \text{ bias}) * 3 \text{ nodes in hidden layer} + 3 \text{ nodes in hidden layer} * 3 \text{ nodes of output layer}$] variables that were weights for the connections in the ANN (solid lines in Fig. 3.1) in its genetic code. The nodes in the output layer defined the movement decision as follows

(Fig. 3.1):

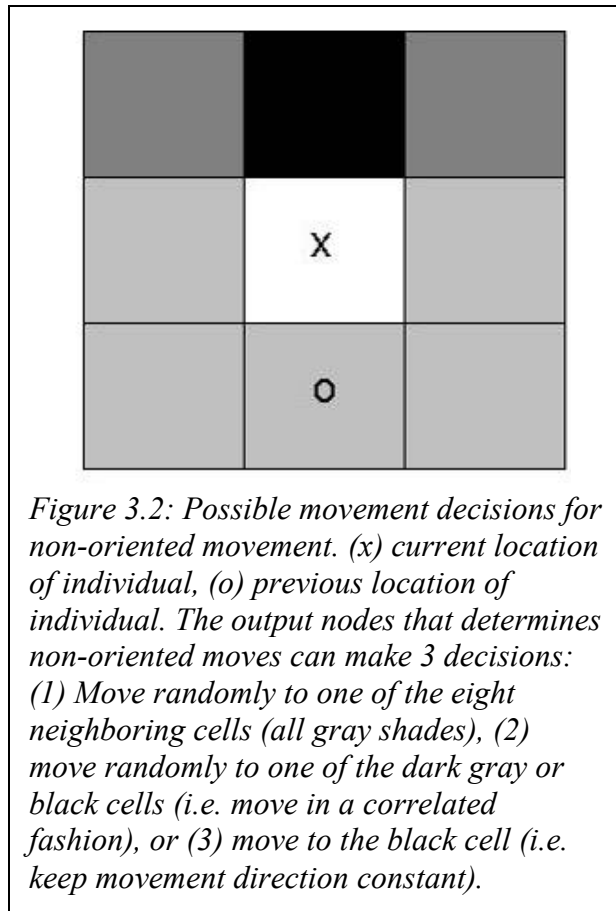


First, one of the three output nodes (node A in Fig. 3.1) determined the general movement type: Based on the value of this first node, individuals either performed a non-oriented, an oriented, or a memory-based movement step and the final outcome was delegated to one of 3 choices (dotted arrows in Fig. 3.1).

(1) Non-oriented movement: in this case the decision was delegated to a second node in the output-layer (upper node B in Fig. 3.1), which made a decision about 3 possible final outcomes: (a) keep the direction and move straight (b) move with correlated turning angle, i.e. randomly choose the cell straight ahead or one of its neighboring cells, (c) move uncorrelated, i.e. randomly choose one of the eight surrounding cells (see Fig. 3.2).

(2) Movement based on memory: here the decision was delegated to a third node in the output layer (lower node B in Fig. 3.1), which made a specific decision to move to one particular cell in its neighborhood.

(3) Oriented movement:
 in this case the individual moved to the cell where a resource was within the perceptual range (outcome C in Fig. 3.1). If no resources were within the perceptual range individuals moved randomly to one of the eight neighboring cells. If multiple resources were detected, one of them was randomly chosen as new location.



Finally an individual

featured a counter that kept track of all resources an individual encountered throughout its lifetime. The value of this counter at the end of an individual's life cycle provided a fitness measure. Each simulation ran 5,000 generations.

Process overview and scheduling: Within each generation 200 individuals consecutively moved 150 steps across landscapes. After all individuals of one generation had finished their moves they reproduced and died.

Design concepts:

Emergence: In contrast to most IBMs, our model included emergence at the level of the individuals: movement decisions and, in turn, movement patterns were emergent and not imposed. In particular, which of the possible output nodes that relate to a specific mechanism were used at a particular movement step and how, i.e. where to move (in case of memory based movements) or what correlation angle to choose (in case non-oriented movement was chosen), were dependent on each individual's weights for the ANN. These weights were not imposed, but evolved. Individuals started with random weights which were reproduced relative to their success in governing movement decision to find resources. If, for example, in memory related movements, weights of a particular individual had values that used the information of its spatiotemporal location to navigate to a certain area, chances for it to reproduce and increase the frequency of those weights were higher if that particular area contained resources. Thus, individuals could learn how to navigate to certain resource locations by evolving weights that allowed them to use information on their current position into movement steps towards locations that had proven advantageous in previous generations (e.g., locations that contained resources).

Adaptation and Fitness: Individuals made adaptive movement decision based on the weights in their ANNs which, in turn, were the result of genetic algorithms. The fitness measure used for the genetic algorithms was total resource uptake at the end of a generation.

Sensing: All mechanism-specific state variables represented sensing and provided critical information each individual used for its movement decisions.

Interaction: The model did not include interaction among individuals, neither direct interactions nor indirect interactions via resource use.

Stochasticity: Stochasticity entered the model in three ways. (1) The starting position of each individual was random. (2) If the individual chose to move non-oriented the movement decision was a random walk, likewise if it decided to move oriented and sensed multiple resource cells in its neighborhood one of these resource locations were chosen randomly and (3) Resource landscapes: If adjusted to be unpredictable, locations of resources were randomly chosen anew for each generation. If adjusted to be predictable resource locations were static within the simulation (i.e., across generations); however at the beginning of each simulation they were also randomly chosen.

Observation: We recorded the average resource gain for the population in each simulation ($n = 100$) for each generation to trace how the overall fitness increased across generations. For the last ten generations, when individuals were adapted to their respective resource landscapes, we also recorded (for a sample of 10 individuals in each of the 100 populations (total $n = 1000$) at each step) which output node of the ANN was used to make a movement decision and traced individual movement paths.

Initialization

Individuals: In the first generation the ANN weights of each individual were randomly initialized with values from 5 to -5. At each generation before an individual started to walk, the starting position was randomly chosen. Also, at the beginning of

each walk the values for perception, tortuosity, and current resource gain were set to zero.

Landscapes: For predictable landscapes the location of resource patches were randomly chosen at the start of each simulation and did not change across generations. Between generations and between runs of different individuals resources got replenished, so that before each run resource landscapes were identical. In unpredictable landscapes the location of resource patches was randomly chosen between each generation. Within a generation though the location of resources patches did not vary and again all resources were replenished between runs of different individuals.

Submodels

Individual movements: At each step an individual could move to one of its eight neighboring grid cells in the binary resource landscape. If its location was at the boundary or corner of the landscape, only five or three neighboring grid cells, respectively, were available. If it encountered a resource the respective landscape cell was set to be empty (i.e., 0) and the resource counter of the individual increased by one (there was no re-growth of resources). The decision to which of the eight possible directions to move was made by the ANN. At each step the individual decided based on the information-providing variables and the individual specific weights (i.e., genetic code), first which mechanism to use and second how to move based on the chosen mechanism. A movement decision was represented by either a specific neighborhood to move to (i.e. if oriented or memory output nodes were chosen) or a correlation angle (if the non-oriented mechanism was chosen). After each movement

step the information-providing state variables were updated. Once an individual had completed all its steps the landscape got reinitialized with resources and the next individual performed its moves.

Reproduction: Once all individuals in a generation had completed their movements, they reproduced. Individuals that had collected more resources were more likely to reproduce than individuals that moved less successfully: We chose to use tournament selection to determine which individuals would be transferred into the next generation (Goldberg and Deb 1991): Always six individuals in a population were compared to each other and the individual that had collected the most resources was selected and copied six times into the new generation. The other five individuals did not reproduce and their genetic code was lost for future generations. The total number of individuals was constant throughout the entire simulation.

As a final step within each generation, after reproduction, the genetic code (i.e., the weight-variables) of each individual of the new generation was modified via crossing-over and mutation. The chance to have a crossover event in an individual was 20 percent and the chance of having a mutation event was set to two percent per locus. For crossing-over events the string of weights for the ANN of a randomly chosen individual was cut-off at a random location and the cut part was exchanged with the respective code of another (randomly chosen) individual. Mutations occurred at a random individual at a random location of the string and resulted in a new random initialization of that particular weight (with values from -5 to 5, see initialization). Crossing over and mutations did not occur in the final 20 generations

to eliminate noise and allow measuring the adaptive fitness of a population at the end of its training/evolution.

Artificial Neural Network: At each movement step the ANN combined values of the mechanism-related state variables with their specific weights of the genetic code to calculate values for the hidden nodes and after that the output nodes which determined the movement decision. To calculate values for each of the three nodes in the hidden layer of the network all values of the input layer were multiplied with their respective weights, summed, and transformed with a sigmoidal function to values between 0 and 1 (Eq. 1).

$$\text{Eq. 1: } \frac{\exp\left(\sum_{j=1}^{nodes} w_j * node_j\right)}{\exp\left(\sum_{j=1}^{nodes} w_j * node_j\right) + 1}$$

Analogously, the values for the three output nodes were calculated by multiplying the values of the hidden layer with their specific weights, summing them and transforming them with a sigmoidal function to values between 0 and 1 (Eq. 1).

A decision of an output node was determined by dividing the range of output values (i.e. values between 0 and 1) in sections, that each represented one of the choices an output node could make. For example, the first output node that decided upon the three subsequent movement mechanisms were determined by dividing the range in three sections, each of which codes for a specific decision: 0 - 0.33 (oriented movement), >.33 - .66 (non-oriented movement), and >.66 – 1 (memory). Similar the decisions for non-oriented movements were achieved by dividing the range from 0-1 in three section that code for straight, correlated or uncorrelated movement. Likewise the output node for memory was divided in eight subsections (0 - 0.125, >0.125-.25,

and so forth) each of which coded for one of the eight possible directions an individual could move.

Tortuosity: We considered tortuosity of a walk as a measure for the search effort an individual was making in its immediate neighborhood (i.e., area restricted search). For a movement step that was oriented or a memory move the value for tortuosity was 0 since we assumed that the individual navigated to a known target rather than search. Likewise, for a non-oriented movement step that was straight we considered the search effort to be minimal and the value for tortuosity for that particular movement step was 0. However, if movement was correlated, the search effort was considered to be medium and the value for tortuosity for that particular step was given the value 1. If the individual was completely random the search effort was considered to be at its maximum and the value was set to 9. Tortuosity values for the past eight movement steps were summed up to provide an individual with information about recent search moves in the input layer of the ANN (Fig. 3.1). In combination with recent resource uptake, tortuosity should be valuable information in patchy landscapes such as those chosen for this study to efficiently search using random walks.

Simulation experiments

We replicated each simulation 100 times to account for idiosyncrasies in the evolutionary training of individuals as well as in particular landscape set-ups. For example, in predictable landscapes, resource location did not change over the course of a simulation, but even so, overall population fitness could vary depending on

whether the two resource patches were distributed far apart from or near to each other.

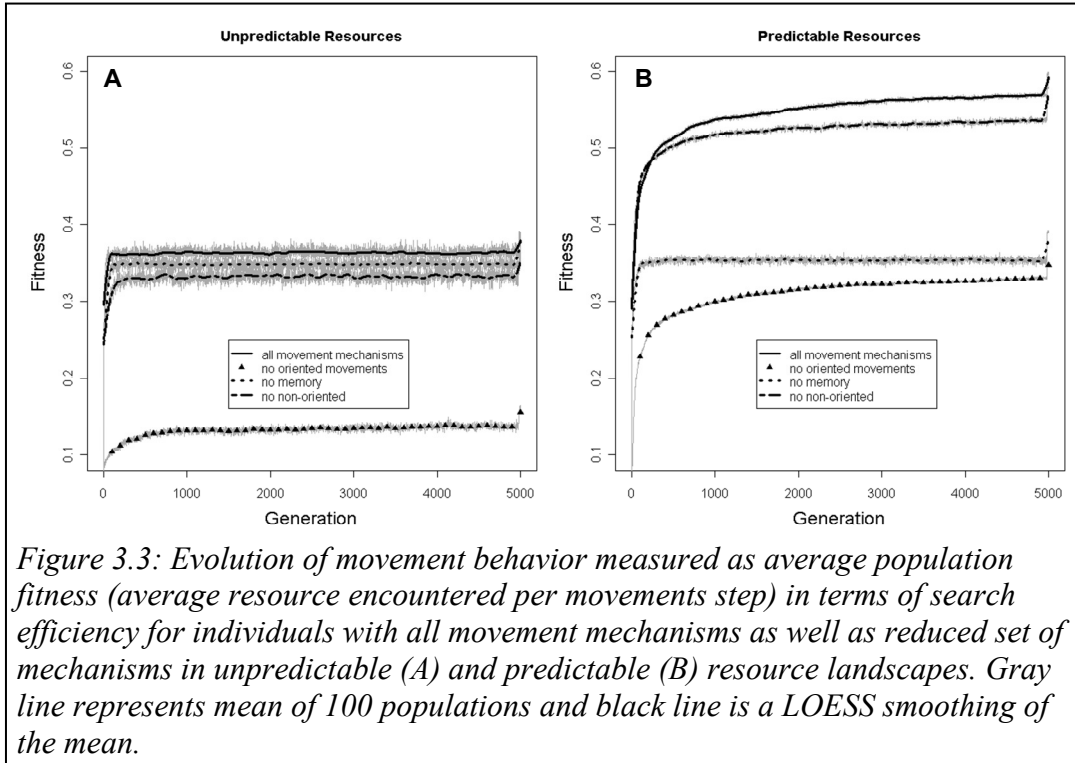
We ran simulations in predictable as well as unpredictable landscapes. In addition to experiments of individuals that had all input information available, we performed experiments that featured individuals where we removed one of the movement mechanisms to test its importance in particular landscape set ups (predictable or unpredictable resources). The network was reduced by the relevant state variables in the input layer as well as by the relevant output nodes.

Results

Individuals usually adapted within a few hundred generations, by which time the overall population fitness in finding resources did not improve any further after an initial steep increase (Fig. 3.3).

An exception included individuals in predictable landscapes that had memory-related state variables available: these populations also exhibited an initial steep increase in fitness but then continued to slowly increase their fitness and adapt to their resource landscapes (Fig. 3.3B). The last 20 generations populations were not exposed to any mutation and crossing-over events which removed any noise. That led to a final jump in fitness for all populations (Fig. 3.3). Generally the proportion of encountered resource cells was much higher compared to unpredictable resource

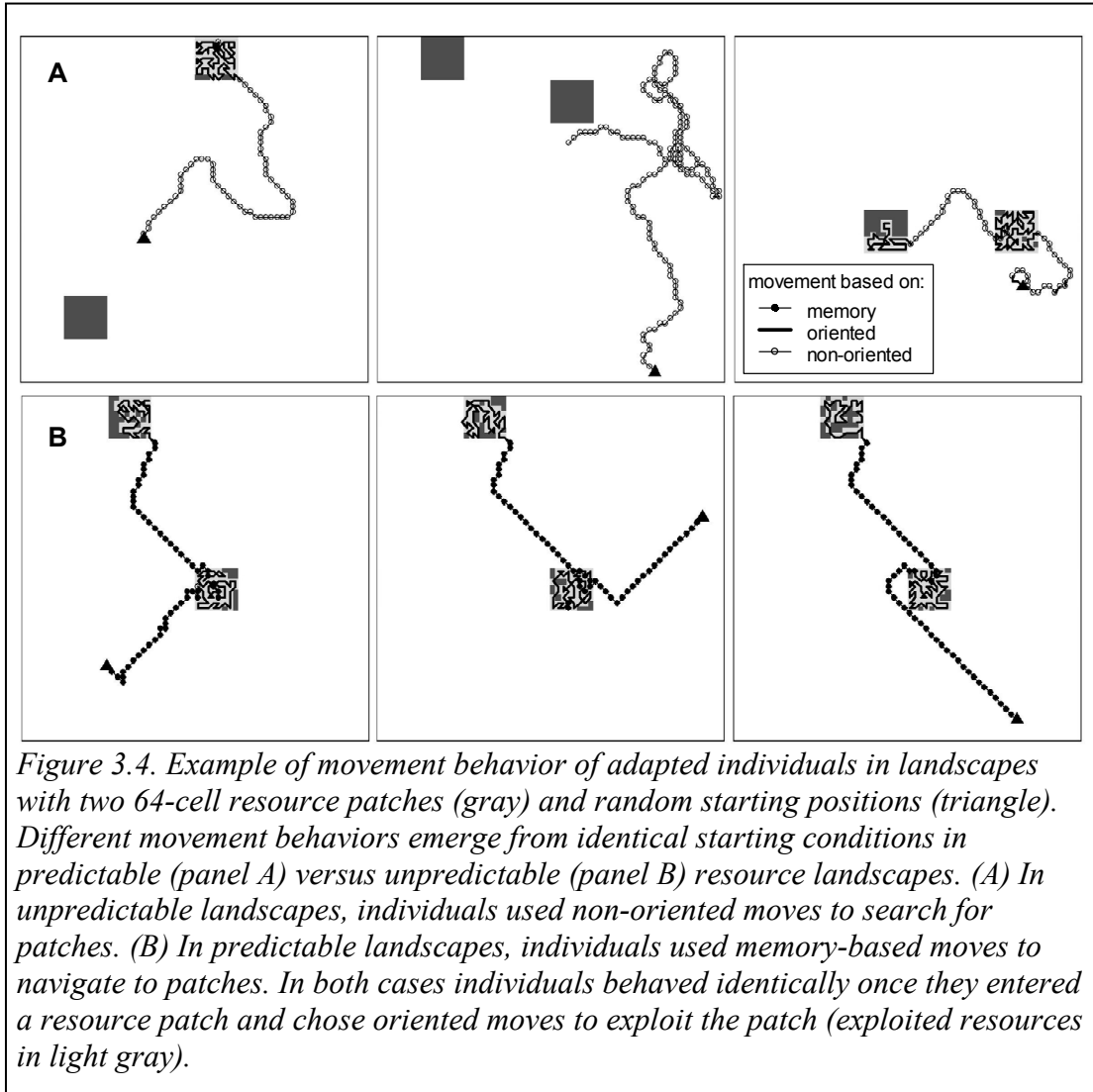
landscapes (Fig. 3.3).



In **unpredictable resource landscapes**, adapted individuals that had all movement mechanisms available usually used non-oriented movements to search for a resource patch (Table 3.1, Fig. 3.4A).

Upon encountering a resource patch individuals utilized oriented moves and returned to non-oriented moves after leaving a patch. A few populations adapted differently and used memory mechanisms to systematically search the landscape in a circular fashion (Table 3.1, Fig. 3.5C). However, upon encountering a resource patch,

they too used oriented movements.



If oriented information was removed from the ANN, most populations adapted to use solely non-oriented movements with correlated walks while searching for patches and uncorrelated “area restricted search” after encountering a patch (Table

3.1, Fig. 3.5A).

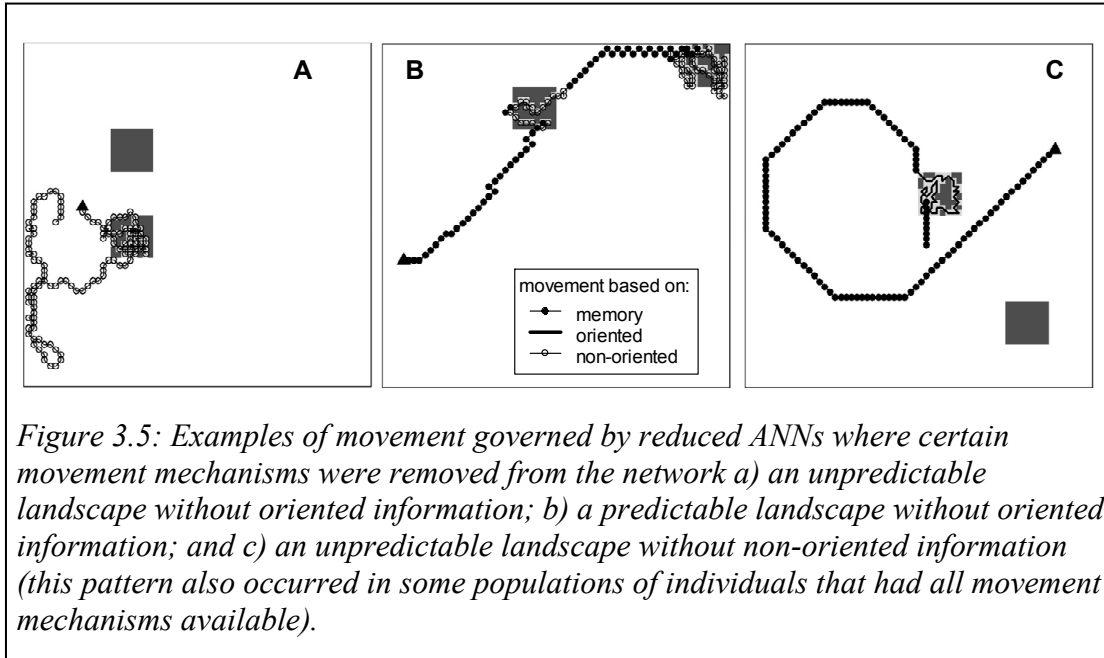


Table 3.1: Proportion of usage of different movement mechanisms (i.e. output nodes of the ANN) in individuals trained with a genetic algorithm. Each row sums to 1.0, reflecting differential reliance on alternative movement mechanisms in the different resource landscapes (predictable resources versus unpredictable resources).

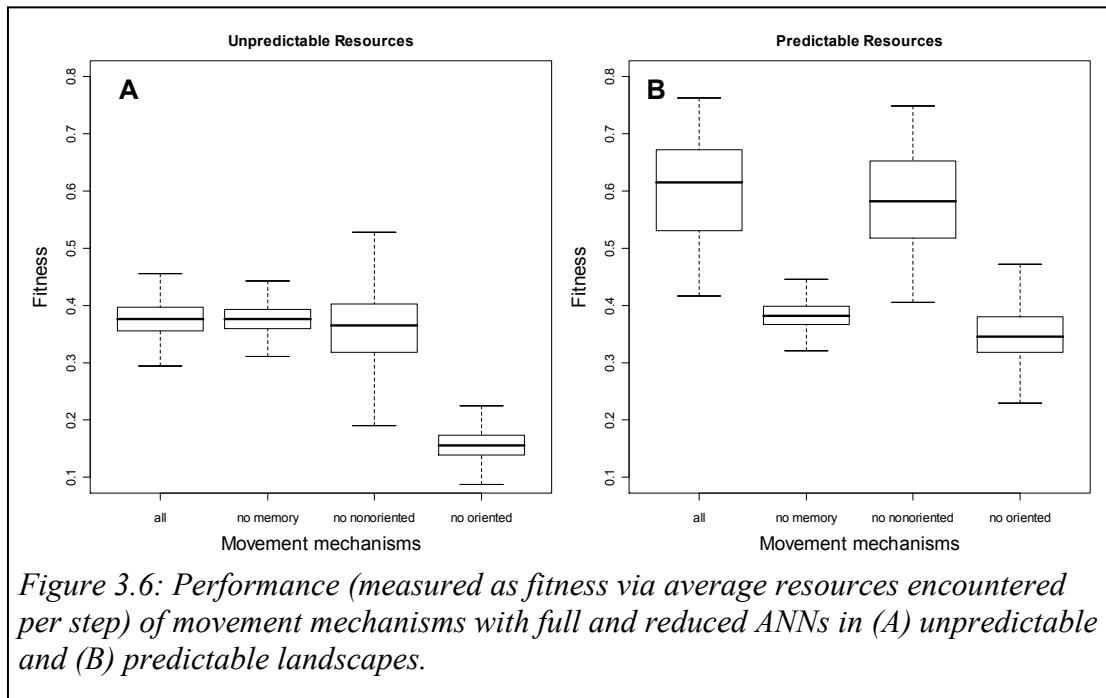
	<u>Movement mechanism utilized</u>		
	memory	oriented	non-oriented
Unpredictable resources			
<i>Available mechanisms:</i>			
All mechanisms	0.199	0.224	0.578
No memory	-	0.175	0.825
No non-oriented	0.630	0.370	-
No oriented	0.266	-	0.734
Predictable resource			
<i>Available mechanisms:</i>			
All mechanisms	0.468	0.492	0.040
No memory	-	0.185	0.815
No non-oriented	0.407	0.593	-
No oriented	0.904	-	0.096

In those populations lacking oriented moves, the drop in fitness in unpredictable landscapes was substantial from an average of 0.383 (SD: 0.056) encountered resource cells per movement step to 0.159 (SD: 0.037; Figs. 3.3A and

3.6A). In contrast there was no drop in fitness for unpredictable landscapes when memory was removed (mean: 0.384; SD: 0.044); memory-less individuals behaved as in the full model, except that no systematic searches occurred as was the case in occasionally in the full model. If non-oriented moves were removed, the average decrease in fitness was minimal (mean: 0.357); however, the standard deviation increased (0.086, Fig. 3.6A). In this case, organisms adapted to perform a circular and systematic search of the resource landscape (Fig. 3.5C), as described above.

In **predictable resource landscapes**, adapted individuals that had all movement mechanisms available used memory movements most of the time to navigate to a resource patch (Table 3.1, Fig. 3.4B). Regardless of the starting location, individuals typically navigated to the same resource patch first, and from there, approached the second patch (provided the starting position was favorable and the two patches were sufficiently close to allow such movement within the 150 step limit) (Fig. 3.4B). This movement behavior was most efficient and allowed the animals to exploit the majority of resource cells (average encountered resource cells per movement step was 0.597; SD: 0.096; Figs. 3.4B and 3.6B). The same efficiency was achieved when non-oriented movements were removed from the ANN (mean: 0.580, SD: 0.082), because non-oriented movements were rarely used in predictable landscapes when all mechanisms were available (Table 3.1). If oriented movement was removed from the ANN, a steep decline in movement efficiency occurred that was similar to that observed in unpredictable landscapes (mean: 0.350, SD: 0.055). In this case, memory was used for inter-patch movements, and once a patch was encountered, either memory or non-oriented movement was used to exploit resources

(Fig. 3.5B). If memory was removed, fitness was identical to the most efficient movement in unpredictable landscapes (mean: 0.390, SD: 0.041). Non-oriented moves were used for broad scale inter-patch searches whereas oriented moves were used to exploit a patch.



Discussion

Here we have demonstrated how qualitatively different movement behaviors can be integrated and compared in models when these behaviors are represented as cognitive information and sensory stimuli, which in turn are implemented as state variables. We used artificial evolution and intelligence techniques to transform these variables into movement decisions. Altering the type of information we provided for the model lead to different behavioral decisions which in turn allowed us to evaluate the value of that information with regard to movement in specific resource landscapes.

In our approach, individuals' movement behaviors were emergent properties: Whether and how individuals used specific information was not pre-defined but instead evolved relative to the available information and the optimization target (i.e., resource uptake). We provided our model organisms with qualitatively different information and output options, but gave the genetic algorithm freedom to combine that information and those options into a single quantitative response. That is a fundamentally different approach to many other models of animal movements in which rules are often predefined (Zollner and Lima 1999a).

In rule-based models, rules are typically defined *a priori* and are thus contingent on the modelers' ability to conceive how and when a particular movement mechanism is used and how it might interact with other mechanisms. The more mechanisms that are considered and the more complex the fitness problem that is defined, the more difficult it is to discern optimal movement rules. This might be a reason, why, despite the fact that the importance of these different movement behaviors is widely recognized, no studies had, to our knowledge, previously combined all three movement behaviors into models (but see Tan et al. 2001, Gautestad and Mysterud 2005, or Moorcroft et al. 2006 for cases where two mechanisms are included).

We presented a simple test scenario involving predictable versus unpredictable landscapes to demonstrate how the genetic algorithm (GA) used specific input information to find near-optimal solutions with regard to a particular movement problem. Individuals used the available information in sensible ways allowing us to evaluate hypotheses about which mechanisms should be most efficient

under specific conditions. As predicted, we found that memory-related variables were most important to individuals attempting to locate resource patches in predictable landscapes. In this case the weights in the GA evolved in a way that guided individuals to employ the memory output node which, in turn, was transformed by weights of the GA to use the information about individuals' spatiotemporal location to direct movement towards a resource patch. On the other hand, information on turn angles and resource uptake was advantageous in unpredictable landscapes, and weights from the GA determined that movement angles tended to be highly correlated to maximize chances of exploring the entire landscape. In both predictable and unpredictable landscapes, oriented movements were used to exploit resources within patches where resources were distributed within perceptual ranges, confirming another prediction.

Although we expected memory-related movement to be unsuitable for unpredictable landscapes, we found that memory related movements appeared to be almost as efficient as non-oriented movements in unpredictable landscapes (Table 3.1). For example, when we removed non-oriented movement from the ANN, average efficiency did not decrease considerable. Furthermore, in some replicates of our simulation studies with the full ANN, memory-related movement evolved when we predicted that non-oriented should have dominated. In these cases individuals evolved systematic circular searches that allowed them to exploit the entire foraging domain. We had not thought of this solution before, but it yielded similar average fitness compared to a non-oriented random walk. However, these systematic searches suffered a disadvantage compared to random walks in that variability in fitness

among different generations and populations was increased in the systematic searchers. Systematic searches with little variability in movement paths among individuals in the same population led to either success or failure of the majority of individuals. Variability in success among generations and populations was much lower if non-oriented movement was performed because each individual within generations moved along entirely different paths and at least some individuals in each generation were always successful to obtain some resources. Populations may have gone extinct if the majority of individuals in one generation would have failed to allocate any resources and non-oriented movement might have been much more advantageous if population sizes were flexible and the fitness target would have been required to maintain minimum energy reserves. However, in our model, population size was kept stable and extinction of populations was not possible. This suggests that the phenomenon of systematic searches would be unlikely to occur in more realistic modeling setups.

While solutions of the GA generally agree with our original predictions, they were not perfect. For example, in predictable landscapes animals navigated to one specific resource patch first independent of the animals' starting positions. Seemingly it would have been more sensible to evolve flexibility and always visit the closest resource patch first. This deviation from our predictions may have arisen from the movement constraints that we placed on model organisms. For example, in our simulation experiments, we assigned a fixed number of movement steps (150) to all individuals. That is, as long as resources were obtained within these steps it did not matter how many of them were actually used (i.e. a solution that exploited a certain

quantity of resources with 150 steps was considered equally good to a solution that exploited the same amount with fewer steps). Other deviations from our predictions may have occurred because our ANN was relatively simple. With a more complex ANN (or with larger population sizes), solutions that would have provided a more flexible solution might have emerged to replace the nearly optimal solutions that we found. Another obvious artifact of our model is that memory-related movements tended to prefer diagonal moves rather than vertical or horizontal (Fig. 3.4b). Since movement decisions were grid-based, larger distances could be covered using diagonal moves leading to greater success in finding a patch.

With our modeling efforts, we sought to demonstrate the general feasibility of implementing mechanistic movement models via INGs when mechanisms are represented as state variables in the input layer of the ANN. Unlike other recent studies that employ evolutionary algorithms and artificial intelligence techniques (e.g. Boone et al. 2006, Morales et al. 2005, Bennett and Tang 2006), we did not attempt to fit empirical movement paths with our model. However these other models did not attempt to investigate the effects of different mechanisms, meaning that we avoided adding more complicated submodels for resource landscapes, individuals, and movements. Future work should seek to add such complexity, however, because more detailed models might be important for capturing the idiosyncrasies of particular empirical settings. For example, in some types of resource landscapes, such as landscapes characterizing forage availability for herbivores, resources may be better represented by continuous rather than binary variables and resources may also replenish after they have been harvested (Farnsworth and Beecham 1999). For these

cases, a detailed resource re-growth model that captures quantity and quality of resources might be more appropriate (Farnsworth and Beecham 1999).

Likewise for individuals and their movements, increased complexity and additional submodels may be necessary to fit an empirical setting for several reasons. First, we limited movements in our model to a certain number of steps, whereas issues of stasis or variability in velocity might be important in other contexts. In addition, our optimization target was relatively simple, and different or more complex targets may be necessary to mimic empirical situations. Alternative optimization targets might include the maintenance of a certain minimum level of resources throughout the entire walk or maximizing the quantity of resources gained before a critical time of year, such as the reproductive season or winter. Finally, future models may want to include predator avoidance (e.g., elk try to avoid wolf packs, Morales et al. 2005) or distance to conspecifics (e.g., social foragers such as pigs, Hancock and Milner-Gulland 2006) as additional important optimization targets to gain model realism and introduce non-resource based motivations for movements.

Considering the movement mechanisms themselves, future modeling may want to go beyond the relatively simple assumptions that we employed. For example, we implemented memory as simple spatiotemporal information of an animal's location, and learning took place only via adaptations of the GA's weights between generations. Such an implementation might be appropriate to fit certain movement types, such as long distance migration behavior in which resources vary predictably across broad scales between few distinct temporal ranges (Boone et al. 2006). However, other environments involve cases where resources vary over shorter time

frames or present more complex spatial problems. Examples include cases where animals visit and feed on inflorescences, such as hummingbirds or flower bats. In those cases, individuals must learn multiple locations of flowers (or artificial feeders) in just a short time (Winter and Stich 2005). Learning in those cases takes place within individuals, rather than across generations, and the memory problem is more complex because knowledge of multiple locations is critical. In this case the current spatiotemporal location of individuals alone would probably not suffice as information to guide memory-related movements. Other representations, such as digital cognitive maps, that would allow implementation of short term episodic memory plus long term reference memory, might be better suited to simulate memory-related movements under these conditions (Bennett and Tang 2006).

Future studies may try to use the concept presented here, representing different movement mechanisms as information-providing state variables in the input layers of ANNs, to fit empirical movement paths. A good fit model may actually reveal the underlying mechanisms of a particular animal or population in an empirical setting. Such models may serve as an important tool for ecological forecasting and might be able to predict how individuals' movements and species' spatiotemporal population dynamics could respond to landscape changes. However, challenges to achieving such an empirical fit lay not only in an adequate modeling of the underlying resource landscapes (Mueller and Fagan 2008), but more importantly in the uncertainty of parameters related to movement. For most animals, we do not know what the perceptual ranges are or how long and precisely they can remember what type of landscape features. Such challenges could possibly be overcome using

pattern-oriented modeling, a technique that uses inverse modeling to identify plausible parameter values by filtering parameterizations that fit multiple patterns derived from field data simultaneously (Grimm et al. 2005, Kramer-Schadt et al. 2007).

References

- Akcakaya, H.R., Radeloff, V.C., Mladenoff, D.J., and He, H.S. 2004. Integrating landscape and metapopulation modeling approaches, Viability of the sharp-tailed grouse in a dynamic landscape. *Cons. Biol.*, 18, 526-537.
- Åkesson, S. and Hedenström, A. 2007. How migrants get there, Migratory performance and orientation. *Bioscience*, 57, 123-133.
- Alerstam, T. 2006. Conflicting evidence about long-distance animal navigation. *Science*, 313, 791-794.
- Alerstam, T., Hedenstrom, A. and Akesson, S. 2003. Long-distance migration, evolution and determinants. *Oikos*, 103, 247-260.
- Asian Development Bank 2002. Strategic development outline for economic cooperation between People's Republic of China and Mongolia. Technical Report, publication stock # 110501. Asian Development Bank, Manila, Philippines.
- Augustin, N. H., Muggleston, M. A., and Buckland, S. T. 1996. An autologistic model for the spatial distribution of wildlife *J. Appl. Ecol.*, 33, 339-347.
- Aumann, C. A., Eby, L. A. and Fagan, W. F. 2006. How transient patches affect population dynamics, The case of hypoxia and blue crabs. *Ecol. Monogr.*, 76, 415-438.
- Bailey, D. W., Gross, J. E., Laca, E. A., Rittenhouse, L. R., Coughenour, M. B., Swift, D. M. and Sims, P. L. 1996. Mechanisms that result in large herbivore grazing distribution patterns. *J. Range Manage.* 49, 386-400.
- Baird D. R. 2001. The Role of Resource Competition in Ungulate Diversity and Community Structure in Africa. PhD thesis, University of Edinburgh.
- Bartumeus, F., Da Luz, M. G. E., Viswanathan, G. M. and Catalan, J. 2005. Animal search strategies, A quantitative random-walk analysis. *Ecology* 86, 3078-3087.
- Bates, D. 2005. Fitting linear mixed models in R. *R News*, 5, 27-30.
- Bekenov, A.B., Grackhev, I.A. and Milner-Gulland, E.J. 1998. The ecology and management of the saiga antelope in Kazakhstan. *Mammal review*, 28, 1-52.
- Bell, W. J. 1991. Searching Behaviour, The Behavioural Ecology of Finding Resources. Chapman and Hall.

- Benhamou, S. 1994. Spatial Memory and Searching Efficiency. *Anim. Behav.*, 47,1423-1433.
- Benhamou, S. and Bovet, P. 1989. How Animals Use Their Environment - a New Look at Kinesis. *Anim. Behav.*, 38, 375-383.
- Bennett, D. A. and Tang, W. 2006. Modelling adaptive, spatially aware, and mobile agents, Elk migration in Yellowstone. *Int. J. Geogr. Inf. Sci.*, 20, 1039-1066.
- Bennetts, R. E. and Kitchens, W. M. 2000. Factors influencing movement probabilities of a nomadic food specialist, proximate foraging benefits or ultimate gains from exploration? *Oikos*, 91, 459-467.
- Berger, J. 2004. The last mile, How to sustain long-distance migrations in mammals. *Cons. Biol.*, 18, 320-331.
- Bergman, C.M., Fryxell, J.M., Cormack Gates, C. and Fortin, D. 2001. Ungulate foraging strategies, energy maximizing or time minimizing? *J. Anim. Ecol.*, 70, 289-300.
- Bilton, D. T., Freeland, J. R. and Okamura, B. 2001. Dispersal in freshwater invertebrates. *Annu. Rev. Ecol. Evol. Syst.*, 32, 159-181.
- Biro, D., Freeman, R., Meade, J., Roberts, S. and Guilford, T. 2007. Pigeons combine compass and landmark guidance in familiar route navigation. *P. Natl. Acad. Sci. USA.* 104, 7471-7476.
- Biro, D., Meade, J. and Guilford, T. 2004. Familiar route loyalty implies visual pilotage in the homing pigeon. *P. Natl. Acad. Sci. USA.*, 101, 17440-17443.
- Boerger, L., B. D. Dalziel, and J. M. Fryxell. 2008. Are there general mechanisms of animal home range behaviour? A review and prospects for future research. *Ecol. Lett.*, 11,637-650.
- Bonadonna, F., Bajzak, C., Benhamou, S., Igloi, K., Jouventin, P., Lipp, H. P. and Dell'Omo, G. 2005. Orientation in the wandering albatross, Interfering with magnetic perception does not affect orientation performance. *P. Roy. Soc. Lond. B. Bio.*, 272, 489-495.
- Boone, R. B., Thirgood, S. J. and Hopcraft, J. G. C. 2006. Serengeti wildebeest migratory patterns modeled from rainfall and new vegetation growth. *Ecology* 87, 1987-1994.
- Bovet, P. and Benhamou, S. 1991. Optimal Sinuosity in Central Place Foraging Movements. *Anim. Behav.*, 42, 57-62.

- Bowen, B. W., Bass, A. L., Chow, S. M., Bostrom, M., Bjorndal, K. A., Bolten, A. B., Okuyama, T., Bolker, B. M., Epperly, S., Lacasella, E., Shaver, D., Dodd, M., Hopkins-Murphy, S. R., Musick, J. A., Swingle, M., Rankin-Baransky, K., Teas, W., Witzell, W. N. and Dutton, P. H. 2004. Natal homing in juvenile loggerhead turtles *Caretta caretta*. *Mol. Ecol.*, 13, 3797-3808.
- Bowler, D. E. and Benton, T. G. 2005. Causes and consequences of animal dispersal strategies, relating individual behaviour to spatial dynamics. *Biol. Rev.*, 80, 205-225.
- Boyce, M.S. and McDonald, L.L. 1999. Relating populations to habitats using resource selection functions. *Trends Ecol. Evol.*, 14, 268-272.
- Boyce, M.S., Mao, J. S., Merrill, E. H., Fortin, D., Turner, M. G., Fryxell, J., and Turchin, P. 2003. Scale and heterogeneity in habitat selection by elk in Yellowstone National Park. *EcoScience*, 10, 421-431.
- Boyle, W. A. and Conway, C. J. 2007. Why migrate? A test of the evolutionary precursor hypothesis. *Am. Nat.*, 169, 344-359.
- Briske, D.D., Fuhlendor, S.D., and Smeins, E.E. 2005. State-and-transition models, thresholds, and rangeland health, A synthesis of ecological concepts and perspectives. *Rangeland Ecology and Management*, 58, 1-10.
- Briske, D.D., Fuhlendorf, S.D., and Smeins, F.E. 2003. Vegetation dynamics on rangelands, a critique of the current paradigms. *J. Appl. Ecol.*, 40, 601-614.
- Brower, L. P. 1996. Monarch butterfly orientation, Missing pieces of a magnificent puzzle. *J. Ex. Bio.*, 199, 93-103.
- Buckland, S.T., Anderson, D.R., Burnham, K.P, Laake, J.L., Borchers, D.L. and Thomas, L. 2001. *Introduction to Distance Sampling, Estimating Abundance of Biological Populations*. Oxford University Press, Oxford, UK.
- Charnov, E. L. 1976. Optimal Foraging, Marginal Value Theorem. *Theor. Popul. Biol.*, 9, 129-136.
- Conradt, L., Zollner, P. A., Roper, T. J., Frank, K. and Thomas, C. D. 2003. Foray search, An effective systematic dispersal strategy in fragmented landscapes. *Am. Nat.*, 161, 905-915.
- Coppolillo, P.B. 2000. The Landscape Ecol. of pastoral herding, Spatial analysis of land use and livestock production in East Africa. *Human Ecology*, 28, 527-560.

- Croney, C. C., Adams, K. M., Washington, C. G. and Stricklin, W. R. 2003. A note on visual, olfactory and spatial cue use in foraging behavior of pigs, indirectly assessing cognitive abilities. *Appl. Anim. Behav. Sci.*, 83, 303-308.
- Csillag, F. and Kabos, S. 2002. Wavelets, boundaries, and the spatial analysis of landscape pattern. *Ecoscience*, 9, 177-190.
- DeWoody, Y.D., Feng, Z.L., and Swihart, R.K. 2005. Merging spatial and temporal structure within a metapopulation model. *Am. Nat.*, 166, 42-55.
- Dingle, H. and Drake, V. A. 2007. What is migration? *Bioscience*, 57, 113-121.
- Edwards, A. M., R. A. Phillips, N. W. Watkins, M. P. Freeman, E. J. Murphy, V. Afanasyev, S. V. Buldyrev et al. 2007. Revisiting Levy flight search patterns of wandering albatrosses, bumblebees and deer. *Nature*, 449, 1044-U1045.
- Estes, R. D. 1991. *The behavior guide to African mammals, including hoofed mammals, carnivores, primates.* University of California Press.
- Fagan, W.F., Lutscher, F. and Schneider, K. 2007. Population and community consequences of spatial subsidies derived from central-place foraging. *Am. Nat.*, 170, 902-915.
- Fahse, L., Wissel, C. and Grimm, V. 1998. Reconciling classical and individual-based approaches in theoretical population ecology, A protocol for extracting population parameters from individual-based models. *Am. Nat.*, 152, 838-852.
- Farnsworth, K. D. and Beecham, J. A. 1999. How do grazers achieve their distribution? A continuum of models from random diffusion to the ideal free distribution using biased random walks. *Am. Nat.*, 153, 509-526.
- Fauchald, P. and Tveraa, T. 2003. Using first-passage time in the analysis of area-restricted search and habitat selection. *Ecology*, 84, 282-288.
- Fauvergue, X., Hopper, K. R. and Antolin, M. F. 1995. Mate Finding Via a Trail Sex-Pheromone by a Parasitoid Wasp. *P. Natl. Acad. Sci. USA*, 92, 900-904.
- Fernandez-Gimenez, M.E. and Allen-Diaz, B. 1999. Testing a non-equilibrium model of rangeland vegetation dynamics in Mongolia. *J. Appl. Ecol.*, 36, 871-885.
- Finch, C. 1996. *Mongolia's wild heritage.* Mongolian Ministry for Nature and the Environment. Hong Kong, Avery Press.

- Fortin M.-J. and M. R. T. Dale 2005. *Spatial Analysis, A Guide for Ecologists*. Cambridge University Press, Cambridge.
- Fortin, D., Beyer, H. L., Boyce, M. S., Smith, D. W., Duchesne, T. and Mao, J. S. 2005. Wolves influence elk movements, Behavior shapes a trophic cascade in Yellowstone National Park. *Ecology*, 86, 1320-1330.
- Fortin, M.-J. and Dale, M. R. T. .2005. *Spatial Analysis, A Guide for Ecologists*. Cambridge University Press.
- Fretwell, S. D. and Lucas, H. L. 1969. On territorial behavior and other factors influencing habitat distribution in birds. *Acta Biotheor.*, 19,16-36.
- Fritz, H., Said, S. and Weimerskirch, H. 2003. Scale-dependent hierarchical adjustments of movement patterns in a long-range foraging seabird. *P. Roy. Soc. Lond. B. Bio.*, 270, 1143-1148.
- Fryxell J.M., Greever, J. and Sinclair, A.R.E. 1988. Why are migratory ungulates so abundant? *Am. Nat.*, 131, 781-798.
- Fryxell, J. M., Mosser, A., Sinclair, A. R. E. and Packer, C. 2007. Group formation stabilizes predator-prey dynamics. *Nature*, 449, 1041-1043.
- Fryxell, J. M., Wilmshurst, J. F. and Sinclair, A. R. E. 2004. Predictive models of movement by Serengeti grazers. *Ecology*, 85, 2429-2435.
- Fryxell, J. M., Wilmshurst, J. F., Sinclair, A. R. E., Haydon, D. T., Holt, R. D. and Abrams, P. A. 2005. Landscape scale, heterogeneity, and the viability of Serengeti grazers. *Ecol. Lett.*, 8, 328-335.
- Fryxell, J.M. 1991. Forage quality and aggregation by large herbivores. *Am. Nat.*, 138, 478-498.
- Fryxell, J.M., Wilmshurst, J., and Sinclair A.R.E. 2004. Predictive models of movement by Serengeti grazers. *Ecology*, 85, 2429-2435.
- Gagliardo, A., Ioale, P. and Bingman, V. P. 1999. Homing in pigeons, The role of the hippocampal formation in the representation of landmarks used for navigation. *J. Neurosci.*, 19, 311-315.
- Gautestad, A. O. and Mysterud, I. 2005. Intrinsic scaling complexity in animal dispersion and abundance. *Am. Nat.*, 165, 44-55.
- Gevrey, M., Dimopoulos, L. and Lek, S. 2003. Review and comparison of methods to study the contribution of variables in artificial neural network models. *Ecol. Model.*, 160, 249-264.

- Goldberg, D.E. 1989. *Genetic Algorithms in Search, Optimization and Machine Learning*. Reading.
- Goldberg, D.E. and Deb, K. 1991. A comparative analysis of selection schemes used in genetic algorithms. In G.J.E. Rawlins ed. *Foundations of genetic algorithms*, pp. 69-93. Morgan Kaufmann.
- Grimm, V. and Railsback, S. F. 2005. *Individual-based Modeling and Ecology*. Princeton University Press.
- Grimm, V., Revilla, E., Berger, U., Jeltsch, F., Mooij, W. M., Railsback, S. F., Thulke, H. H., Weiner, J., Wiegand, T. and DeAngelis, D. L. 2005. Pattern-oriented modeling of agent-based complex systems, Lessons from ecology. *Science*, 310, 987-991.
- Grimm, V., U. Berger, F. Bastiansen, S. Eliassen, V. Ginot, J. Giske, J. Goss-Custard et al. 2006. A standard protocol for describing individual-based and agent-based models. *Ecol. Modell.*, 198, 115-126.
- Grünbaum, D. 2000. Advection-diffusion equations for internal state-mediated random walks. *Siam J. Appl. Math.*, 61, 43-73.
- Gunin, P., Vostokova, E., Dorofeyuk, N., Tarasov P., and Black, C. 2000. Assessing present day plant cover dynamics. *Vegetation dynamics of Mongolia, Geobotany*, 26. eds Gunin, P., Vostokova, E., Dorofeyuk, N., Tarasov, P. and Black, C., Kluwer Academic Publishers.
- Hancock, P. A. and Milner-Gulland, E. J. 2006. Optimal movement strategies for social foragers in unpredictable environments. *Ecology*, 87, 2094-2102.
- Hanski, I. 1999. Habitat connectivity, habitat continuity, and metapopulations in dynamic landscapes. *Oikos*, 87, 209-219.
- Haskell, J. P., Ritchie, M. E. and Olf, H. 2002. Fractal geometry predicts varying body size scaling relationships for mammal and bird home ranges. *Nature*, 418, 527-530.
- Haugen, T. O., Winfield, I. J., Vollestad, L. A., Fletcher, J. M., James, J. B. and Stenseth, N. C. 2006. The ideal free pike, 50 years of fitness-maximizing dispersal in Windermere. *P. Roy. Soc. Lond. B. Bio*, 273, 2917-2924.
- Higgins, S.I., Richardson, D.M., and Cowling, R.M. 2000. Using a dynamic landscape model for planning the management of alien plant invasions. *Ecol. Appl.*, 10, 1833-1848.

- Hobbs, N. T., and Swift, D. M. 1988. Grazing in herds - when are nutritional benefits realized? *Am. Nat.*, 131, 760-764.
- Holden, C. 2006. Inching toward movement ecology. *Science*, 313, 779-+.
- Hooper, D.U. and Vitousek, P.M. 1998. Effects of plant composition and diversity on nutrient cycling. *Ecol. Monogr.*, 68, 121-149.
- Hopfield, J. J. 1982. Neural networks and physical systems with emergent collective computational abilities. *P. Natl. Acad. Sci. USA.*, 79,2554-2558.
- Huete, A., Didan, K., Miura, T., Rodriguez, E.P., Gao, X. and Ferreira L.G. 2002. Overview of the radiometric and biophysical performance of the MODIS vegetation indices. *Remote Sens. Environ.*, 83, 195-213.
- Huse, G., Strand, E. and Giske, J. 1999. Implementing behaviour in individual-based models using neural networks and genetic algorithms. *Evol. Ecol.*, 13, 469-483.
- Ito, T.Y., Miura, N., Lhagvasuren, B., Enkhbileg, D., Takatsuki, S., Tsunekawa, A., and Jiang, Z. 2006. Satellite tracking of Mongolian gazelles *Procapra gutturosa*. and habitat shifts in their seasonal ranges. *J. Zool.*, 269, 291-298.
- Ito, T.Y., Miura, N., Lhagvasuren, B., Enkhbileg, D., Takatsuki, S., Tsunekawa, A., and Jiang, Z.W. 2005. Preliminary evidence of a barrier effect of a railroad on the migration of Mongolian gazelles. *Cons. Biol.*, 19, 945-948.
- Jahn, A. E., Levey, D. J. and Smith, K. G. 2004. Reflections across hemispheres, A system-wide approach to new world bird migration. *Auk* 121, 1005-1013.
- Jiang, G., Liu, M., Han, N., Zhang, Q., and Li, W. 2003. Potential for restoration of degraded steppe in the Xilingol Biosphere Reserve through urbanization. *Environmental Conservation*, 30, 304-310.
- Jiang, Z., Takatsuki, S., Li, J.S., Wang, W., Gao, Z.X., and Ma, J.Z. 2002a. Seasonal variations in foods and digestion of Mongolian gazelles in China. *J. Wildl. Manage.*, 66, 40-47.
- Jiang, Z., Takatsuki, S., Li, J.S., Wang, W., Ma, J.Z., and Gao, Z.X. 2002b. Feeding type and seasonal digestive strategy of Mongolian gazelles in China. *J. Mammal.*, 83, 91-98.
- Jiang, Z., Takatsuki, S., Wang, W., Li, J.S., Jin, K., and Gao, Z.X. 2003. Seasonal changes in parotid and rumen papillary development in Mongolian gazelle *Procapra gutturosa* Pallas. *Ecological Research*, 18, 65-72.

- Jonsen, I. D., Flenming, J. M. and Myers, R. A. 2005. Robust state-space modeling of animal movement data. *Ecology*, 86, 2874-2880.
- Kareiva, P. and Odell, G. 1987. Swarms of predators exhibit preytaxis if individual predators use area-restricted search. *Am. Nat.*, 130, 233-270.
- Kawamura, K., Akiyama, T., Watanabe, O., Hasegawa, H., Zhang, F.P., Yokota, H. and Wang, S. 2003. Estimation of aboveground biomass in Xilingol steppe, Inner Mongolia using NOAA/NDVI. *Grassland Science*, 49, 1-9.
- Kawamura, K., Akiyama, T., Yokota, H., Tsutsumi, M., Yasuda, T., Watanabe, O., Hasegawa, H., Zhang, F.P., and Wang, S. 2005b. Comparing MODIS vegetation indices with AVHRR NDVI for monitoring forage quantity and quality in Inner Mongolia grassland, China. *Grassland Science*, 51, 33-40.
- Kawamura, K., Akiyama, T., Yokota, H., Tsutsumi, M., Yasuda, T., Watanabe, O., Wang, G., and Wang, S. 2005a. Monitoring of forage conditions with MODIS imagery in the Xilingol steppe, Inner Mongolia. *Int. J. Remote Sens.*, 26, 1423-1436.
- Keitt, T. H. 2000. Spectral representation of neutral landscapes. *Landscape Ecol.*, 15, 479-493.
- Keymer, J.E., Marquet, P.A., Velasco-Hernandez, J.X., and Levin, S.A. 2000. Extinction thresholds and metapopulation persistence in dynamic landscapes. *Am. Nat.*, 156, 478-494.
- Kramer-Schadt, S., E. Revilla, T. Wiegand, and V. Grimm. 2007. Patterns for parameters in simulation models. *Ecol. Modell.*, 204,553-556.
- Lee, R., Yu, F., Price, K.P., Ellis, J. and Shi P. 2002. Evaluating vegetation phenological patterns in Inner Mongolia using NDVI time-series analysis. *Int. J. Remote Sens.*, 23, 2505-2512.
- Leimgruber, P., McShea, W.J., Brooks, C.J., Bolor-Erdene, Wemmer, C. and Larson, C. 2001. Spatial patterns in relative primary productivity and gazelle migration in the eastern steppes of Mongolia. *Biological Conservation*, 102, 205-212.
- Lhagvasuren, B., and Milner-Gulland, E.J. 1997. The status and management of the Mongolian gazelle, *Procapra gutturosa*, population. *Oryx*, 31, 127-134.
- Lovell, S. F. and Lein, M. R. 2004. Neighbor-stranger discrimination by song in a suboscine bird, the alder flycatcher, *Empidonax alnorum*. *Behav. Ecol.*, 15, 799-804.

- Maher, C. R. and Lott, D. F. 2000. A review of ecological determinants of territoriality within vertebrate species. *Am. Midl. Nat.*, 143, 1-29.
- Manly, V.F.J., McDonald, L.L., Thomas, D.L., McDonald, T.L., and Erickson, W.P. 2002. Resource selection by animals, statistical analysis and design for field studies. Second Edition Kluwer, Boston, USA.
- McNaughton, S.J. 1984. Grazing lawns, animals in herds, plant form and coevolution. *Am. Nat.*, 124, 863-886.
- McNaughton, S.J. 1985. Ecology of a grazing ecosystem, The Serengeti. *Ecol. Monogr.*, 55, 259-294.
- Mech, S.G. and Zollner, P.A. 2002. Using body size to predict perceptual range. *Oikos*, 98, 47-52.
- Milner-Gulland, E.J. and Lhagvasuren, B. 1998. Population dynamics of the Mongolian gazelle *Procapra gutturosa*, an historical analysis. *J. Appl. Ecol.*, 35, 240-251.
- Milner-Gulland, E.J. 1994. A Population-Model for the Management of the Saiga Antelope. *J. Appl. Ecol.*, 31, 25-39.
- Moe, S.J., Stelzer, R.S., Forman, M.R., Harpole, W.S., Daufresne, T., and Yoshida, T. 2005. Recent advances in ecological stoichiometry, Insights for population and community ecology. *Oikos*, 109, 29-39.
- Moorcroft, P. R., Lewis, M. A. and Crabtree, R. L. 1999. Home range analysis using a mechanistic home range model. *Ecology*, 80, 1656-1665.
- Moorcroft, P. R., Lewis, M. A. and Crabtree, R. L. 2006. Mechanistic home range models capture spatial patterns and dynamics of coyote territories in Yellowstone. *P. Roy. Soc. B Bio.*, 273, 1651-1659.
- Morales, J. M., Fortin, D., Frair, J. L. and Merrill, E. H. 2005. Adaptive models for large herbivore movements in heterogeneous landscapes. *Landscape Ecol.* 20, 301-316.
- Morales, J. M., Haydon, D. T., Frair, J., Holsinger, K. E. and Fryxell, J. M. 2004. Extracting more out of relocation data, Building movement models as mixtures of random walks. *Ecology*, 85, 2436-2445.
- Morrell, L. J. and Kokko, H. 2005. Bridging the gap between mechanistic and adaptive explanations of territory formation. *Behav. Ecol. Sociobiol.*, 57, 381-390.

- Mueller T. and W.F. Fagan. 2008. Search and navigation in dynamic environments - from individual behaviors to population distributions. *Oikos*, 117, 654-664.
- Mueller, T., Olson, K., Fuller, T.K. Schaller, G.B., Murray, M.G. and Leimgruber, P. 2008. In search of forage, predicting dynamic habitats of Mongolian gazelles using satellite-based estimates of vegetation productivity. *J. Appl. Ecol.*, 45, 649-658.
- Murray, M.G. and Brown, D. 1993. Niche separation of grazing ungulates in the Serengeti, An experimental test. *J. Anim. Ecol.*, 62, 380-389.
- Murray, M.G. and Illius, A.W. 2000. Vegetation modification and resource competition in grazing ungulates. *Oikos*, 89, 501-508.
- Murray, M.G. 1995. Specific nutrient requirements and migration of wildebeest. In, *Serengeti II- Dynamics, Management, and Conservation of an Ecosystem* eds A. R. E. Sinclair and P. Arcese., pp. 231-256. University of Chicago Press, Chicago, USA.
- Murray, M.G., and Illius, A.W. 1996. Multispecies grazing in the Serengeti. In, *The Ecology and Management of Grazing Systems*, eds J. Hodgson and A. W. Illius., pp. 247-272. CAB International.
- Musiega, D. and Kazadi, S. 2004. Simulating the East African wildebeest migration patterns using GIS and remote sensing. *African Journal of Ecology*, 42, 355-362.
- Nams, V. O. 2006. Detecting oriented movement of animals. *Anim. Behav.* 72,1197-1203.
- Nellemann, C. and Cameron, R.D. 1998. Cumulative impacts of an evolving oil-field complex on the distribution of calving caribou. *Canadian J. Zool.*, 76, 1425-1430.
- Oosterheld, M., DiBella, C.M. and Kerdiles, H. 1998. Relation between NOAA-AVHRR satellite data and stocking rate of rangelands. *Ecol. Appl.*, 8, 207-212.
- Olden, J. D., Schooley, R. L., Monroe, J. B. and Poff, N. L. 2004. Context-dependent perceptual ranges and their relevance to animal movements in landscapes. *J. Anim. Ecol.*, 73, 1190-1194.
- Olson, K.A., Fuller, T.K., Schaller, G.B., Lhagvasuren, B. and Odonkhoo D. 2005b. Reproduction, neonatal weights, and first-year survival of Mongolian gazelles *Procapra gutturosa*. *J. Zool.*, 265, 227-233.

- Olson, K.A., Fuller, T.K., Schaller, G.B., Odonkhuu D. and Murray M. 2005a. Population density of Mongolian gazelles as estimated by driving long-distance transects. *Oryx*, 39, 164-169.
- Patterson, T. A., L. Thomas, C. Wilcox, O. Ovaskainen, and J. Matthiopoulos. 2008. State-space models of individual animal movement. *Trend. Ecol. Evol.*, 23,87-94.
- Payero, J.O., Neale, C.M.U. and Wright, J.L. 2004. Comparison of eleven vegetation indices for estimating plant height of alfalfa and grass. *Applied Engineering in Agriculture*, 20, 385-393.
- Pentilla, W.C. 1994. The recoverable oil and gas resources of Mongolia. *Journal of Petroleum Geology*, 17, 89-98.
- Pettorelli, N., Vik, J. O., Mysterud, A., Gaillard, J. M., Tucker, C. J. and Stenseth, N. C. 2005. Using the satellite-derived NDVI to assess ecological responses to environmental change. *Trends Ecol. Evol.*, 20, 503-510.
- Pettorelli, N., Vik, J.O., Mysterud, A., Gaillard, J.M., Tucker, C.J. and Stenseth, N.C. 2005. Using the satellite-derived NDVI to assess ecological responses to environmental change. *Trends Ecol. Evol.*, 20, 503-510.
- Pyke, G. H. 1984. Optimal Foraging Theory - a Critical-Review. *Annual Rev. Ecol. Syst.* 15, 523-575.
- R Development Core Team 2006. R, A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. URL <http://www.R-project.org>.
- Ramenofsky, M. and Wingfield, J. C. 2007. Regulation of migration. *Bioscience*, 57, 135-143.
- Reading, R.P., Mix, H., Lhagvasuren, B. and Tseveenmyadag, N. 1998. The commercial harvest of wildlife in Dornod Aimag, Mongolia. *J. Wildl. Manage.*, 62, 59-71.
- Reed, B.C., Brown, J.F., VanderZee, D., Loveland, T., Merchant, J.W. and Ohlen, D. 1994. Measuring phenological variability from satellite imagery. *Journal of Vegetation Science*, 5, 703-714.
- Reich, P.B., Tilman, D., Craine, J., Ellsworth, D., Tjoelker, M.G., Knops, J., Wedin, D., Naeem, S., Bahaeddin, D., Goth, J., Bengtson, W., and Lee, T.D. 2001. Do species and functional groups differ in acquisition and use of C, N and water under varying atmospheric CO₂ and N availability regimes? A field test with 16 grassland species. *New Phytologist*, 150, 435-448.

- Revilla, E., Wiegand, T., Palomares, F., Ferreras, P. and Delibes, M. 2004. Effects of matrix heterogeneity on animal dispersal, From individual behavior to metapopulation-level parameters. *Am. Nat.*, 164, E130-E153.
- Reynolds, J. H. and Ford, E. D. 1999. Multi-criteria assessment of ecological process models. *Ecology*, 80, 538-553.
- Riley, J. R., Greggers, U., Smith, A. D., Reynolds, D. R. and Menzel, R. 2005. The flight paths of honeybees recruited by the waggle dance. *Nature*, 435, 205-207.
- Roshier, D. A. and Reid, J. R. W. 2003. On animal distributions in dynamic landscapes. *Ecography*, 26, 539-544.
- Ruckstuhl, K. E. and Neuhaus, P. 2002. Sexual segregation in ungulates, a comparative test of three hypotheses. *Biol. Rev.*, 77, 77-96.
- Schaller, G.B. 1998a. *Wildlife of the Tibetan Steppe*. University of Chicago Press, Chicago, USA.
- Schaller, G.B. 1998b. Mongolia's golden horde, a million migrating gazelles. *Wildlife Conservation*, November/December, 36-41.
- Schooley, R. L. and Wiens, J. A. 2003. Finding habitat patches and directional connectivity. *Oikos*, 102, 559-570.
- Serneels S. and Lambin, E.F. 2001. Impact of land-use changes on the wildebeest migration in the northern part of the Serengeti-Mara ecosystem. *Journal of Biogeography*, 28, 391-407.
- Sinclair, A.R.E. and Arcese, P. 1995. *Serengeti II- Dynamics, management, and conservation of an ecosystem*. University of Chicago Press, Chicago, USA.
- Sinclair, A.R.E. 1983. The function of distance movements in vertebrates pp. 248-258. In, Swingland I.R. and P. J. Greenwood. *The Ecology of Animal Movement*. Clarendon Press, Oxford.
- Sinclair, A.R.E. 1983. The function of distance movements in vertebrates. - In, Swingland, I.R. and Greenwood, P. J. *The Ecology of Animal Movement*. Clarendon Press, pp. 248-258.
- Sneath, D. 1998. State policy and pasture degradation in inner Asia. *Science*, 281, 1147-1148.

- Strand, E., Huse, G. and Giske, J. 2002. Artificial evolution of life history and Behavior. *Am. Nat.*, 159, 624-644.
- Sutherland, W. J. 1983. Aggregation and the Ideal Free Distribution. *J. Anim. Ecol.*, 52, 821-828.
- Tan, Z.J., Zou, X.W., Huang, S.Y., Zhang, W. and Jin, Z.Z. 2002. Random walk with memory enhancement and decay. *Phys. Rev. E*, 65, 1-5.
- Thirgood, S., Mosser, A., Tham, S., Hopcraft, G., Mwangomo, E., Mlengeya, T., Kilewo, M., Fryxell, J., Sinclair, A.R.E. and Borner, M. 2004. Can parks protect migratory ungulates? The case of the Serengeti wildebeest. *Anim. Conserv.*, 7, 113-120.
- Thrun, S., Montemerlo, M., Dahlkamp H., Stavens, D., Aron, A., Diebel, J., Fong, P., Gale, J., Halpenny, M., Hoffmann, G., Lau, K., Oakley, C., Palatucci, M., Pratt, V., Stang, P., Strohband, S., Dupont, C., Jendrossek, L.-E., Markey, C. C., Rummel, C., van Niekerk, J., Jensen, E., Alessandrini, P., Bradski, G., Davies, B., Ettinger, S., Kaehler, A., Nefian, A., and Mahoney, P., 2006. Stanley, the robot that won the DARPA grand challenge. *Journal of Field Robotics*, 23, 661-692.
- Tong, C., Wu, J., Yong, S., Yang, J. and Yong, W. 2004. A landscape-scale assessment of steppe degradation in the Xilin River Basin, Inner Mongolia, China. *Journal of Arid Environments*, 59, 133-149.
- Toupin, B., Huot, J. and Manseau, M. 1996. Effect of insect harassment on the behavior of the Riviere George caribou. *Arctic*, 49, 375-382.
- Turchin, P. 1998. Quantitative analysis of movement, measuring and modeling population redistribution in animals and plants. Sinauer Associates.
- Tyre, A. J., Tenhumberg, B., Field, S. A., Niejalke, D., Parris, K., and Possingham, H. P. 2003. Improving precision and reducing bias in biological surveys, Estimating false-negative error rates. *Ecol. Appl.*, 13, 1790-1801.
- Van Bommel, F.P.J., Heitkonig, I.M.A., Epema, G.F., Ringrose, S., Bonyongo, C., Veenendaal, E.M. 2006. Remotely sensed habitat indicators for predicting distribution of impala *Aepyceros melampus*. in the Okavango Delta, Botswana. *Journal of Tropical Ecology*, 22, 101-110.
- van Gils, J. A., Spaans, B., Dekinga, A. and Piersma, T. 2006. Foraging in a tidally structured environment by red knots *Calidris canutus*. Ideal, but not free. *Ecology*, 87, 1189-1202.

- Van Soest, P.J. 1994. *Nutritional Ecology of the Ruminant*, 2nd edition. Cornell University Press, Ithaca.
- VanderMeer, J. and Ens, B. J. 1997. Models of interference and their consequences for the spatial distribution of ideal and free predators. *J. Anim. Ecol.* 66, 846-858.
- Vaughan, I.P., and Ormerod, S. J. 2005. The continuing challenges of testing species distribution models. *J. Appl. Ecol.*, 42, 720-730.
- Verheyen, K., Vellend, M., Van Calster, H., Peterken, G., and Hermy, M. 2004. Metapopulation dynamics in changing landscapes, A new spatially realistic model for forest plants. *Ecology*, 85, 3302-3312.
- Verlinden, A. and Masogo, R. 1997. Satellite remote sensing of habitat suitability for ungulates and ostrich in the Kalahari of Botswana. *Journal of Arid Environments*, 35, 563-574.
- Vickerstaff, R. J. and Di Paolo, E. A. 2005. Evolving neural models of path integration. *J. Exp. Biol.*, 208, 3349-3366.
- Viswanathan, G. M., Buldyrev, S. V., Havlin, S., da Luz, M. G. E., Raposo, E. P. and Stanley, H. E. 1999. Optimizing the success of random searches. *Nature*, 401, 911-914.
- von Frisch, K. 1967. *Dance language and orientation of the honey bee*. Harvard Univ. Press.
- Wahlberg, N., Klemetti, T., and Hanski, I. 2002. Dynamic populations in a dynamic landscape, the metapopulation structure of the marsh fritillary butterfly. *Ecography*, 25, 224-232.
- Walsh, N.E., Fancy, S.G., McCabe, T.R. and Pank, L.F. 1992. Habitat use by the Porcupine Caribou Herd during predicted insect harassment. *J. Wildl. Manage.*, 56, 465-473.
- Wang, M. and Grimm, V. 2007. Home range dynamics and population regulation, an individual-based model of the common shrew *Sorex araneus*. *Ecol. Modell.*, 205, 397-409.
- Wang, X., Helin, S., Junghui, B. and Ming, L. 1997. Recent history and status of the Mongolian gazelle in Inner Mongolia, China. *Oryx*, 31, 120-126.
- Weladji, R.B., Holand, Ø., and Almøy, T. 2003. Use of climatic data to assess the effect of insect harassment on the autumn weight of reindeer *Rangifer tarandus* calves. *J. Zool.*, 260, 79-85.

- Wiegand, T., Jeltsch, F., Hanski, I. and Grimm, V. 2003. Using pattern-oriented modeling for revealing hidden information, a key for reconciling ecological theory and application. *Oikos*, 100, 209-222.
- Wiegand, T., Revilla, E. and Knauer, F. 2004. Dealing with uncertainty in spatially explicit population models. *Biodiversity and Conservation*, 13, 53-78.
- Williams, D.M. 1996. Grassland enclosures, catalyst of land degradation in Inner Mongolia. *Human Organization*, 55, 307-313.
- Wilmschurst, J.F., Fryxell, J.M., and Bergman, C.M. 2000. The allometry of patch selection in ruminants. *P. Roy. Soc. Lond. B. Bio.*, 267, 345-349.
- Wilmschurst, J.F., Fryxell, J.M., Farm, B.P., Sinclair, A.R.E. and Henschel, C.P. 1999. Spatial distribution of Serengeti wildebeest in relation to resources. *Canadian J. Zool.*, 77, 1223-1232.
- Wiltschko, R. and Wiltschko, W. 2006. Magnetoreception. - *Bioessays* 28, 157-168.
- Winter, Y., and K. P. Stich. 2005. Foraging in a complex naturalistic environment, capacity of spatial working memory in flower bats. *J. Ex. Biol.*, 208,539-548.
- Wintle, B.A., Bekessy, S.A., Venier, L.A., Pearce, J.L., and Chisholm, R.A. 2005. Utility of dynamic-landscape metapopulation models for sustainable forest management. *Cons. Biol.*, 19, 1930-1943.
- With, K. A. and King, A. W. 1997. The use and misuse of neutral landscape models in ecology. *Oikos*, 79, 219-229.
- Xu, D.S., Feng, Z.L., Allen, L.J.S., and Swihart, R.K. 2006. A spatially structured metapopulation model with patch dynamics. *Journal of Theoretical Biology*, 239, 469-481.
- Yao, X. 1999. Evolving artificial neural networks. *PIEEE* 87, 1423-1447.
- Yu, F.F., Price, K., Ellis, J. and Shi, P. 2003. Response of seasonal vegetation development to climatic variations in eastern central Asia. *Remote Sens. Environ.*, 87,42-54.
- Zahler P., Olson K., Ganzorig K., Boldbaatar B., Schaller G.B., Grigg G., Pople T., Payne N., Draisma M., Hopwood, P. and Odonkhuu, D. 2004. Management of Mongolian gazelles as a sustainable resource. *Mongolian Journal of Biological Sciences*, 1, 48-55.

Zollner, P. A. and Lima, S. L. 1999a Search strategies for landscape-level interpatch movements. *Ecology*, 80, 1019-1030.

Zollner, P. A. and Lima, S. L. 1999b. Orientational data and perceptual range, real mice aren't blind. *Oikos*, 84, 164-166.