

**The roles of Resources and Conspecifics in Shaping Consumer Movement: From
Individual Processes to Population Patterns**

by

Daniel Cory Kuefler

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ABSTRACT

THE ROLES OF RESOURCES AND CONSPECIFICS IN SHAPING CONSUMER MOVEMENT: FROM INDIVIDUAL PROCESSES TO POPULATION PATTERNS

Daniel Cory Kuefler
University of Guelph, 2013

Advisor:
John M. Fryxell

Animal movement patterns provide a rich source of information for examining a wide range of ecological interactions that span ecological scales from foraging behaviours of individuals to the spread of populations across landscapes. I investigated the causes and consequences of consumer movement, from the localized movements of individuals to the patterns of spread of populations across landscapes, using a series of complementary microcosm experiments with a model consumer-resource system. In Chapter One, I conducted a series of experiments designed to test differences in the fine-scale movement characteristics of swimming rotifers under experimental manipulations of local resource and conspecific abundance. Individual turn frequencies increased in resource-rich environments but were unaffected by competitor density. In contrast, individual swimming speeds increased at high competitor densities but were unaffected by resources. I demonstrated how these contrasting behaviours could be integrated to form predictions of population spread under different ecological scenarios. In Chapter Two, I tested the predictions established in Chapter One by directly measuring the rates of spread of many replicate populations of rotifers in one-dimensional environments.

Experimental treatments included a wide range of resource and conspecific densities, and starved versus sated rotifers in the presence versus absence of predator chemical cues. Rates of population spread were negatively correlated with resource abundance, especially when conspecific density was high, and rates of population spread of both starved and risk-exposed populations were significantly lower than controls. In Chapter Three, I tested the effect of resource patchiness, conspecific density, and their interaction, on population spread through a two dimensional landscapes. I found that rates of population spread decayed over time indicative of a sub-diffusive movement processes that can be well explained by positive density-dependent movement responses. Neither the rate of spread nor the magnitude of its decay differed between patchy and evenly distributed resource treatments, despite observed rotifer preferences for patches. These findings suggest that under certain ecological circumstances resource distribution may be less crucial in predicting population spread than density-dependence. Overall, my research demonstrates mechanistic links between the behavioural responses of individuals to their environment and the resulting larger scale phenomena of population-level movement patterns.

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PROLOGUE

The animal movement Hydra: A brief history of resource- and conspecific dependent animal movement with comparisons across the empirical literature

Background

Animal movement can be defined as a physical action exerted by a whole organism that serves to displace the organism in space and time. This action plays a fundamental role in how organisms interact with each other and their environment and is consequently central to many ecological processes at the level of individuals, groups, and populations. Movement is an element common to basic ecological theories, from simple population regulation, through species interactions and the structure and diversity of communities, to ecosystem processes such as habitat engineering, pollination, and seed dispersal (e.g., Allee 1931; Huffaker 1958; MacArthur & Wilson 1967; Levey *et al.* 2005; Hastings *et al.* 2007).

From the perspective of an individual organism, movement may be both a causal precursor to, and a consequence of, behavioural interactions that underpin components of fitness. Successful reproduction is largely determined by one's ability to seek out or remain in proximity to potential mates. Mate encounters, even in the simplest mass-action models, are positively correlated with motility (Duvall & Schuett 1997; Kiorboe & Bagoien 2005; Hutchinson & Waser 2007). Survival and growth are limited by sufficient food or varied diets which are in turn determined by movement decisions that enable the acquisition of resources scattered across space. Mortality due to predation may be

mediated via evasion, risk dilution through grouping (Hamilton 1971; Kiltie 1980), or selection for predator-free refugia (Bergerud 1990).

Individual fitness consequences are ultimately reflected in demography, yet movement studies at the level of populations often ignore the effects of movement on demographic parameters. Largely due to fundamental methodological differences (discussed in the following section), population-level movement studies tend to focus on the effects of movement on broad scale distributional patterns, rates of range expansions, habitat selection, or rates of flux between distinct habitat patches. In application, the management of animal populations relies on an understanding of both individual and population movement processes to inform decisions over broad issues, such as how to provide functional connectivity for species of concern in increasingly fragmented landscapes (Schultz 1998) or how to control the spread of invasive species or agricultural pests (Philips *et al.* 2007; Nakayama, Ojanguren & Fuiman 2011). Given the wide range of ecological implications and the clear potential for application in wildlife management and conservation, a refined understanding of both the determinants and consequences of animal movement continues to be sought.

In this regard, the ecological literature has seen an explosive proliferation of studies dedicated to animal movement, including an estimated 26,000 papers in the previous decade alone (Holyoak 2008). This proliferation earmarks a balkanization of movement studies into various sub-disciplines which have merited reviews unto themselves. These sub-disciplines include, for example, the study of foraging behaviour (Pyke 1984), natal dispersal (Bowler & Benton 2005; Matthesen 2005), migration

(Fryxell & Sinclair 1988; Dingle 2006), and influences of physical landscape structure on movement (Ockinger & Smith 2007). Few attempts have been made to draw comparisons across this sprawling literature, however, because the motivations for movement studies strongly differ in their ecological context and are often species- or system-specific. Here, I attempt to address this gap by providing an overview of the empirical movement literature with relevant comparisons across several movement sub-disciplines.

The primary goal of this overview is to provide the reader with a general sense of the theoretical background and empirical literature surrounding resource and conspecific-dependent movement. An initial brief introduction to the two fundamentally different ways in which ecologists measure movement is provided, highlighting some of the relative strengths and limitations of each approach. I then highlight findings from empirical papers that satisfied the generic criteria of measuring any type of movement metric in response to resource abundance/quality, conspecific presence/density, or combinations of both. Although this selection is by no means exhaustive, my goal is to provide a snapshot of the literature sufficient to illuminate similarities and differences between resource- and conspecific-dependent movement studies across sub-disciplines.

Two approaches to movement

There are two fundamental perspectives from which ecologists study animal movement. From a 'Lagrangian' perspective (commonly borrowed from Joseph Louis Lagrange's ideas of mechanical physics), the movement trajectory of an entity - often an individual animal - is tracked across many points in space. This perspective has advantages in testing behavioural mechanisms driving movement patterns (Turchin 1998;

Grimm 1999; DeAngelis & Mooij 2005). Under a Lagrangian approach, however, population level inferences can typically only be reached by either scaling up models of individual movement to phenomenological models of diffusive spread (e.g., Grunbaum 1994), or by simulating the movements of many individuals based on complicated mechanisms. The major disadvantage of inferring population responses from this approach is that observations are nearly always restricted to a limited sample of individuals (relative to the size of entire populations) and are subsequently confounded by the stochastic element of individual variation (Morales & Ellner 2002; Hawkes 2009).

The most commonly used models of animal movement from the Lagrangian perspective include a family of ‘random walk’ models based on the concept of Brownian motion (Einstein 1905). Various forms of random walk models can accommodate more or less complexity in movement processes – ‘simple’ random walks assume that the direction of every sequential step is random, ‘correlated’ random walks accommodate some degree of directional persistence between steps, and ‘biased’ random walks accommodate global directional biases (for a review of these models see Codling, Plank & Benhamou 2008). More recently, a special form of random movement model, the ‘Levy-flight’ or ‘Levy-walk’ model, has received much theoretical and empirical attention. The Levy-walk model differs from Brownian models in that it assumes a power-law (i.e. fat-tailed) distribution of step lengths (rather than the Brownian assumption of an exponential distribution), such that Levy walks are characterized by a higher probability of making occasional long-distance steps. It has been empirically demonstrated that many animal movement patterns are well-described by this model,

particularly when animals are foraging in areas where resources are patchily distributed (e.g. Bartumeus *et al.* 2003; de Knecht *et al.* 2007). Much contention surrounds the debate of whether and when the ‘Levy-flight’ movement process should be considered an “adaptive” deviant from simpler random walk processes under certain foraging conditions (Viswanathan *et al.* 1999; Benhamou 2007; Reynolds 2008; Plank & Codling 2009; Edwards 2011). While the full range of this debate is outside of the scope of this review, it is important to note that the question of how best to model individual animal movement processes in complex environments remains unresolved.

The ‘Eulerian’ perspective (commonly borrowed from Leonhard Euler’s ideas of fluid mechanics) offers an approach that is potentially broader in scope but often more general in practice. From this perspective, the flux of a group or population of individuals is tracked through a given area or across fixed points in space. The major advantage of this approach is that because it treats movement as the dynamic density gradient of an entire population over space and time, it offers a greater analytical accessibility for pairing with demographic models (Skellam 1951; Okubo 1980). Some of the best examples of this approach can be found in mass mark-recapture studies of invertebrates introduced to novel environments, which investigate the spread of animals across fixed, explicitly-defined, points in space (e.g., Kareiva 1982; Turchin & Theony 1993).

More commonly seen is a simplified form of the Eulerian approach that is often used in dispersal studies. In these cases, population metrics are described as a proportion of individuals emigrating out of, or immigrating into, a single point (or patch). While patch-based data are useful for modelling transitional movement dynamics between

discrete patches, they have limited usefulness in identifying specific mechanisms underlying the movement transitions that occur between patches. Furthermore, because of the relative difficulty involved with experimentally measuring the flux of entire populations, this approach is often limited to very low levels of experimental replication.

In practice, ecological questions are often about populations while observations are only available at the level of individuals. For example, if we want to ask a question about how a population expands across an area, it is easier to think about range expansion in terms of diffusive movement or wave fronts, yet we may only be able to observe the explicit behaviour of a few individual dispersers. Logistical trade-offs must be made between collecting individual data that may better inform mechanistic processes versus population data that may better capture cumulative movement patterns. In short, questions about the detailed movement mechanics underlying individual movement patterns always utilize Lagrangian models while questions of population spatial patterns take an Eulerian approach.

Resource-dependent Movement

Some of the earliest formalized hypotheses regarding resource-dependent animal movement stem from an optimal foraging paradigm (McArthur & Pianka 1966; Charnov 1976). The basic assertion of this foraging theory is that individual animals will adjust their movements to maximize their overall foraging efficiency depending on the quality or distribution of their food resources. These behaviours are predicted to increase fitness and subsequently be maintained through natural selection (Pyke 1984; Farnsworth & Beecham 1999). While direct links to increased fitness have yet to be documented,

several studies have empirically demonstrated significantly greater intake rates for animals that move in a manner consistent with an optimal foraging strategy. For example, Klaassen, Nolet and Bankert (2006) demonstrated that swans were more likely to move greater distances between foraging bouts if the area in which they were foraging was below a critical tuber density, and shorter distances into adjacent areas if the tuber density was high. This foraging strategy resulted in a 38% gain in long-term intake rate compared to if they sampled all areas equally. Similarly, Fryxell, Wilmshurst and Sinclair (2004) demonstrated that nomadic movements by Thomson's gazelles were predictable on the basis of local energy gain. Gazelles closely tracked changes in the spatial distribution of short grass swards and left short grass patches when local daily energy intake dropped below the expected intake averaged across the landscape. The resulting patterns of gazelle redistribution among neighboring patches were proportional to daily rates of energy intake in each patch.

The individual movement characteristics underlying these efficient foraging strategies are contemporarily referred to as "area-restricted" search behaviours, following a study by Tinbergen (1976) who noted that many avian predators react to the discovery of a prey item with an intensified search effort in the area around the initial prey encounter. Models of searching animals' trajectories typically characterize these behaviours as differences in speed and path tortuosity (Benahmou & Bovet 1987; Kareiva & Odell 1987; Dicke & Burrough 1988; Turchin 1998). Animals that move at slower speeds or with more tortuous movement paths achieve a lower net displacement and thereby increase their search intensity in a given area per unit time (Kareiva & Shigesada

1983). While Tinbergen (1976) initially applied the term to describe an extremely localized phenomenon, these types of movement behaviours have been extensively studied at a variety of spatial scales, for numerous taxa, in aquatic and terrestrial systems alike (e.g., Austin *et al.* 2006; Bailey & Thompson 2006; Klaassen, Nolet & Bankert 2006; Snider & Gilliam 2008; Vanninni *et al.* 2008; Brouwers & Newton 2010; Kuefler *et al.* 2010; Skarin *et al.* 2010; Papastamatiou *et al.* 2011). Significant increases in path tortuosity have been documented for gray seals foraging over spatial scales of >20 km day (Austin *et al.* 2006), nymphalid butterflies moving through areas of high host plant density at scales of > 20 m (Kuefler & Haddad 2006), and terrestrial isopods searching for nitrogenous leaves at scales of > 20 mm (Tuck & Hassall 2004). This approach has been used to test how different species of browsing ungulates perceive prevalent components of plant communities (Etzenhowzer *et al.* 1998), whether painted turtles (Bowne & White 2004) or Antarctic petrels (Fauchald & Tverra 2006) exhibit scale-dependent search strategies, and to what degree the interplay between state-conditioning and environmental cues influence the foraging behaviour of houseflies (White, Tobin & Bell 1984). Regardless of the focal taxon, spatial extent, or context of these studies on individual movement, one strikingly consistent result is that movement metrics are generally negatively correlated with resource metrics. In agreement with optimal foraging theory, empirical tests have widely shown that individual consumers generally decrease their rates of movement in order to linger where resources are abundant and increase their rates of movement to efficiently explore areas where resources are scarce.

Generalized predictions become more complicated, however, when one shifts the unit of observation from an individual forager to a group or population of animals residing in discrete patches. Theories regarding resource-dependent movement at the level of patches stem from a larger body of work including transitional dynamics between mainland-island (MacArthur & Wilson 1967), source-sink (Levin 1974; Pulliam 1988) and metapopulation systems (Hanski & Gilpin 1991). Empirical tests of these theories tend to focus on movement as the rates of emigration from, immigration to, or transition between discrete habitat patches. One hypothesis is that as per capita resource availability within a patch decreases, individuals will experience a greater motivation to seek out areas of higher quality or lower competition in order to maximize their fitness (Fretwell & Lucas 1970; Farnsworth & Beecham 1999). This hypothesis predicts that patch emigration or transition between distinct areas should be negatively correlated with the abundance or quality of resources in an animal's initial patch. In practice, however, it is difficult to disentangle the effects of diminishing resources on movement from those of increasing population size or density (but see Mares *et al.* 1982). Correlations between movement and resources may appear to be negative when high quality but low density patches motivate animals to stay (Murray 1967; Waser 1985; Odendall, Turchin & Stermitz 1989), and appear to be positive where high quality and (subsequently) high density patches motivate animals to move (Levins 1969; Pulliam 1988; Dias 1996; Gunderson & Andreassen 1998). Clearly, at the patch-level, the relationship between movement and resources is both a dynamic and potentially cyclic one that is dependent on the state of the patch demography.

At the spatial scale of movement across landscapes, a third, and more recent, branch of movement literature surrounds the concept of landscape connectivity (Taylor & Fahrig 1993; Kindlemann & Burell 2008; Mortelliti, Amori & Boitani 2010), which theorizes that relatively small chunks of high quality habitat embedded within otherwise inhospitable landscapes facilitate long-distance movement processes by providing resources, protection from predators, and/or structural familiarity to dispersing animals. Numerous empirical studies have demonstrated that resource-rich patches function as movement conduits in the form of ‘corridors’ (Haddad 1999; Danielson & Hubbard 2000; Jonsen & Taylor 2000; Bergerren, Birath & Kindvall 2002), ‘stepping stones’ (Shultz 1998; Boscolo *et al.* 2008) or ‘least-cost pathways’ (McRae & Bier 2007; Zeller, McGarigal & Whiteley 2012). Empirical investigations of this theory typically focus on the positive associations between resource-rich conduits and animal movements through them (Ockinger & Smith 2007), but few investigate the mechanisms underlying slow movement through unfamiliar terrain. A rather unique finding by Jackson *et al.* (2009) demonstrated that the displacement rate, velocity, and path linearity of saproxylic beetle movement paths were 50-100% greater in resource-rich forests compared to resource-poor pasture. While this result contradicts foraging theory, it is well-explained by connectivity theory. In unfamiliar pasture, beetles paused frequently to stand on the tops of grass blades and leaf litter with raised heads and active antennae, indicating attempts to scan the inhospitable and unfamiliar environment (Jackson *et al.* 2009).

Two independent studies on the fungivorous soil collembolan, *Protaphorura armata*, offer an excellent example of how resource-dependent movement can be

interpreted differently depending on the ecological context motivating the study and/or the spatial scale over which it is conducted. Westerberg *et al.* (2008) conducted an experimental study of collembolan foraging-behaviour during which the movements of individuals were monitored within a 20 x 20 mm arena in the presence versus absence of food. In the presence of food, individual collembolans moved less frequently and with sharper turns. In a complementary study, researchers experimentally measured collembolan dispersal rates at much larger spatial scales (~40 cm), following release in fungus-enriched soils (Bengtsson, Hedlund & Rundgren 2008). They observed that when soils were enriched with fungus patches, mean dispersal rates were four times greater compared to controls, which suggests that the ability to sense and move towards resource-rich patches may stimulate long-distance forays for collembolans. This comparison demonstrates that the conclusions arrived at by empirical studies depends on both the perspective of the animal and the researcher; localized movements may be interpreted as negatively correlated with resource abundance within a single departure patch while dispersal movements are interpreted as being positively correlated with the abundance of resource-rich recipient patches embedded within the landscape.

Conspecific-dependent movement

The presence of conspecifics can have a profound impact on the movement patterns we observe in nature even in cases where the movement responses of individuals are not specifically dictated by their encounters with conspecifics, *per se*. For example, theory predicts that when each individual in a group of foragers moves in accordance with 'area-restricted' behaviour, tightly aggregated, migratory waves of consumers can

arise (Gueron & Liron 1989; Wilson & Richards 2000). An aggregation of consumers is predicted because individuals at the front of a group will slow down in the presence of high densities of food. Individuals that lag behind will speed up because they are moving through areas that have already been depleted. This relatively simple, resource-mediated movement response has been demonstrated to generate travelling bands of chemotactic bacteria (Schribner, Segel & Rogers 1974), seasonal migrations of schooling pelagic fish (Fauchald, Mauritzen & Gjosaeter 2006) and sea urchin feeding fronts (Abraham 2007; Dumont, Himmelman & Robinson 2007). Not all aggregative foraging patterns, however, can be described by deceptively simple rules. Using an observational study of urchins on resource-rich versus barren substrates, Luazon-Guay, Scheibling and Barbeau (2006) demonstrated that the aggregative patterns of the green sea urchin, *Strongylocentrotus droebachiensis*, were not resource-dependent. Foraging urchins showed no response to resources, but rather moved more slowly and with smaller step lengths in the presence of conspecifics, offering an alternative mechanism underlying dense urchin feeding fronts. Stoner and Lally (1994) similarly refuted the resource-mediated aggregative movement hypothesis by demonstrating that aggregative movements by conch (*Strombus gigas*) were not resource-dependent but rather were motivated by a lower predatory mortality experienced by groups. In sum, while a group of conspecifics moving in response to resources may result in aggregative movement patterns via their sheer abundance alone, a richer array of individual behaviours may underlie these, and many other, patterns of conspecific-dependent movement.

Individual movement characteristics may be influenced by a number of conspecific-dependent processes, including competition for food (Dethier & MacArthur 1964), competition for mates (Kussaari *et al.* 1998), and the avoidance of predators (Lima & Dill 1990). There are few general predictions regarding how individuals should relate to the presence or density of conspecifics, however, because individuals may respond positively or negatively towards conspecifics depending on the ecological circumstances. As a competitive movement strategy, for example, individual Carabid beetles move with greater velocities and straighter movement paths in the presence of conspecific cues in order to minimize searching in areas previously visited by others (Guy *et al.* 2008). Domestic sheep demonstrate an alternative strategy by moving smaller distances and taking shorter steps in the presence of conspecifics in order to graze more intensively (Mobaek *et al.* 2012). At low densities, the same sheep moved further with longer step lengths, indicating an increase in exploratory behaviour and dietary choosiness when they were released from competitive pressure. In contrast to studies demonstrating the negative aspects of conspecific competitors, Kiester (1979) demonstrated that conspecifics may function as a proxy for familiar habitat in novel settings by showing that anoles selectively moved towards compartments occupied by conspecifics when released in resource-poor cages. Kawaguchi *et al.* (2006) further demonstrated that conspecific cues can facilitate foraging efficiency in the bumblebee, *Bombus terrestris*. Using a set of manipulative experiments upon which dead conspecifics were tethered onto plastic versus real flowers, Kawaguchi (2006) demonstrated that bumblebees preferentially move towards flowers occupied by conspecifics. In this example, the

behaviours exhibited by individual bees were in agreement with the authors' hypothesis that movement towards conspecifics can result in significantly lower food detection times and greater foraging efficiency.

Numerous movement studies have measured the influence of conspecific density on rates of emigration from, and immigration into, discrete habitat patches (Bowler & Benson 2005; Matthysen 2005). Positive density-dependent emigration rates have been demonstrated to arise from, for example, exploitative competition in bruchid beetles (Stevens & Bonsall 2011) and reproductive interference (via male harassment) in butterflies (Baguette, Convie & Neve 1996). Patterns of negative density-dependent patch emigration (Kussaari, Nieminem & Hanski 1996; Andreassen & Ims 2001; Rabasa, Gutierrez & Escudero 2007) and positive density-dependent patch immigration (Kiester 1979; Serrano & Tella 2003; Robinson, Larson & Kerr 2011) are often driven by less transparent processes. For example, whenever conspecific density is correlated with other patch characteristics such as area (Rabasa, Gutierrez & Escudero 2007) or quality (Kussaari, Nieminem & Hanski 1996), it may not be clear whether increased rates of movement out of high density patches are a result of increased encounters with patch boundaries or competitive interactions with conspecifics (Enfjall & Leimer 2005). Alternatively, increased rates of movement into high density patches may occur if the presence of conspecifics functions as a proximate descriptor of patch quality. Serrano and Tverra (2003) demonstrated that after statistically controlling for patch quality, lesser kestrels were more likely to emigrate out of source patches with fewer breeding pairs, and more likely to immigrate into recipient patches with more breeding pairs. This rare

example demonstrates how conspecific attraction can be a strong determinant of inter-patch transition dynamics in both the source and recipient patch.

Empirical studies that explicitly test, *in situ*, the influence of conspecifics on movement processes occurring over landscape extents are extremely rare, with the exception of a few studies on released populations of invertebrates (e.g., Cronin, Hyland & Abrahamson 2001; Van Hezewijk & Bouchier 2005; Chapman & Dyson 2007; Henne & Johnson 2011). While Henne and Johnson (2011) reported that the estimated diffusion rate of released parasitic flies was notably higher in a single high-density trial, Hezewijk and Bouchier (2005) reported that spread rates of flea beetles were not sensitive to initial release densities that varied over several orders of magnitude in replicated release studies. No studies of released invertebrates reported statistically significant evidence of density-dependent movement rates.

More common are studies that are defined in a landscape context but measure the influences of conspecifics on the initiation or maintenance of long-distance dispersal events (Rosenberg *et al.* 1997; French & Travis 2001; Rouquette & Thompson 2007; Senger, Roitberg & Thistlewood 2007; De Meester & Bonte 2010). In such studies, dispersal movements are considered to be key building blocks of population spread, for which detailed mechanisms can be explored. Long-distance dispersal in agrobiont spiders, for example, was found to be stimulated by social information rather than rearing density (De Meester & Bonte 2010), whereby spiders initiated significantly greater long-distance ballooning events when exposed to the presence of leftover silk at potential departure points. Senger, Roitberg and Thistlewood (2007) tested whether the long

distance dispersal of fruit flies was dependent on conspecific density by measuring the flights of flies tethered to an artificial “flight mill” under experimental manipulations of fly density. They determined that crowded fruit flies flew 1.5 times further and with significantly fewer stops than isolated flies (at scales relevant to long-distance movements within cherry orchards). No studies, to my knowledge, took the extra step towards linking these types of novel mechanisms underlying the initiation of dispersal with the density-dependent processes of spread across large areas.

Synthesis

From collembolans to caribou, animals demonstrate movement responses to stimuli across different temporal and spatial scales. Foraging ungulates, for example, switch between multiple behaviours at different spatiotemporal scales that span many orders of magnitude (Fryxell *et al.* 2008). Conspecific interactions change dynamically across spatial scales as consumers balance trade-offs between intraspecific competition and the benefits of living in groups (Fortin *et al.* 2009; Folmer, Olf & Piersma 2012). Recent unifying frameworks (Nathan *et al.* 2008; Schick *et al.* 2008) may prove useful in establishing a common language across spatiotemporal scales or ecological sub-disciplines and facilitate the interpretation of movement as one of the *primum movens* of greater ecological processes. The challenge remains for empiricists to design studies that are able to unravel these facets of movement and demonstrate the important linkages between individual behaviours, the spatial and temporal dynamics of populations, and ultimately redistribution processes that shape the abundance and distribution of species across space.

In order for this to happen, more studies are needed that are able to tease apart co-varying effects of environmental variables in generalized ecological contexts that are relevant across species or systems. In application, studies are needed that probe specific behavioural mechanisms while supplying parameters that can be readily integrated into models of spatial population dynamics and community interactions. My dissertation research addresses the general lack of syntheses in empirical movement research by investigating the behaviour of a model consumer-resource system across multiple scales. In Chapter One, I conducted experiments with individual rotifers to test whether and how random walk characteristics of consumers differ in response to controlled manipulations of consumer density versus resource density. This chapter is in review at *Functional Ecology*, coauthored by T. Avgar and J. M. Fryxell. Chapter Two addresses similar questions of resource- and density dependent movement at the population level by measuring the spreading behaviour of replicate rotifer populations through homogeneous one-dimensional environments. Chapter Two is published in the *Journal of Animal Ecology*, coauthored by T. Avgar and J. M. Fryxell. In Chapter Three, which is in preparation for submission coauthored by T. Avgar and J. M. Fryxell, I evaluated the robustness of the population responses observed in Chapter Two by testing whether density-dependence or resource configuration influences rates of spread within much larger, two-dimensional, heterogeneous landscapes.

Combined, these experiments demonstrate how contrasting individual movement responses can be integrated into predictions of diffusive population spread, provide direct and novel evidence that biological diffusion is conditional upon consumer density,

resource density, body condition, and predation risk, and demonstrate variation in population-level responses to these important ecological state variables. In doing so, these experiments link ecological conditions to local behavioural responses of individuals and subsequent patterns of population spread across heterogeneous landscapes.

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CHAPTER ONE

Movement behaviours of individual rotifers: density – and resource- dependent random walk characteristics

Abstract

Theory predicts that consumers can increase their energy intake by spending more time within resource-rich areas and/or by avoiding areas where local competitor densities are high. A consumer whose movements are described by a simple random walk can achieve these objectives by adjusting its turn frequency and/or speed. We recorded movements, as series of steps, by 180 individual rotifers (*Brachionus calyciflorus*) in glass capillary tubes to test the influence of resource density, competitor density, and their statistical interaction on these two movement parameters. Four treatments contrasted opposing levels of algae (resource) and conspecific density in a 2x2 factorial design. Our results indicate that density- and resource-dependent behaviours act through different mechanisms to shape patterns of rotifer movement. Turn frequency increased up to two-fold in resource-rich treatments, depending on the presence or absence of competitors. In contrast, swimming speed was 50% greater in the presence of competitors under all treatments, but was only slightly depressed by the presence of resources alone. We show how these two different movement mechanisms may be integrated into predictions of consumer population spread as resource and competitor densities vary. We discuss implications of the contrasting and complementary nature of these different movement mechanisms and their possible adaptations to different environmental stimuli.

Introduction

Foraging theory suggests that individuals should manipulate their searching behaviour to increase the proportion of time spent in resource rich patches (Tinbergen, Impekovén & Frank 1967; Fretwell & Lucas 1970; Charnov 1976; Benhamou 2007). From the perspective of the forager, the currency through which one must make decisions about localized movements is intake rate, with the prevailing theoretical expectation that an animal should alter behaviour in order to increase energetic gain. Explicit relationships between resources and movement are well established within this framework (Chandler 1969; Mason 1975; Heinrich 1979; Carter & Dixon 1982; Charoy & Clement 1993; Tuck & Hassall 2004).

On the other hand, competition theory suggests that individuals should distribute themselves through space to avoid interference or exploitative competition (Morista; 1952; Hutchison 1957; Taylor 1976; Leibold 1995). Hence, the presence or density of conspecific competitors should also have a strong influence on the intake rate of any given forager, and play an equally important role in dictating behaviour. Investigations of individual movement trajectories conditional on conspecific density are rare in the current literature, particularly empirical studies. In contrast, there is an extensive literature on animal abundances in space with respect to ideal free distribution theory (Fretwell & Lucas 1970) as well as density-dependent dispersal, much of which addresses neonatal dispersal among discrete patches in the landscape (Sutherland, Gill & Norris 2002; Matthysen 2005; Bowler & Benton 2005). Rather than considering simple spatial distributions or the probability of transfer among patches, we focus here on the explicit movement trajectories exhibited by individuals travelling continuously through

homogeneous environments of low or high competitor density. In this way, we can distinguish the influence of conspecific competitors, per se, on detailed individual movement characteristics.

Despite the obvious conceptual linkage between resource and competitor density, these two variables are rarely considered together with respect to movement. While population-based studies suggest a positive relationship between competitor population density and rates of movement (Baguette, Convie & Neve 1996; Matthysen 2005), it is not clear whether or how that relationship is affected by resource density. By contrast, individual-based studies have demonstrated that organisms behaviourally respond to resource density (Ricketts 2001; Roshier, Doerr & Doerr 2008), but it is unclear how this behaviour is affected by conspecific competition. Moreover, we suggest that there is little synthetic theory regarding the combined effect of resource- and conspecific-dependent movement. There are few general predictions of how foraging individuals should relate to the presence or density of conspecifics. By considering the influence of resources and conspecifics in tandem, movement studies may be designed to link more complex ecological conditions to detailed behavioral responses and to highlight new directions for theory.

Here we try to bridge this gap with a balanced experimental design that tests whether behavioural responses to food availability are conditional on competitor density, and vice versa, using experimental treatments ranging between abundant food and few competitors to scarce food and abundant competitors. We compare individual behaviours

using conventional metrics of movement and briefly discuss the implications of our results within the context of these differing ecological conditions.

Methods

We propagated and maintained batch cultures of our study species, the rotifer *Brachionus calyciflorus* on *Monoraphidium minutum* (green algae) in COMBO medium (Kilham *et al.* 1998). These stocks were originally isolated from natural populations in Germany by the Institute for Freshwater Ecology and Inland Fisheries and donated to us by G. Fussmann (McGill University). This rotifer strain has been cultured for greater than 10 years in laboratory populations and we maintained cultures for a minimum of 6 months in our lab prior to conducting experiments, making no attempt to isolate particular clonal strains. We did not observe any evidence of sexual reproduction in our rotifer cultures. New cultures, inoculated biweekly, typically contained algal and rotifer densities of approximately 2×10^6 /ml and 2/ml, respectively, and were housed in a continuously illuminated incubator at 20 degrees (the light regime following Gilbert 1970). For experiments, we randomly chose one culture to use each day, providing it was between 2 and 4 weeks old (since inoculation).

We crossed low and high algae densities with low and high rotifer densities within replicate tubes in a 2x2 factorial design. Immediately prior to conducting observations, we prepared one of each type of solution into four separate wells on a standard well tray. To prepare the solutions, we added pure COMBO medium to 2 wells (no algae) and an algal solution to 2 wells (3.14×10^6 cells/ml $\pm 4 \times 10^4$ algal cells [mean + SE]). This resource density was selected for practical reasons (it was roughly the algal

stock density) and for being demonstrably sufficient to influence rotifer movement behavior (Charoy & Clement 1993). We isolated rotifers from a single culture using a 20 micron filter trap, while washing the concentrate once with COMBO to remove any algae from the dense rotifer concentrate. Rotifers were then added to the wells to produce a low and high rotifer density treatment for each algae treatment. All subsequent observations were conducted within 2 hours of the preparation, and the order of observations was randomized to eliminate bias in pre-conditioning duration across treatments. All experiments were completed within a three-month period with at least one replication of each treatment tested during each sampling bout, to block for any potential temporal biases.

We obtained precise measures of conspecific density *post hoc* by counting the rotifers in every tube following observations. Low rotifer density treatments averaged 15 rotifers/ml (12 ± 1 rotifers per tube) whereas high density treatments averaged 150 rotifers/ml (120 ± 3 rotifers per tube). These densities are higher than those commonly observed in natural populations so it remains to be tested whether density-dependent responses can be found under field conditions or whether the responses shown here are only sensitive to these experimental densities. Our visual observations indicated that individuals in the low density treatments rarely, if ever, experienced contact with conspecifics whereas individuals in the high density treatments experienced frequent encounters with other individuals while swimming. Similarly, individuals experienced either an environment with no algae present or one with homogeneously distributed algae while swimming.

For a given replicate, we started by injecting one of the four experimental solutions into a glass capillary tube (1m long by 1mm inside diameter) and immediately capping both ends. This process ensured that rotifers within the tube were dispersed along the entire tube upon filling. A transparent ruler with 1 mm increments was placed alongside the capillary tube to calibrate rotifer movements. After the tube was filled, a single rotifer was randomly identified for observation by choosing the closest moving individual to a predetermined increment on the ruler. We measured movement parameters for 3 individuals per tube, roughly one in the center and one >20 cm of either side of center, taking care to avoid observing the same individual twice. Preliminary data exploration indicated that tube identity had no effect on our results. Hence, individuals were treated as independent observations. We observed a total of 45 individuals (15 tubes) per treatment, for a collective total of 180 independent observations. We followed the movement path of each focal individual using a 3X hand lens, recording data via a keystroke-logging script that recorded the time (in seconds) that elapsed for each passage of 1 mm according to the adjacent ruler. Movements to the left were arbitrarily recorded as negative displacements and movements to the right were recorded as positives. We set an arbitrary time limitation of a maximum of 5 minutes for each individual although some could not be followed for the entire duration (mean of 266 ± 5 seconds across all individuals). We discontinued observations if an individual swam within 5 cm of the end of the tube.

We conducted observations of rotifers swimming in 1 m long glass capillary tubes that were wide enough (1 mm) to allow turning and side-by-side passage of multiple

rotifers (which are approx. 0.2 mm in body length) but narrow enough to restrict displacements within the tube to essentially one dimension. The restriction of movements to a single dimension simplified the movement process such that an individual could control its rate of displacement through the adjustment of its speed, its turn frequency, or both. To measure turn frequency, a single step can be operationally defined as the distance traveled and time elapsed between turns (Kareiva & Shigesada 1983; Turchin 1998). We defined a turn as a reversal in movement direction (i.e., shifting from positive to negative displacement or the converse) at 1 mm resolution. We ignored the first step (originating at a random point in time) and the last step (ending after a random duration) to guarantee that the start and end points were determined by the organism. Turn frequency (turns per second) was calculated as the number of reversals (i.e. the total number of steps minus one) over time. For every individual, mean speed (in mm per second) was calculated as the total cumulative distance travelled divided by the entire observation period. We used Levene's test to confirm homogeneity of variance across treatments, which required log-transformation of turn frequencies but not swimming speeds. We tested for the effect of resources, competitors and their interaction on distributions of these two movement characteristics using general linear models. Partial R-squares for each of the predictors ($SS_{Treatment} / SS_{Total}$, where SS is the residual sum of squares) were calculated according to Cohen (1973; for ecological precedents see Murray, Eberly & Pusey 2006; Stankowich 2009; Krojerova-Prokesova *et al.* 2010).

We used observed individual characteristics to predict how analogous populations of individuals should spread through space by comparing the rate of change of the mean

squared displacement (MSD) across binned time intervals for groups of individuals pooled by treatment. The rate of spread of a population of organisms whose movements are well-described by random walk models is proportionate to the rate of change of the mean squared displacement (MSD) over time (Kareiva & Shigesada 1983; Turchin 1998).

To estimate rates of spread, we first calculated the squared displacement for each individual at 20 sec intervals. Given our experimental design, however, the squared displacement for a given individual at a given point in time is dependent on movements that occurred earlier in the observation period. To eliminate this bias, we used bootstrapped samples, where for each treatment we randomly selected a single squared displacement value for each of 45 individuals at a randomly chosen time interval. This process was repeated 1000 times to generate bootstrapped confidence intervals around the slope, that were then used to compare treatments. All statistical analyses were performed with R 2.2.0 (R Core Development Team, <http://www.r-project.org>).

Results

Our results from a generalized linear model fitted through turn frequency as a function of resource density (low or high), conspecific density (low or high), and their interaction, show that these three factors explain a significant amount of variation in turn frequencies ($F_{3,176} = 12.77$, $P < 0.001$, Adjusted $R^2 = 0.17$; Figure 1a). When resources were absent, turn frequencies were low regardless of competitor density (Figure 1a). When resources were abundant, however, turn frequencies were consistently higher and this response was enhanced by abundant conspecifics (Figure 1a). The significant

interaction between resources and conspecifics resulted in a 50% increase in turn frequency when resources were present but competitors were scarce compared to a 200% increase in turn frequency when both resources and competitors were abundant (Figure 1a). Partial R-square values suggest that more variation in turn frequency was explained by resource density (0.13) than either the interaction term (0.04) or the presence of conspecifics (0.01).

Swimming speeds were roughly 50% faster in the presence of conspecifics and 20% slower in the presence of resources ($F_{3,176} = 20.52$, $P < 0.001$, Adjusted $R^2 = 0.25$; Figure 1b). Partial R-square values suggest that more variation in swimming speed was explained by competitor density (0.24) than either resource density (0.01) or the interaction term (< 0.01). Some of the residual variation may be attributable to different individuals' body length or size, which are known to influence swimming speed in *Brachionus* spp. (Epp & Lewis 1984; Yufera, Pascual & Olivares 2005).

When individuals were pooled by treatment, the resulting mean squared displacements over time were well described by a linear model (Figure 2). Mean adjusted R^2 values for linear models fit through bootstrapped mean squared displacements as function of time ranged between 0.34-0.45 across treatments. The bootstrapped 90% confidence intervals for slopes of the regression lines did not overlap between treatments with the highest and lowest rates of spread, but there was significant overlap among slopes for the other treatments.

Discussion

Locomotory studies have traditionally categorized an animal's control of its movement into angular regulation (i.e. klinokinesis) and velocity regulation (i.e. orthokinesis; Fraenkel & Gunn 1961). More recently, these two components of movement regulation have been placed in a broader ecological context as elementary mechanisms that are sensitive to ecological conditions (Benhamou & Bovet 1989; Bartumeus *et al.* 2008). However, the two mechanisms are often difficult to tease apart based on animal movement data (Benhamou & Bovet 1989). Building on the existing literature, this study is the first to our knowledge to measure turn frequency and speed via experimental manipulations of conspecific and food densities, providing further insights into the link between movement mechanisms and ecological conditions.

Our results show that rotifers should spread at a slower rate in resource-rich environments (Figure 2) primarily because of high rates of turning that are conditional upon the presence or absence of conspecifics (Figure 1a). This is consistent with both theoretical (e.g., Benhamou & Bovet 1989; Barraquand & Benhamou 2008; Avgar, Kuefler & Fryxell 2011) and observational (e.g., Fryxell *et al.* 2008; Sei 2009; Kuefler *et al.* 2010) studies suggesting that organisms spread more slowly or have a higher residency time in resource rich areas by increasing path tortuosity. Previous observations of the swimming behaviors of *B. calyciflorus* have shown that individuals turn at sharper angles and show significant reductions in swimming speed in algal suspensions versus pure water (Charoy & Clement 1993; Charoy 1995). Although our results qualitatively agree with the previous studies, we found that the presence of resources explained a relatively small amount of the variation in swimming speed compared to the presence or

absence of conspecific competitors. Some of this difference may be due to methodological differences between studies, whereby our coarser grained observations and the restriction of rotifers to a single dimension may have reduced our ability to discern subtle differences in speed. Our trials show, nonetheless, a much stronger effect of resource density on turn rate than on speed, emphasizing a biologically significant difference in behavioural response that warrants further mechanistic inquiry.

Using computer simulations of foragers employing a resource-dependent, correlated random walk in a patchy environment, Stillman & Sutherland (1990) demonstrate that decreasing speeds in higher quality patches should positively influence intake rates, whereas changes in turn angles or directional biases should have a negligible impact on intake rates, in part because increased turning enhances the probability of departing a newly-entered patch. Consistent with their model, our results showed that rotifers did indeed reduce their swimming speed in resource-rich treatments. Contrary to their model predictions, we observed substantial increase in turn frequency when resources were abundant. It is important to note that in our experimental design there is no cost of turning away from patches because the environment is homogeneous. A robust test of Stillman and Sutherland's (1990) model would require a patchwork of cells with widely varying resource abundance, which was not possible in our experimental design.

We found that the presence of conspecifics induced a significant increase in rotifer swimming speeds in all treatments, but influenced turn frequencies only when resources were abundant. Intuitively, increases in speed in response to local competitor densities would serve to space out individuals and could represent a competitively

advantageous movement strategy when resources are limiting (French & Travis 2001; Yee, Taylor & Vamosi 2009). The enhancing effect of conspecific presence on movement tortuosity in resource rich environments provides additional support for the notion that competition for resources motivates observed movement patterns in our system. Less intuitive is the contrast between the strongest movement responses invoked by abundant conspecific competitors (i.e. increased speeds) and those invoked by abundant resources (i.e. increased directional changes). Note that the energetic cost of the first mechanism, speed regulation, is likely higher than the cost of the alternative mechanism, turn frequency regulation. Thus, the two responses may differ not only in their underlying stimuli but also in their ecological consequences. A possible explanation for this difference might lie in the different spatial scale of these two stimuli. The avoidance of a competitor requires getting away from a certain point in space, affectively achieved by speeding up along a straight line. Conversely, the adherence to a profitable resource patch involves remaining in a certain region, rather than a single point in space. Generally, increasing one's turn frequency would accommodate search in a local area while a decrease in speed would lead to decreased search, and potentially lower intake rates (White, Tobin & Bell 1984; Benhamou & Bovet 1989; Barraquand & Benhamou 2008; but see Stillman & Sutherland 1990).

Distinguishing turn frequency from movement speed is often a challenging task because of the difficulty of delineating discrete steps from continuous animal trajectories. At a sufficiently coarse scale, for example, one would not be able to distinguish frequent turns from slow movements. One disadvantage of our approach is that by measuring the

position of animals at fixed locations in space we are unable to explicitly determine the behaviour of the animal between those 1 mm intervals. One major advantage of our approach, however, is that the one-dimensional design allowed us to use the turning behaviour of each animal to precisely define its ‘natural’ steps, as opposed to the common practice of defining movement steps using arbitrary end-points, thus avoiding issues of autocorrelation in the movement process associated with the resolution at which the movement data are collected (Turchin 1998). Consequently, at the scale of our measurements, turn frequency and speed can be considered independent attributes of the animal’s movement behaviour. Such independence is rarely attainable, however, without continuous monitoring of movement in two or three dimensions (Karieva & Shigesada 1983; Turchin 1998).

While empirical links between individual and population movement processes are rarely possible, well-established analytical tools exist. Conventional approaches in spatial ecology use a family of models based on discrete Brownian (random) motion to describe animal movements based on steps and turns. Brownian walk models are powerful because they can be used to translate discrete individual movement into continuous population characteristics. For a population of random walkers, the movement behaviour of individuals can be directly translated into the rate of spread of a population (Turchin 1991; Grunbaum 1994; Hawkes 2009). Although our data do not allow direct comparisons with natural rotifer populations, inferences from this study are complementary to our previous work on laboratory rotifer populations demonstrating that the rate of spread of replicate populations differed significantly as a result of

experimentally controlled changes in conspecific and resource density (Kuefler, Avgar & Fryxell 2012). These outcomes are well predicted by the behavioural responses demonstrated in the current study in which increased speed and less frequent turns generate the highest rates of spread under conditions of extreme competition (i.e. both high competitor densities and scarce food). Under opposing conditions, in which rotifers experience high per capita food availability, decreased speed and frequent turns generate low rates of spread (Figure 2). The demonstration that diffusion processes reflect contrasting movement characteristics in rotifers under these different scenarios thus links ecological conditions to behavioural responses of individuals and subsequent patterns of population spread.

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Figure Legends

Figure 1a – Mean individual turning frequencies with upper and lower confidence intervals ($1.96 \times \text{SE}$) for four experimental treatments. For every individual, turning frequencies were measured as number of changes in direction (measured at a 1mm resolution) of the individual over the interval of observation (approx. 5 min). These values were then averaged across all individuals ($n=45$) for each of the four treatments (presence and absence of algal resources paired with the presence and absence of conspecific competitors).

Figure 1b – Mean individual swimming speeds with upper and lower confidence intervals for four experimental treatments. For every individual, speeds were measured as the total distance travelled (in mm) over the interval of observation (approx. 5 min). These values were then averaged across all individuals ($n=45$) for each of the treatments.

Figure 2 - Mean squared displacements of rotifers at consecutive 20 second time intervals under four experimental treatments. For each treatment, symbols indicate the mean squared displacements averaged across all of the individuals ($n=45$). Solid lines show the best fit linear model through mean values of bootstrapped populations ($n=1000$). Treatments include the presence and absence of algal resources (triangles vs. circles) paired with the presence and absence of conspecific competitors (hollow vs. filled). Treatments marked by “‡” showed no overlap between 90% confidence intervals around bootstrapped mean slopes.

Figures

Figure 1 a-b

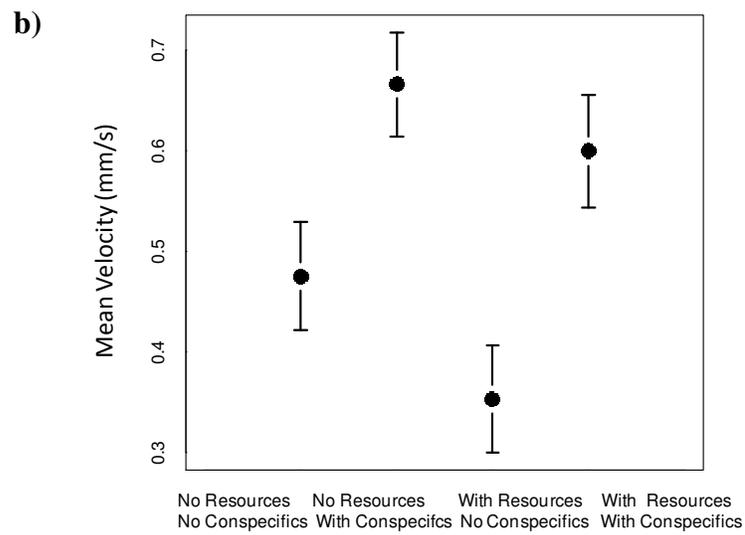
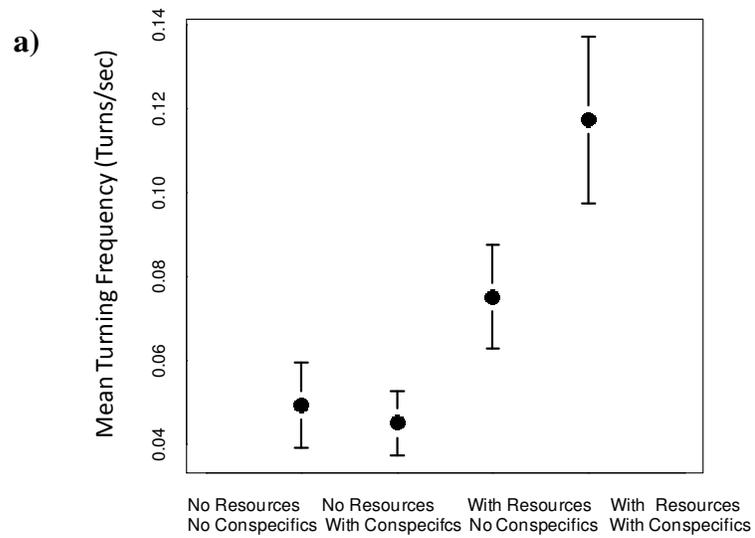
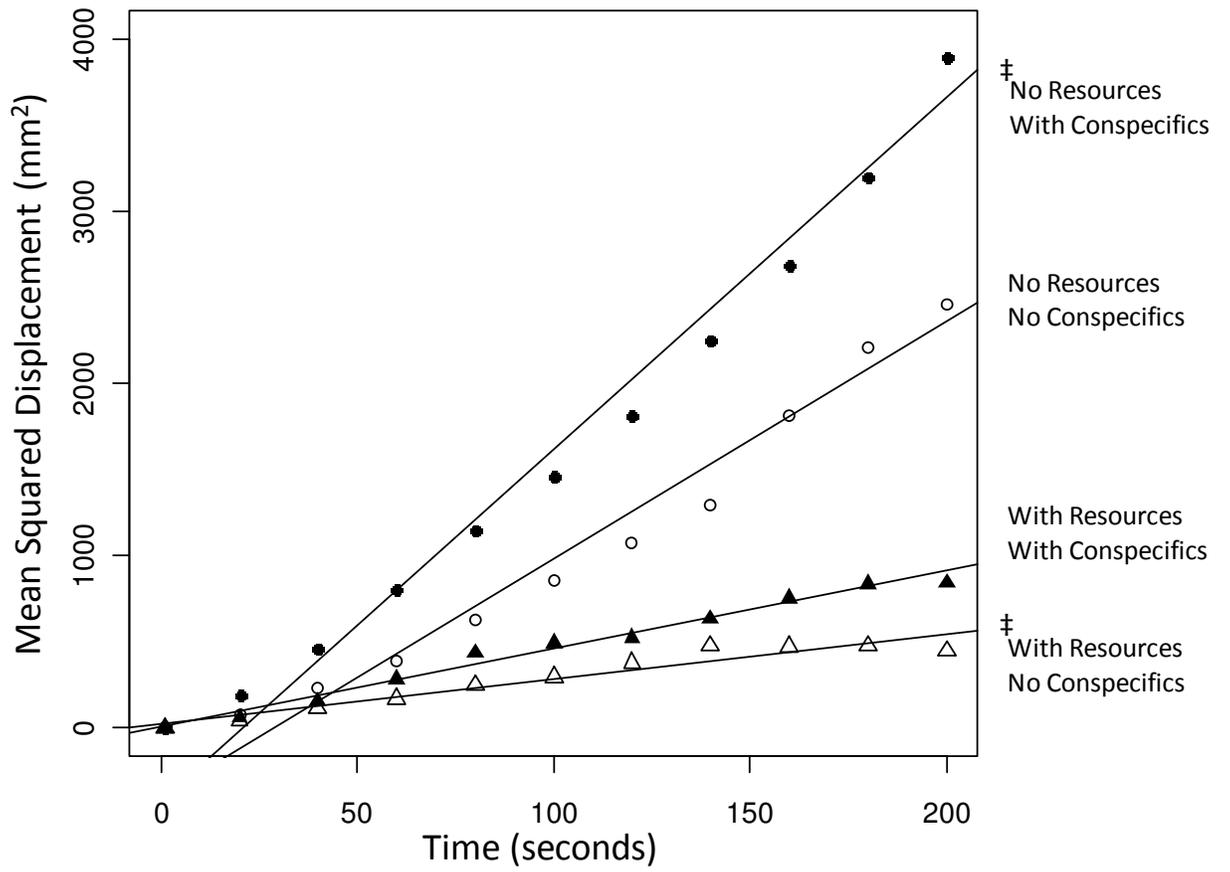


Figure 2



CHAPTER TWO

Rotifer population spread in relation to food, density and predation risk in an experimental system

Abstract

Despite the popular use of diffusion models to predict the spatial spread of populations over time, we currently know little about how diffusion rates change with the state of the environment or the internal condition of individuals. To address this gap in our understanding, we measured rates of spread for many populations of the rotifer *Brachionus calyciflorus* in a suite of well-replicated experiments. In one set of experiments, we manipulated food availability and population density along a continuous range of densities. In a second set, we manipulated the internal state of entire populations via food deprivation and exposure to predator kairomones. Across replicate populations, diffusion rates were positively correlated with conspecific density. Diffusion rates were negatively correlated with food availability, especially when conspecific density was high. Diffusion rates of food-deprived populations or those exposed to predation risk were lower than controls. Our results provide direct experimental evidence that rates of population spread are conditional on population density, food availability, body condition, and predation risk.

Introduction

A central challenge in ecology is linking animal movement with external and internal factors to predict patterns of population redistribution across space. Simple diffusion

models are a fundamental method of predicting continuous patterns of population spatial redistribution over time and have been successfully applied to both experimental and observational data (Skellam 1951; Andow *et al.* 1990; Turchin & Theony 1993; Moorcroft & Lewis 2006; Ovaskainen *et al.* 2008). Diffusion processes are central to spatially dynamic population interactions and pattern formation across large spatial scales (Lubina & Levin 1988; Holmes *et al.* 1994). The same processes govern rates of biological invasions including the spread of silvicultural and agricultural pests, with potentially severe economic consequences (Holmes 1993; Turchin & Theony 1993; Dwyer & Morris 2006; Urban *et al.* 2008).

Despite much theoretical precedence, few empirical studies have progressed beyond simple representations of diffusion because it is extremely difficult to measure variation in diffusion rates under complex field conditions with free-ranging individuals. Here we take a novel empirical approach to measure diffusion under controlled experimental conditions in order to test how diffusion rates are influenced by continuous variation in external environmental conditions and also the internal state of individuals. We use simple, one dimensional, microcosms to test state-dependent diffusion in over 200 populations of the rotifer (*Brachionus calyciflorus*). By using small scale, but highly replicated, experiments we were able to measure the degree of sensitivity of the diffusion process to consumer population density, resource abundance, and levels of hunger and predation risk experienced by the diffusing individuals, and evaluate whether interactions exist among either external (environmental) or internal (organismal) state variables.

Resource-dependent movement processes logically dictate that consumers spend more foraging time in locations with abundant resources than in those with lower resource density. Everything else being equal, populations of consumers can achieve this by reducing diffusion rates when resources are locally abundant and increasing diffusion rates when resources are scarce, as assumed in numerous theoretical models (Kareiva & Odell 1987; Morris & Kareiva 1991; Grunbaum 1998; Wilson & Richards 2000; Dwyer & Morris 2006; Avgar, Kuefler & Fryxell 2011). Population density-dependent processes may be expected to either suppress or inflate diffusion rates depending on the ecological circumstances. If rotifers move away from conspecifics to reduce competition for locally available resources, then diffusion rates may increase with population density (Shigesada, Kawasaki & Teramoto 1979; Turchin 1989). On the other hand, if rotifers are sensitive to predation risk, they may move towards conspecifics and thus diffuse less at higher densities (Courchamp, Clutton-Brock & Grenfell 1999). We tested these predictions by estimating rotifer diffusion coefficients across a range of experimentally-manipulated population and resource densities.

The internal state of organisms is a key component of movement behaviour (Nathan *et al.* 2008). Theory suggests that predation risk and starvation should influence optimal patterns of habitat use (Sih 1980; Mangel & Clark 1986; McNamara & Houston 1986; Lima & Dill 1990). In the presence of risk, population diffusion rates should increase if individuals in the risk-exposed population actively disperse to avoid predators (Taylor 1976; Ferguson, Bergerud & Ferguson 1988) or decrease if individuals either cluster to seek refuge (Caldwell 1986; Colishaw 1997) or simply reduce movement to

minimise predator encounters (Hutchinson & Waser 2007; Avgar, Kuefler & Fryxell 2011). Food deprivation could reduce population diffusion rates if animals in starved populations forgo exploration or are energetically challenged (McIntyre & Wiens 1999). Conversely, food deprivation could increase population diffusion rates if animals in starved populations are motivated to seek resources in unexplored areas (White, Tobin & Bell 1984). We therefore extended our experimental design to compare the diffusion coefficients of starved rotifer populations, those exposed to predator kairomones, and those exposed to increased risk of both starvation and predation.

Methods

Focal Species

Our experimental system consisted of a single resource species, the freshwater green alga *Monoraphidium minutum*, and a single consumer species, the planktonic rotifer *Brachionus calyciflorus*. These rotifers were originally isolated from natural population in Germany by the Institute for Freshwater Ecology and Inland Fisheries and donated to us by Prof. G. Fussmann (McGill University). This strain has been cultured for greater than 10 years in laboratory populations and we maintained cultures for a minimum of 6 months in our lab prior to conducting experiments, making no attempt to isolate particular clonal strains. Adults of this rotifer species self-propel via a band of ciliary cells that serve to capture food and generate movement (Clement 1987; Wallace *et al.* 2006). Given the extremely narrow perceptual field of this species (Salt 1987) and lack of prior observations of directed movement, we assume that the movement of any individual in the population approximates an uncorrelated, unbiased movement that is

well described (at the population level) by the simple Fokker-Planck diffusion model. Our experiments reflect primarily the behaviours, and not demographic dynamics, of these populations as the average generational time of this species under similar environmental conditions is approximately 5 days (Guo, Snell & Yang 2011), whereas our experiments were conducted over a span of 8 hours.

The resource, *M. minutum*, was batch cultured on COMBO medium (Kilham *et al.* 1998). New cultures were inoculated biweekly, as experimental volume demanded, and old cultures were immediately discarded if contamination was detected. The consumer, *B. calyciflorus*, was likewise propagated and maintained in batches on *M. minutum* in COMBO. We used only asexual females in experiments based on our visual observations that there were no males or resting-egg bearing females in the cultures used for experiments. New cultures were inoculated in 250-ml Erlenmeyer flasks weekly and, upon initial inoculation, contained algal and rotifer densities of approximately 2×10^6 / ml and 2 / ml, respectively. As a source of predator kairomones for risk-conditioned experiments, we maintained cultures of the rotifer *Asplanchna brightwelli* (a natural predator of *B. calyciflorus*) in COMBO medium with the alga *Cryptomonas erosa* as a food source. These *A. brightwelli* were originally isolated in 2000 from a natural population in a pond system near Munich, Germany (J.J. Gilbert *personal communication*). We propagated batch cultures of *A. brightwelli* approximately bi-weekly in 250-ml Erlenmeyer flasks, making no attempt to isolate particular clonal strains. Media conditioned with this predator has a demonstrated effect on the consumer's defensive spine formation (Gilbert & Waage 1967) and growth rates (Guo, Snell & Yang

2011), but has not previously been demonstrated to influence movement behaviours. All cultures were housed in a 20°C incubator with 24-hr light.

Experimental Apparatus

To estimate diffusion coefficients we measured changes in rotifer distribution within capillary tubes over time. Parallel rows of 20 glass capillary tubes were supported on a levelled 1 m x 1 m platform. The clear plastic material and architecture of the platform eliminated shadows on the tubes, which were suspended in slots cut in the platform. Each tube was 1m long, with a 2 mm outside diameter and 1 mm inside diameter. Individual tubes were spaced 3 cm apart. The entire apparatus was positioned on a lab bench beneath laboratory ceiling lights such that all experiments were conducted under constant temperature and lighting conditions. For each trial, we injected rotifers from the same stock culture into five replicate tubes filled with an algal solution. A different tube was censused every two hours by breaking it into 10 equal segments and counting the rotifers in each segment. Each set of five tubes was analyzed as a single independent trial, yielding one set of time-sequenced snapshots of rotifer redistribution along a one-dimensional axis.

External (Environmental) Factors

We conducted experiments to assess the influence of resource and conspecific density on rates of rotifer redistribution, spanning a wide range of resource (0.3 to 4×10^6 algae cells / ml) and consumer (20 to 600 rotifers / ml) densities. Densities of both algae and rotifers were manipulated to achieve a continuous, evenly-distributed range of

experimental densities rather than prescribed bins of different density treatments. To manipulate algal density, we diluted algal solutions with fresh medium to meet a specific density ($\pm 5\%$), measured using a Partec CyFlow® flow cytometer. Tubes were pre-filled with these solutions, taking care to avoid injecting any air pockets. Algal concentrations were measured only once at the onset of every trial. To manipulate rotifer density, we concentrated rotifers into a dense solution by gently filtering an entire population through a small funnel capped with a 20- μm Nitex filter, which allowed for the passage of algal solution while trapping rotifers in the funnel. This rotifer concentrate was then diluted with fresh medium to meet a specific rotifer density. We used new randomly assigned populations of rotifers each day. Newly inoculated cultures or very old cultures were discarded. For this first set of experiments, we counted rotifers in 460 tubes to calculate the numbers of individuals at certain distances after certain time intervals. The absolute densities of individual rotifers varied from tube to tube, ranging between 20 individuals per tube and 580 per tube across all trials, with a mean density of 174 (± 13 SE) individuals per tube. At the lower extreme, these densities overlap with those observed in lab-reared populations and at the upper extreme we used the highest densities we could achieve experimentally in order to increase our power to detect treatment responses. Nonetheless, as the rotifer densities we tested are higher than those commonly observed in natural populations, further studies are needed to test whether similar density-dependent responses can be found under field conditions or whether the responses shown here are only sensitive to these experimental densities. The absolute number of rotifers in any single 10 cm tube segment varied according to the absolute tube density and the rate

of spread. The range of absolute densities in any single tube segment for a given time intervals varied between 0 per section (e.g. in the section furthest from the injection site at $t=0$) to 279 per section (e.g. in the section nearest to the injection site at $t=0$). For standardisation, rotifer counts in each segment were divided by the overall population size (i.e., the sum of counts from all segments).

We initiated each trial by injecting 0.07 ml of rotifers in solution (the volume of a 10 cm tube segment is 0.0785 ml) into one end of five algal-filled capillary tubes, and immediately capped both ends of the tubes to prevent drainage. We processed one tube immediately at the beginning of each trial to determine the initial distribution of rotifers and subsequently sampled a new tube every two hours to measure how the distribution had changed over time. Processing involved breakage of the tubes at 10 cm increments. We did this by scoring the tube with a diamond edged glass cutter, snapping sections apart, and flushing the contents of each section into glass well trays while diluting the samples with 0.5 ml of fresh medium. Rotifers in each well were counted using a dissecting microscope. When rotifer densities were markedly high (>30 / ml) we subdivided the contents of each well into several new wells to facilitate more accurate counting. This procedure yielded five single snapshots of rotifer spatial distribution over the course of eight hours for each experimental trial.

Internal (Organismal State-Conditioning) Factors

We conducted a second set of experiments to assess the influence of food-deprivation and risk exposure on diffusion rates. For these experiments, we pre-

conditioned rotifers via one of four treatments for 15 hours prior to conducting trials, but otherwise followed the protocol described above. State-conditioning treatments included a control (i.e. no treatment), food-deprivation, risk-exposure, and the latter combined. Food-deprivation was achieved by filtering rotifers from a stock population into a new flask containing the same volume of fresh medium, but with no algae present, and returning to the incubator for 15-16 hours. Risk-exposure was achieved by injecting 10 ml of media laden with predator kairomones into a population before returning to the incubator for 15-16 hours. We extracted the predator-conditioned media from our cultures of *A. brightwelli* (density >5 / ml) and filtered samples through glass fibre paper to ensure no actual predators or their algal food (*C. erosa*) physically entered the *B. calyciflorus* stock, but only kairomones. The alga *C. erosa* does not exude any chemical cue perceived by *B. calyciflorus* that we are aware of based on a review of the literature. Across replicates, we varied the state-conditioning treatments while holding the algae and rotifer densities roughly constant. The algae and rotifer densities used in these state-conditioning experiments were approximately mid-range of the levels used in the first set of experiments described above (i.e., at 2.06×10^6 algae / ml $\pm 4.2 \times 10^4$ SE and 115 rotifers / ml ± 4.6 SE, respectively).

For the resource- and density- influenced diffusion rates we analysed 92 independent trials, for which we measured redistributions at 2-hour time intervals. For the predator- and starvation- dependent diffusion rates we analysed 120 independent s (30 independent trials for each treatment), for which we measured redistributions at 2-hour time intervals. Each independent trial generated a time-series of population proportions at

different distances from the initial point of origin (Figure 1a). Using a maximum likelihood approach, we fitted a one-dimensional Fokker-Planck diffusion model (see Appendix) to these distributions (Figure 1b) to estimate the most likely diffusion coefficient (Figure 1d). The discretized approximation to the Fokker-Planck diffusion model generally fit our experimental data quite well (Figure 1c) – out of 212 trials, none of the R^2 values were less than 0.5 and most exceeded 0.8.

For experiments that manipulated a continuous range of external factors, variation in diffusion rates across trials was analyzed using a set of nested linear regression models with resource density, consumer density, and their interaction as potential explanatory variables. A likelihood ratio test was then used to determine the best model. For the second set of experiments that manipulated only discrete organismal state-variables across constant environmental conditions, we used ANOVA to assess the influence of food deprivation and predator exposure on estimated diffusion coefficients. All statistical analyses were performed with R ver. 2.2.0 software (R Core Development Team, <http://www.r-project.org>).

Results

For external factors, likelihood ratio tests show that the full model (rotifer diffusion rate as a function of rotifer density, resource density, and an interaction term) explained significantly more variation in the data than any of the nested models (full model vs. density-dependent model: $\chi^2 = 46.1$, $P < 0.001$; full model vs. resource-dependent model: $\chi^2 = 86.0$, $P < 0.001$; full model vs. density- and resource-dependent additive model: $\chi^2 = 33.4$, $P < 0.001$). The full model, including resource density,

consumer density, and their interaction, explained 63% (adjusted R^2) of the variability in observed diffusion rates ($F_{3,88} = 51.7$, $P < 0.001$). Rotifer diffusion rates increased with consumer density but decreased with resource density (Figure 2). A negative interaction between these two factors resulted in a stronger influence of resource density when consumers were most dense and a likewise stronger influence of consumer density when resources were scarce. In other words, rotifer movement rates were highest at high competitor densities, but low resource densities (Figure 2).

We found significant variability in diffusion coefficients between state conditioning treatments. Movement rates were significantly lower for food-deprived populations relative to controls ($F_{1,117} = 16.5$, $P < 0.001$) and marginally lower for risk-exposed populations relative to controls ($F_{1,117} = 3.4$, $P = 0.07$; Figure 3). However, we did not find statistically significant evidence of an interaction between starvation and predation risk on diffusion rates ($F_{1,117} = 2.1$, $P = 0.15$; Figure 3).

Discussion

In this study, we have directly tested whether rates of population spread are sensitive to environmental conditions and the internal state of individuals in consumer populations. Our results demonstrate clearly that biological diffusion is conditional upon consumer density, resource density, body condition, and predation risk. There is a substantial empirical literature on organismal movement, particularly natal dispersal (Holyoak *et al.* 2008). Proximate mechanisms associated with individual dispersal probabilities or distance traveled by individual dispersers, for example, include factors such as age, body size, sex, personality type, local population density, resource density,

and degree of relatedness to other members in a population (Johnson & Gaines 1990; Clobert *et al.* 2001; Lambin, Aars & Piernet 2001; Bowler & Benton 2005; Mattheysen 2005; Clobert *et al.* 2009). Our experimental approach extends this growing literature by measuring the rate of population spread (i.e. the diffusion coefficient) under controlled experimental conditions. This is a necessary first step to parameterizing more complex continuous models of diffusive spread under heterogeneous environmental conditions (Patlack 1953; Gurney & Nisbet 1975; Kareiva & Odell 1987; Grunbaum 1998; Moorcroft & Lewis 2006).

Our finding that diffusion rates decrease with resource abundance adds an Eulerian perspective to the ample evidence that individual consumers travel faster through resource poor areas and linger in resource rich ones (Barraquand & Benhamou 2008; Avgar, Kuefler & Fryxell 2011 and references therein). Theory suggests that a negative relationship between diffusion rates and resource abundance would be expected if consumers adaptively respond to high resource density by taking shorter steps or making more frequent turns (Okubo 1986; Kareiva & Odell 1987; Morris & Kareiva 1991; Moorcroft & Lewis 2006). Numerous empirical studies have demonstrated that at the level of individuals such behavioural responses can serve to increase time spent in favourable patches (Grunbaum 1998; Viet 1999; Wilson & Richards 2000; Klaassen, Nolet & Bankert 2006; Kuefler & Haddad 2006; Fryxell *et al.* 2008; Dias, Granadeiro & Palmeirim 2009). Recent theoretical work has demonstrated that such patterns may simply reflect the mechanical truncation of step lengths between resource encounters and thus do not require any decisive behavioural response (Avgar, Kuefler & Fryxell 2011).

Regardless of the mechanisms involved, our work demonstrates empirically that a common pattern of resource-dependent movement is translated, at the population level, to resource-dependent diffusion and may thus play a crucial role in determining population redistribution patterns. Our experimental objective was to assess population responses to conditions that remained relatively constant through time. In our study, however, it is possible that resource densities within capillary tubes changed over time due to algal growth or rotifer consumption. Such changes are likely monotonic (as demonstrated by Fussmann *et al.* 2005) and should thus have no qualitative effect on the overall form of the population response surface we observed (Figure 2).

Our finding that diffusion rates increase with conspecific density is in agreement with speculations in the literature about the adaptive value of conspecific repulsion promoting more rapid diffusion as densities increase (Shigesada, Kawasaki & Teremoto 1979). This might suggest a pre-emptive adaptive response to competition for resources that become more rapidly depleted as local competitor densities increase. As with the response to resource density, the explicit mechanisms underlying these observed patterns may be informed by more detailed studies of individual movement. In a related paper, we describe a set of experiments demonstrating that rotifers vary their turning frequencies and swimming velocities. Interestingly, these two different movement mechanisms, turning regulation and velocity regulation, are each influenced uniquely by densities of either resources or conspecific competitors, respectively (Kuefler, Avgar & Fryxell *unpublished data*). These different mechanisms may reflect different selection regimes operating on these two determinants of population spread rates: escaping competition

through increased movement when conspecific density is high and enhancing intake through decreased movement when resource density is high.

The results from our state-conditioning treatments suggest that nutritional stress and predation risk also influenced patterns of movement in rotifers. Reduced diffusion rates exhibited by starved populations of *B. calyciflorus* may reflect a metabolic deficit due to starvation superimposed upon a relatively heavy cost of swimming (Epp & Lewis 1984; Charoy & Clement 1993; Charoy 1995). The lower diffusion rates of rotifer populations exposed to predation risk may be attributable to a reduction in swimming velocity to minimize predator encounters (Charoy & Clement 1993; Preston, Cecchine & Snell 1999) or a retraction of the swimming appendage (i.e., the corona) to reduce detectable vibrations (Wallace *et al.* 2006). Such suppressive effects of both starvation and predation on local diffusion rates could have significant ecological implications for foodweb interactions, by altering the spatial structure of populations.

Biological diffusion has received a great deal of theoretical attention (Turchin 1998; Okubo & Levin 2001), but far less empirical study. Empirical studies have begun to examine how individual movement characteristics respond to external drivers (Haddad 1999; Fortin *et al.* 2005; Morales *et al.* 2005; Klaassen, Nolet & Bankert 2006; Dalziel, Morales & Fryxell 2008; Kuefler *et al.* 2010). Extending observations of individuals to derive patterns of population spread is hampered, however, by the challenging task of scaling up individual animal movements to a landscape scale, particularly for ecological state variables that vary over time and space (Morales & Ellner 2002; Moorcraft & Lewis 2006). Other studies have modelled changes in the spatial distribution of a single

population over time in relation to resource abundance, rates of energy gain, or predation risk (Kareiva & Odell 1987; Morales & Ellner 2002; Fryxell, Wilmshurst & Sinclair 2004). Such field studies are often challenging to interpret, because of complex patterns of spatial heterogeneity in key environmental variables. Single realizations of a spatial process yield limited insight into the degree of variability in behavioural responses and are rarely suitable for testing for interactions among state variables. While physiological or motivational states have long been thought to influence the movement behaviour of individuals in an energy-seeking versus risk-avoiding framework (Sih 1980; Mangel & Clark 1986; McNamara & Houston 1986) our understanding of how internal state affects patterns of population redistribution is often obscured by other aspects of individual variation. We suggest that experimental studies may help in meeting these substantial challenges.

Predictions of population spread in rotifers were improved by considering diffusion as a function of both population density and resource density, tempered by predation risk and body condition experienced in the past by individuals. The implementation of such processes in diffusion models could conceivably improve our ability to predict how populations spread over time and space. Such models would be conditioned on past resource levels experienced by dispersers, local resource densities as the population spreads across space, as well as gradients in density of competing consumers and predators. In sum, our experimental results suggest richer state-dependent models of diffusion are worthy of deeper consideration.

Appendix

Matlab code for estimating movement parameters according to a random walk model, with spatially homogeneous diffusion parameters:

```
%*****parameters*****  
**  
  
clear all;  
imax = 10;  
jmax = 5;  
  
%*****initialization*****  
  
step = 0;  
randn('state',sum(100*clock));  
stepmax = 10000;  
bestNLL = 10000;  
predictN = zeros(imax,jmax);  
%NLL = zeros(stepmax);  
%Dpar = zeros(stepmax);  
residual = zeros(imax,jmax);  
  
%*****read data file*****  
datafile = input('Enter data filename (e.g. T27.txt): ','s');  
datafile  
A = load(datafile);  
for i=1:imax,  
    distance(i) = A(i,1);  
    for (j=1:jmax),  
        N(i,j) = A(i,j+1);  
    end  
end  
tmax=[0 120 240 360 480];  
  
%***** subroutine to estimate diffusion parameter *****  
  
for D=0.0001:0.0001:0.2000,  
    step = step + 1;
```

```

devsq = zeros(imax,jmax);
for j=1:jmax,
    Y = zeros(imax);
    Y(1) = 1.0;
    oldY = Y;
    for t=0:tmax(j),
        Y(1) = (1-D)*oldY(1)+D*Y(2);
        for i=2:imax-1,
            Y(i) = (1-(2*D))*oldY(i)+D*(oldY(i-1)+oldY(i+1));
        end
        Y(imax) = (1-D)*oldY(imax)+D*oldY(imax-1);
        oldY = Y;
    end
    for i=1:imax,
        predictN(i,j) = Y(i);
    end
    devsq = (predictN - N).^2;
end
mse = sum(sum(devsq))/(imax*jmax);
sigma = sqrt(mse);
Dpar(step) = D;
NLL(step) = (imax*jmax)*(log(sigma)+0.5*log(2*pi))+(sum(sum(devsq))/(2*mse));
if NLL(step)<bestNLL
    bestNLL = NLL(step);
    bestD = D;
    residual = predictN - N;
end
step
end
bestNLL
bestD
D = bestD;

%***** subroutine to observations over time *****
hold on;
subplot(2,2,1)
plot(distance,N,'ok',distance,N,'-k','Markersize',5)
axis([0 100 0 1])
xlabel('Distance (cm)','FontSize',14)

```

```

ylabel('Observed','FontSize',14)
hold off;
%***** subroutine to model predictions over time *****
subplot(2,2,2)
hold on
predictY = zeros(imax,jmax);
box on;
for j=1:jmax,
    Y = zeros(imax,1);
    Y(1,1) = 1.0;
    oldY = Y;
    for t=0:tmax(j),
        Y(1,1) = (1-D)*oldY(1,1)+D*Y(2,1);
        for i=2:imax-1,
            Y(i,1) = (1-(2*D))*oldY(i,1)+D*(oldY(i-1,1)+oldY(i+1,1));
        end
        Y(imax,1) = (1-D)*oldY(imax,1)+D*oldY(imax-1,1);
        oldY = Y;
    end
    predictY(:,j) = Y;
    plot(distance,Y,'-k',distance,Y,'sk','Markersize',5);
    axis([0 100 0 1])
    xlabel('Distance (cm)','FontSize',14)
    ylabel('Predicted','FontSize',14)
end
hold off
%**** subroutine to calculate R-squared between observations vs predictions*****
Rmatrix = corrcoef(N,predictY);
Rsquare = Rmatrix(1,2).^2

%***** subroutine to plot observations vs predictions *****
subplot(2,2,3)
plot(N,predictY,'ok','Markersize',5)
xlabel('Observed','FontSize',14);
ylabel('Predicted','FontSize',14);

%***** subroutine to plot neg log likelihood profile *****
subplot(2,2,4)
plot(Dpar,NLL,'-k')

```

```
xlabel('Estimate of D',FontSize,14);  
ylabel('NLL',FontSize,14);
```

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Figure Legends

Figure 1 – An example of observed (a) and predicted (b) changes over time in the proportion of rotifers at increasing distance from the point of origin for a single experimental trial. The five different lines indicate observed (a) and predicted (b) values for five sequential two-hour time intervals. Typically most of the variation in observed values was well-predicted by the best-fit Fokker-Planck model (c), with a clearly resolved negative log-likelihood (NLL) function (d) for the diffusion parameter.

Figure 2 – Transparent grid lines show the predicted relationship between rotifer diffusion rates, rotifer density, and resource density. Filled symbols connected with lines to the grid surface depict the observed values generated by experiments.

Figure 3 – Filled circles show the rotifer diffusion coefficient estimates (mean \pm 1 SE) associated with each of four state-conditioning treatments, averaged across all replicates for each treatment. Error bars indicate standard error of the mean for each treatment.

Figure 1

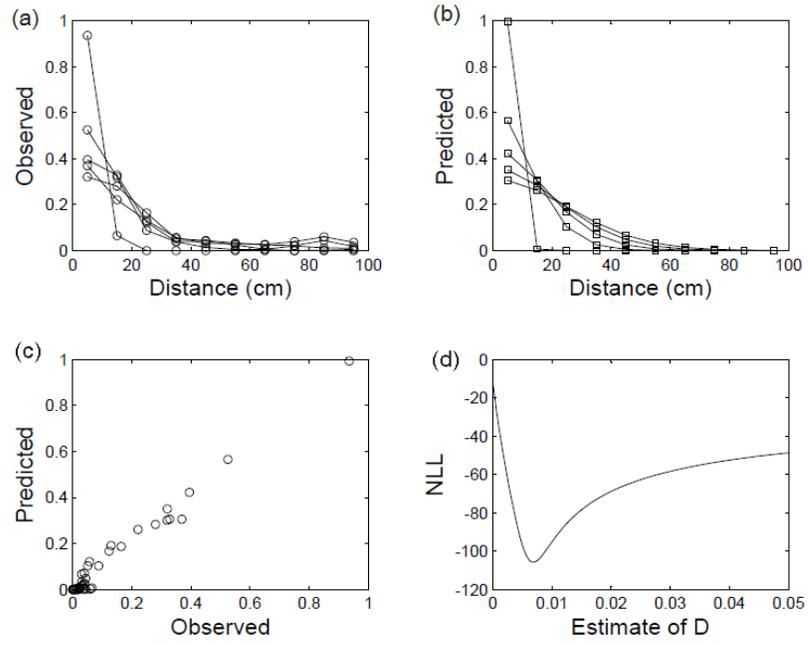


Figure 2

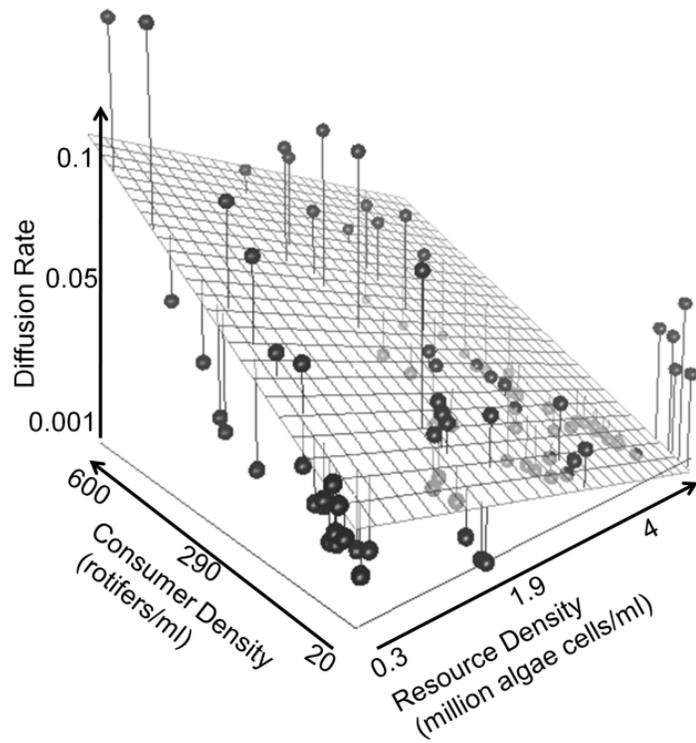
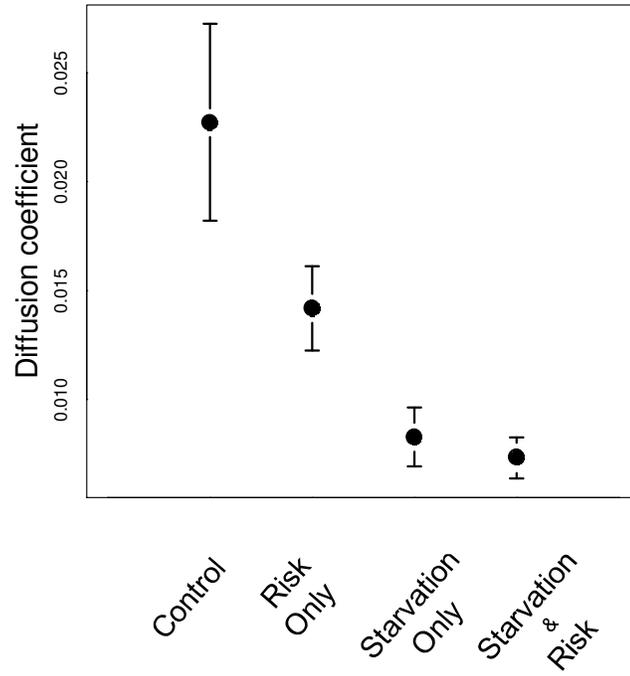


Figure 3



CHAPTER THREE

Density-dependence, resource distribution and rates of rotifer population spread following reintroduction in experimental microcosm landscapes

Abstract

Understanding how spatial variation in consumer density and resource distribution influences the spread of consumer populations is a central challenge to many important areas in ecology, including species conservation and the management of invasive species or agricultural pests. Here, we monitored the rates of spread of populations of the rotifer *Brachionus calyciflorus* in experimental microcosms with patchy versus evenly distributed algal food resources. We found that rates of population spread decayed over time indicative of sub-diffusive movement processes that can be well explained by positive density-dependent movement responses. Neither the rate of spread nor the magnitude of its decay differed, however, between patchy and evenly distributed resource treatments, despite observed rotifer preferences for patches. Our findings suggest that resource distribution was less crucial in predicting population spread than density-dependence.

Introduction

The challenge of understanding the complex relationships among population density, resource distribution, and rates of population spread is central to many facets of ecology. These relationships guide our understanding of spatially-structured population dynamics (Apps & McLellen 2006; Schooley & Branch 2009), animal reintroductions (Yott *et al.* 2010; Morgia *et al.* 2011; Henne & Johnson 2011) and the control of biological pests (Turchin & Theony 1993; Jonsen, Bouchier & Roland 2001; Urban *et al.* 2008; Wilson, Dorcas & Snow 2011). Although there have been many empirical advances in our understanding of how animal movement behaviours are shaped by key landscape elements (Dancose, Fortin & Guo 2011; Hudgens *et al.* 2012; Schultz, Franco & Crone 2012), few studies have measured whether and how localized movement behaviours relate to patterns of population spread across landscapes. We used controlled experiments with populations of the rotifer *Brachionus calyciflorus* in experimental landscapes with homogeneous versus patchy prey distribution to test the effects of consumer density and resource dispersion on rates of population spread.

Conspecific abundance has frequently been shown to stimulate dispersal (Bowler & Benton 2005; Matthysen 2005), where movements are thought to reduce competition. At local (within-patch) scales, conspecific repulsion (Rosenberg *et al.* 1997) and changes in movement characteristics (Sword 2005; Kuefler, Avgar & Frxell 2013) have been demonstrated to increase movement rates when competitor densities are high. This suggests that rates of population spread may be initially rapid following point introductions but decline as introduced animals spread over time. On the other hand,

social-attraction can mitigate competitive repulsion (Kuussaari, Nieminem & Hanski 1996; Andreassen & Ims 2001; Haydon *et al.* 2008), resulting in inversely density-dependent rates of spread.

Resource patchiness can also influence patterns of population spread in ways that may or may not be tied to population density. In a series of point-release experiments with flea beetles, for example, Hezewijk and Bouchier (2005) demonstrated that while individual beetles aggregated in areas with higher densities of their host plant, rates of spread were not significantly influenced by initial release densities ranging over several orders of magnitude. Under these conditions, rates of spread following point introductions will appear constant irrespective of changes in local competitor density. Here we test whether rates of population spread of the rotifer *Brachionus calyciflorus* are influenced by resource patchiness and/or local conspecific density for individuals introduced into a novel environment. In the simplest case, where there is a linear relationship between rates of spread and resource density, rates of spread averaged across homogeneous environments will not differ from those averaged across patchy environments because fast movements through resource poor areas will be balanced by proportionally slower movements through resource rich areas. Hence, resource patchiness, per se, may not have any effect on the population's rate of spread through the landscape.

If resource patches are to have any detectable difference on rates of population spread, a sufficient number of animals will need to encounter and respond to patch areas. Following release into a novel patchy environment, the number of animals encountering

patches – and hence the influence of patches on population spread - inevitably increases through time as animals spread out. Once a sufficient portion of the released population has encountered patches, any non-linear relationship between diffusion rates and local resource density should result in different rates of population spread across homogeneous versus patchy landscapes. Nonlinear movement responses may occur, for example, when consumers adopt area restricted search behaviour (Tinbergen, Impekoven & Franck 1967) as a threshold-response to the rate of resource encounters, thus displaying suppressed movement rates only at a high resource density (Focardi, Marcellini & Montanaro 1996; Fryxell *et al.* 2008). Note however that in practice we rarely observe the full spectrum of these relationships and hence the effect of resource patchiness on the population's rate of spread may depend not only on the shape of the relationship but also on the considered range of resource densities and the time span over which the effect is measured.

Previous work with rotifers has shown that linear density- and resource-dependent diffusion models provided a good fit to patterns of rotifer population spread in homogeneous, one-dimensional environments (Kuefler, Avgar & Fryxell 2012). The goal of this study was to test whether similar patterns of rotifer population spread result from point releases in the center of two-dimensional microcosms with or without resource patchiness. Our first objective was to test whether patterns of spread were better described by density-dependent or density-independent movement processes, depicted by constant versus decaying rates of spread over time. Our second objective was to ask whether this process is influenced by resource patchiness. By conducting repeated

experiments in microcosms with contrasting distributions (but constant abundances) of resources, we tested which of these predictions of resource-dependent movement would be supported when population spread was measured over composite landscapes.

Methods

Focal species

Our experimental system consisted of a single resource species, the freshwater green algae *Chlorella vulgaris*, and a single consumer species, the planktonic rotifer *Brachionus calyciflorus*. These rotifers were originally isolated from natural population in Germany by the Institute for Freshwater Ecology and Inland Fisheries and donated to us by Prof. G. Fussmann (McGill University). This strain has been cultured for > 10 years in laboratory populations and we maintained cultures for a minimum of 6 months in our lab prior to conducting experiments, making no attempt to isolate particular clonal strains. Adults of this rotifer species self-propel via a band of ciliary cells that serve to capture food and generate movement (Clement 1987; Wallace, Snell & Ricci 2006). Given the extremely narrow perceptual field of this species (Salt 1987) and lack of prior observations of directed movement, we assume that the movement of any individual in the population approximates an uncorrelated, unbiased movement which is well described (at the population level) by a simple Fokker-Planck diffusion model. Our experiments reflect primarily rotifer behaviour, and not demographic dynamics, since the average generation time of *Brachionus calyciflorus* under similar environmental conditions is approximately 5 days (Guo, Snell & Yang 2011), whereas our experiments were conducted over a span of 4 hours.

The resource (*Chlorella vulgaris*) was batch cultured on COMBO medium (Kilham *et al.* 1998). New cultures were inoculated biweekly, as experimental volume demanded, and old cultures were immediately discarded if contamination was detected. The consumer, *B. calyciflorus*, was likewise propagated and maintained in batches on *C. vulgaris* in COMBO. Our visual observations indicate that there were no males or resting-egg bearing females in the cultures used for experiments. New cultures were inoculated in 250-ml Erlenmeyer flasks weekly and, upon initial inoculation, contained algal and rotifer densities of approximately 2×10^6 / ml and 2 / ml, respectively. All cultures were housed in a 20°C incubator with 24hr light.

Experimental Apparatus

Our microcosm landscape (see Figure 1) consisted of a shallow aquarium made of Plexiglas with a 1.05 m² base and 15 cm walls. A clear 1 m² acrylic sheet, 3 mm thick, was cut to fit inside the inner walls of the aquarium. Several thin rubber grommets, 1.2 mm thick, were fixed with silicone to the acrylic sheet to provide even spacing between the base and the cover sheet. We filled the aquarium with 1450 ml of solution and carefully placed the cover sheet to trap an aqueous layer approximately 1.2 mm deep. Weighted bars were placed around the edges of the top sheet to ensure that a uniform depth was maintained throughout the apparatus. The shallow depth of our aquarium was purposefully designed so that our analysis of rotifer movement within the aquarium could reasonably be restricted to two dimensions. The aquarium was supported by a 95-cm² wooden frame fitted with 3 Plexiglas joists to minimize shadows on the base of the aquarium. The frame, in turn, was suspended from levelled steel supports over a lab

bench on which fluorescent lights were placed. Diffuser panels were used to uniformly distribute the light across the bottom of the aquarium.

We observed the rates of spread for ten rotifer populations introduced into landscapes with homogeneously distributed algae and another ten introduced to landscapes with algal patches. Algal densities were estimated using a haemocytometer immediately prior to use and diluted to meet consistent experimental levels. For a homogeneous landscape, we mixed algae with fresh COMBO media prior to filling the aquarium, so that algae cells were randomly distributed across the aquarium at a mean density of 1.40×10^6 cells / ml ($\pm 7.9 \times 10^4$ S.E.M.). To create a heterogeneous (patchy) landscape, we filled the aquarium with fresh medium first, set the cover sheet on, and then injected 24, 0.2 ml doses of dense algae into evenly spaced holes in the sheet. The resulting algal patches were approximately 2 cm in diameter and 15 cm apart. Patchy landscapes contained a mean density of 1.12×10^6 cells / ml ($\pm 1.16 \times 10^5$ S.E.M.) averaged across the entire aquarium area. These two treatments hence differed in the spatial distribution of algae, but not in mean algal abundance. We did not measure changes in algal densities across the arena over time for any single trial as it would have been impossible to do so without disturbing the set-up. The patches were readily visible to the naked eye and subsequent observations suggested that algal patches spread out very little over the course of a given four hour trial.

Immediately after the algae had been added to the experimental arena, we injected 0.2 ml of solution containing rotifers into the center of the arena. Detailed methods on concentrating rotifer populations via filtration are described in Kuefler, Avgar & Fryxell

(2012). The number of rotifers injected was consistent across all trials (3973 individuals \pm 214 SEM), corresponding to an approximate density of 3 rotifers per ml.

We used digital cameras for estimating the pattern of spread of the rotifer population over time. The steel frame supporting the aquarium also provided a central pivot for an axle attached to a bar on which six digital cameras were mounted (Figure 1). The pivot point of the boom was positioned directly above the center of the aquarium where rotifers were released. This boom rotated 360° parallel to the surface of the aquarium such that each of the digital cameras sampled rotifer abundance at their constant distance from the point of introduction. Cameras were held at an even height above the surface, close enough to enable macro settings for video capturing. Within a 1-4 mm focal distance above the aqueous solution, our 9.0 megapixel cameras (Canon Powershot SX110) with manual macro video setting had adequate resolution to enable us to distinguish individual swimming rotifers on video.

Data processing and analysis

To enable consistent video sampling, ten equally-spaced radial positions were marked around at the edge of the aquarium so that we could repeatedly count rotifers at the same spatial positions. The six cameras were fixed to the boom so that the distance between the lens centers of any two cameras was 5.5 cm. Each camera captured a frame area of 2.1 x 2.9 cm, so the distance between any two frames was 2.5 cm. As the boom rotated, the first camera along the boom captured video snapshots at a 4-cm radius from the rotifer release point, and the most distant camera captured video snapshots at a 35-cm

radius from the rotifer release point. Each camera hence sampled a concentric ring with a wide buffer between the farthest camera and the edge of the 1m x 1m aquarium. To take video samples, we turned on all the cameras and captured a constant stream of video footage while moving the boom clockwise between marked positions, with a 20-second pause at each position. In this way, we captured 20-second video samples at 10 spatial positions at 6 different distances from the release point.

Within 2 minutes of injecting rotifers into the landscape, we took an initial sample of the rotifer distribution and repeatedly sampled the same locations at 20 min intervals, over a total period of 200 minutes. Videos were processed manually whereby an observer recorded the number of rotifers within a given frame during the 20 second video segment for any given spatial position at any time. Each experimental trial generated 600 snapshots of rotifer abundance across time and space (10 spatial positions x 10 time intervals x 6 distances from a release point).

To evaluate whether rotifers exhibited preferences for algae patches at the spatial resolution of an individual camera frame, we compared counts of rotifers in patch versus non-patch areas using data from the patchy resource s. For this analysis, we used only data from a single camera and single time interval so that we compared rotifer counts at the same distance from the initial release site and at the same time interval (3 hours following release). We binned 100 count samples (1 sample per camera frame) among 10 replicate trials, into counts from camera frames that captured any part of an algae patch in the field-of-view (n=28) versus frames where no patch was detectable (n=72). We used a linear mixed effect model to compare whether counts differed as a function of patchiness,

using log-transformed count data to minimize heteroscedasticity. We assigned a random effect on the intercept with respect to the trial identity, as each trial contained 10 nested observations.

We used counts from the complete set of video segments to calculate the mean squared displacement (*MSD*) of the population of rotifers from the point of release at each time interval. The linear rate of change of *MSD* over time provides a metric that is proportional to the rate of diffusive spread of a population of organisms whose movements are well-described by random walk models (Kareiva & Shigesada 1983; Turchin 1998). To calculate the *MSD* for a single population at one time interval, we summed the total number of rotifers observed at each of the 6 radial positions relative to the release point. For each radial position, we then multiplied the square of the radial distance from the point of origin by the number of individuals observed at that distance. We then summed the resulting values over the six radial positions and divided by the overall number of rotifers observed to produce an estimate of the mean squared displacement for the population. This process of weighted averaging was repeated for each of the ten time intervals in each trial.

In order to accommodate potential deviations from simple linear diffusion, we used the following curvilinear model:

$$MSD = e^A \cdot t^B, \tag{Eq. 1}$$

where e^A represents the linear rate of change of the *MSD* over time, t is time, and B is the curvature coefficient. When $B > 1$ the population's rate of spread increases with time

(i.e., super-diffusive) whereas when $B < 1$ the population's rate of spread decreases with time (i.e., sub-diffusive). When $B = 1$ our model converges to the standard linear diffusion model where the population's rate of spread is constant through time.

We expanded Eq. 1 to further accommodate potential effects of patchiness on the linear rate of spread and the curvature as follows:

$$MSD = e^{(A + \alpha \cdot I(patchy))} \cdot t^{(B + \beta \cdot I(patchy))}, \quad \text{Eq. 2}$$

where α represents the effect of landscape patchiness on the linear rate of spread, β represents the effect of patchiness on the curvature, and $I(patchy)$ is a dummy variable that takes the value of 1 when the landscape is patchy and 0 when the landscape is homogeneous. We log-transformed Eq.2 to facilitate statistical analysis by linear regression. The full statistical model was formulated as:

$$\ln(MSD) = A + B \cdot \ln(t) + \alpha \cdot I(patchy) + \beta \cdot \ln(t) \cdot I(patchy), \quad \text{Eq. 3}$$

where t is the time elapsed (in seconds) since the initial release of rotifers.

To account for the hierarchical nature of our data, we included random effects of trial identity (10 per treatment) on A and B . Accounting for random effects is necessary as our MSD observations were not fully independent, but rather nested within each experimental population in a repeated measures design. We compared a nested suite of linear mixed effect models by AIC weight (Burnham & Anderson 2002) to evaluate whether the movement process was best described by a linear (diffusive) or non-linear (sub- or super-diffusive) relationship between the MSD and time, and whether the rate of

population spread or its curvature differed between landscapes with patchy versus homogeneous resource distributions. All statistical analysis was done using function *lme* (package *nlme*) in R (<http://www.r-project.org/>).

Results

Prior to estimating rates of spread of populations, we evaluated whether rotifers exhibited preferences for algal patches at the spatial resolution of an individual camera frame. Mean rotifer counts were higher in frames where patches were present (35 ± 4 SE, $n=28$) versus those where patches were absent (13 ± 1 SE, $n=72$). A comparison of these data with a linear mixed-effect models showed that this differences was significant ($t=7.66$, $df= 89$, $p<0.001$) after controlling for trial identity. This suggests that rotifers were not evenly distributed through space but rather they were more abundant in algal patches (Figure 2).

Our evaluation of spread across entire microcosms showed that the best-fit model did include significant curvature but did not include any effects of patchiness on either the linear rate of spread or the curvature. Parameter values (and 95% confidence intervals) for the fixed effects of the intercept (A) and the curvature coefficient (B) were estimated as 3.51 (3.44 - 3.59) and 0.33 (0.30 - 0.37) respectively. Hence, the mean squared displacement increased with time at a basal rate of $e^{3.51}$ which then decays through time (Figure 3).

The overall explanatory power of our full model (derived from a linear regression of observed vs. predicted mean squared displacements) was 94 %. We estimated the

relative explanatory power provided by the fixed effects by subtracting the variance of *MSD* values predicted based on the fixed effects alone from the variance of observed *MSD* values, and dividing by the latter. This ratio provides a relative goodness-of-fit measure, suggesting that approximately 65% of the variation in the *MSD* was explained by time. The remaining variation (29%) reflects the contribution of the random effects.

Discussion

The observation that curvilinear models of rotifer redistribution through time fit better than linear models reflects a movement process that is more complex than simple diffusion (Turchin 1989; Turchin 1998). Decaying rates of spread are common following population introductions as initial release effects abate over time (Henne & Johnson 2011). Alternatively, initial phases of active exploration and learning in novel environments may precede settlement (Bar-David, Saltz & Dayan 2005; Fryxell *et al.* 2008; Yott *et al.* 2010; Berger-Tal & Avgar 2012). In rotifers, previous behavioural studies suggest that increased swimming velocities are attributable to high competitor density (Kuefler, Avgar & Fryxell 2013). Such density-dependent movement behaviour is expected to result in a decelerating rate of population spread from an initial point release as local densities decline over time. Our experimental results corroborate this expectation.

Many organisms, from butterflies (Shultz, Franco & Crone 2012) to bison (Dancose, Fortin & Guo 2011), demonstrate individual movement behaviours that are conditioned on the configuration of landscape elements. It is often difficult to distinguish between the combined effects of landscape features on population spread because of the

enormous number of possible environmental variables contributing to movement processes. This is further complicated by the many different ways by which organisms interact with their environment at landscape scales. These phenomena include – but are not limited to - animal cognition or memory (Dalziel, Morales & Fryxell 2008; Mueller & Fagan 2008), the physical effects of landscape structure (Haddad 1999; Morales & Ellner 2002; Hudgens *et al.* 2012), energy-maximizing tradeoffs (Grunbaum 1998; Morales *et al.* 2005; Garcia *et al.* 2007), or combinations of behavioural and physical factors (McIntyre & Weins 1999; Dancose, Fortin & Guo 2011). In particular, the effects of resource distribution can be difficult to distinguish from the effects of resource abundance (Fahrig 2007; Mortelliti & Boitani 2008; Pe'er *et al.* 2011) mainly in human-altered landscapes where fragmentation is almost always positively correlated with a reduction in available resources (Collinge 1996; Tischendorf 2001; Koper, Schmiegelow & Merrill 2007). Our experimental design offers a substantial advantage over field-based studies by contrasting opposing levels of resource distribution (homogeneous versus patchy) while controlling for the absolute resource abundance (total number of algal cells) across all landscapes. By using replicated microcosms we were able to reduce landscape complexity to a single variable – the distribution of food resources – in order to conduct a generalized test of the influence of resource distribution on population spread.

Our findings show that rates of population spread do not differ in patchy (i.e., fragmented) versus homogeneous environments. Previous studies clearly demonstrated that *Brachionus* movement rates decline with increasing algal densities in spatially homogeneous systems (Charoy & Clement 1993; Charoy 1995; Kuefler, Avgar & Fryxell

2012, 2013). Moreover, these findings are corroborated in the current study where rotifers were found to occur more in resource patches compared to inter-patch matrix (Figure 2). The observation that these strong behavioural responses do not translate into landscape configuration-dependent diffusion rates suggests that the relationship between movement rates and resource abundance is approximately linear (see Introduction). Hence, fast movements through resource poor areas are balanced by proportionally slower movements through resource rich areas. This supports the notion that the qualitative effect of landscape fragmentation on a population rate of spread may depend on the shape of the functional relationship between movement behaviour and resource abundance.

An alternative explanation to the observed landscape configuration-independent diffusion rates may lie in the strong conspecific density effect. If this effect is strong enough, as suggested by the strong non-linearity in our data (Figure 3), it might overwhelm weaker resource-dependent responses. Indeed, we have previously found that while both resource and conspecific densities affect one-dimensional rates of rotifer population spread, the latter is the dominant effect (Kuefler, Avgar & Fryxell 2012). That said, the duration of our experiments was long enough to allow a landscape configuration-dependent effect on the diffusion rate to be evident, if such an effect exist. We thus believe that the observed lack of sensitivity to landscape patchiness reflects a linear relationship between resource abundance and rotifer diffusion rate. Note that such a linear relationship might actually stem from a complex behavioural response to environmental conditions as a simpler, behaviour-free mechanism is expected to result in a negative exponential functional form (Avgar, Kuefler & Fryxell 2011).

Predictions of population spread depend on, to varying degree, differences among individual movement characteristics within populations (Sheppard *et al.* 2006; Roshier, Doerr & Doerr 2008; Petrovskii, Mashanova & Jansen 2011). By demonstrating the challenges of scaling up individual movements in heterogeneous landscapes, Morales & Ellner (2002) argued that accurate predictions of population spread at the landscape scale require models that can accommodate the complexities of individual behaviour. In the present case, while mechanics of individual rotifer movement are known to be sensitive to local resource density (Figure 2; Charoy 1995; Kuefler, Avgar & Fryxell 2012), we found no effect of resource patchiness on overall rates of rotifer population spread. Our results suggest that in some cases, details about individual responses to local resource variation may have an undetectable impact on rates of population spread at larger spatial scales. This may be particularly in those cases where the movement response to resource abundance is approximately linear.

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Figure Legends

Figure 1 – Experimental microcosm landscape. Video snapshots of swimming rotifers were collected using an array of digital cameras mounted on a pivoting boom. A shallow (1mm deep) aquarium with a clear acrylic top sheet approximated a 2-D landscape. Treatments contrasted landscapes with homogeneously distributed algae versus equivalent amounts algae distributed in small patches injected through the top sheet.

Figure 2 – Boxplots indicate the mode, upper and lower quartiles for counts of rotifers observed in binned video samples. Data were binned from 100 total samples of rotifer counts, among 10 replicate trials, in frames that either included algae patches (n=28) or those where no algae patches were visible (n=72). All data are from samples taken at the same distance from the initial release site at the same time interval (3 hours following release). The expected count size based on a uniform distribution of individuals (total counts averaged over all frames) is shown by the dotted line. A linear mixed model (including trial identity as a random effect on the slope) fit through the data show that the presence of patches had a significant positive effect ($p > 0.001$) on the count size, indicating that rotifers were counted more frequently in algae patches.

Figure 3 – Circles indicate observed values of mean squared displacements for multiple unique populations (N=20) at 20 min time intervals. Hollow circles show observed values

for 10 populations spreading across replicate microcosm landscapes with homogeneously distributed algal resources. Filled circles show observed values for 10 populations spreading across replicate microcosm landscapes with algae concentrated into small patches. Total algal abundance was held constant across all landscapes replicates, regardless of resource configuration. The overall predicted rate of spread (solid line) is based on our best-fit model, which shows significant decay of the rate of spread through time but no distinction between landscape types.

Figures

Figure 1

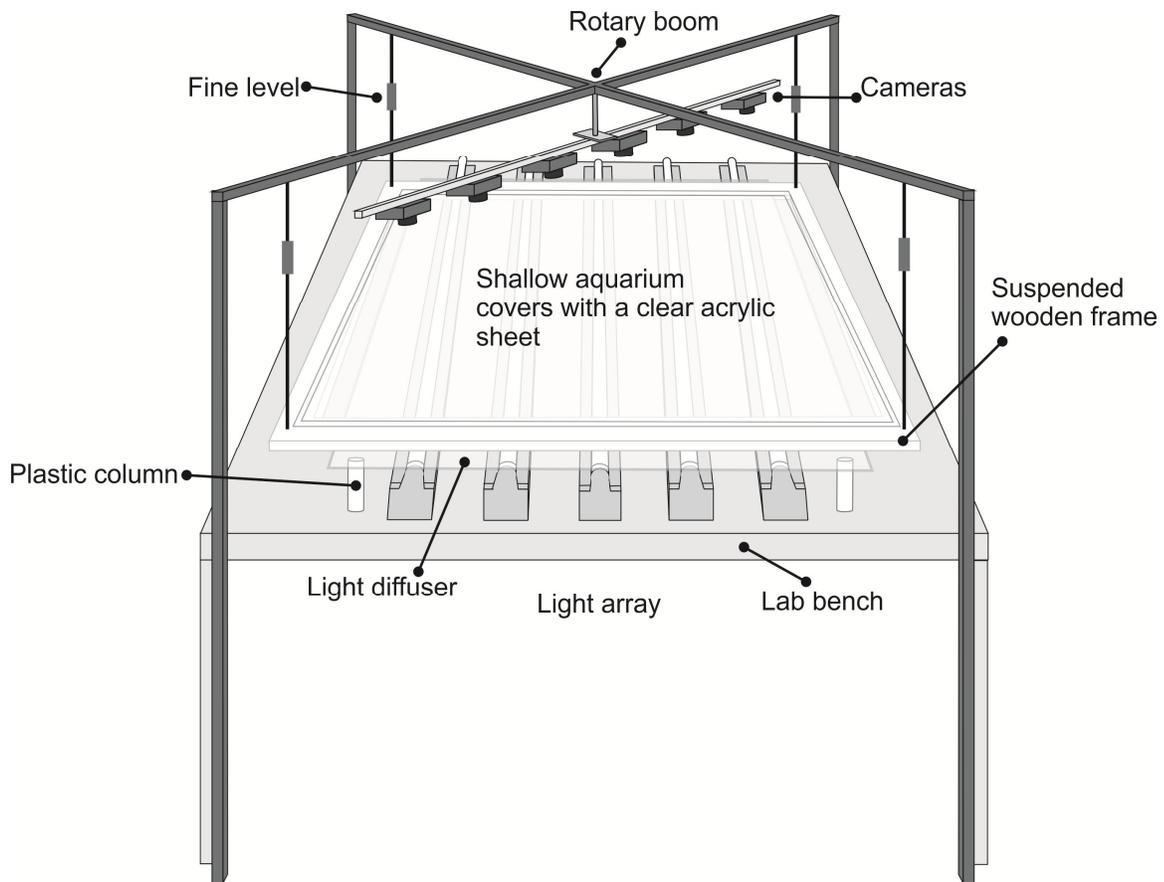


Figure 2

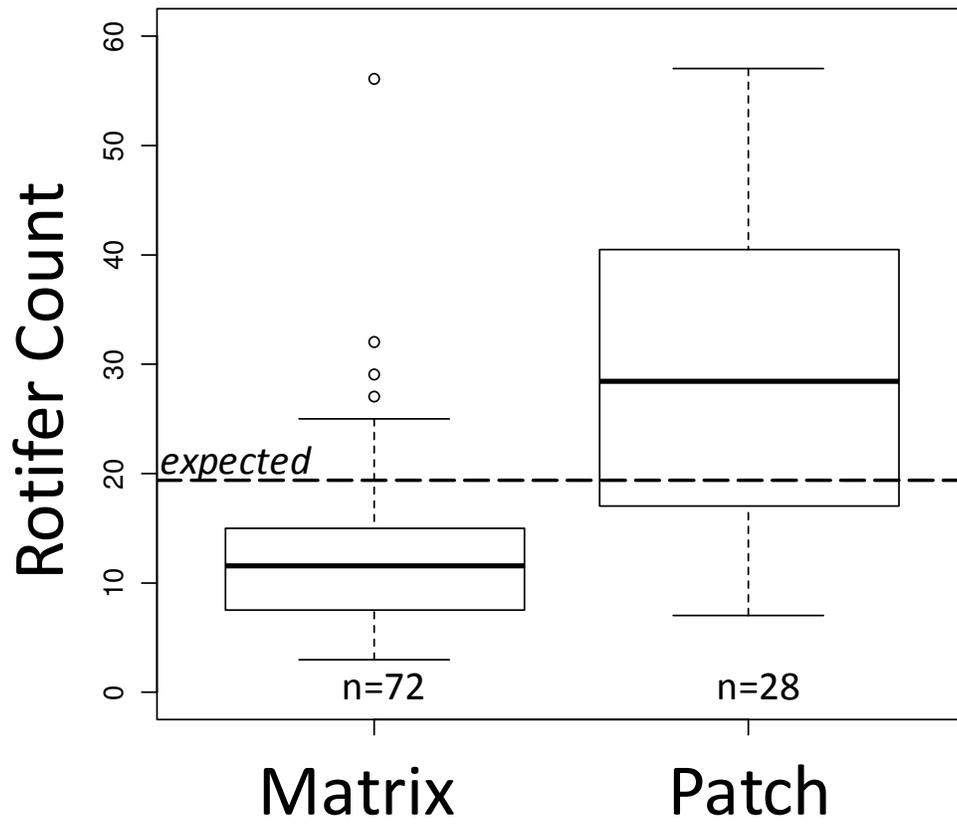
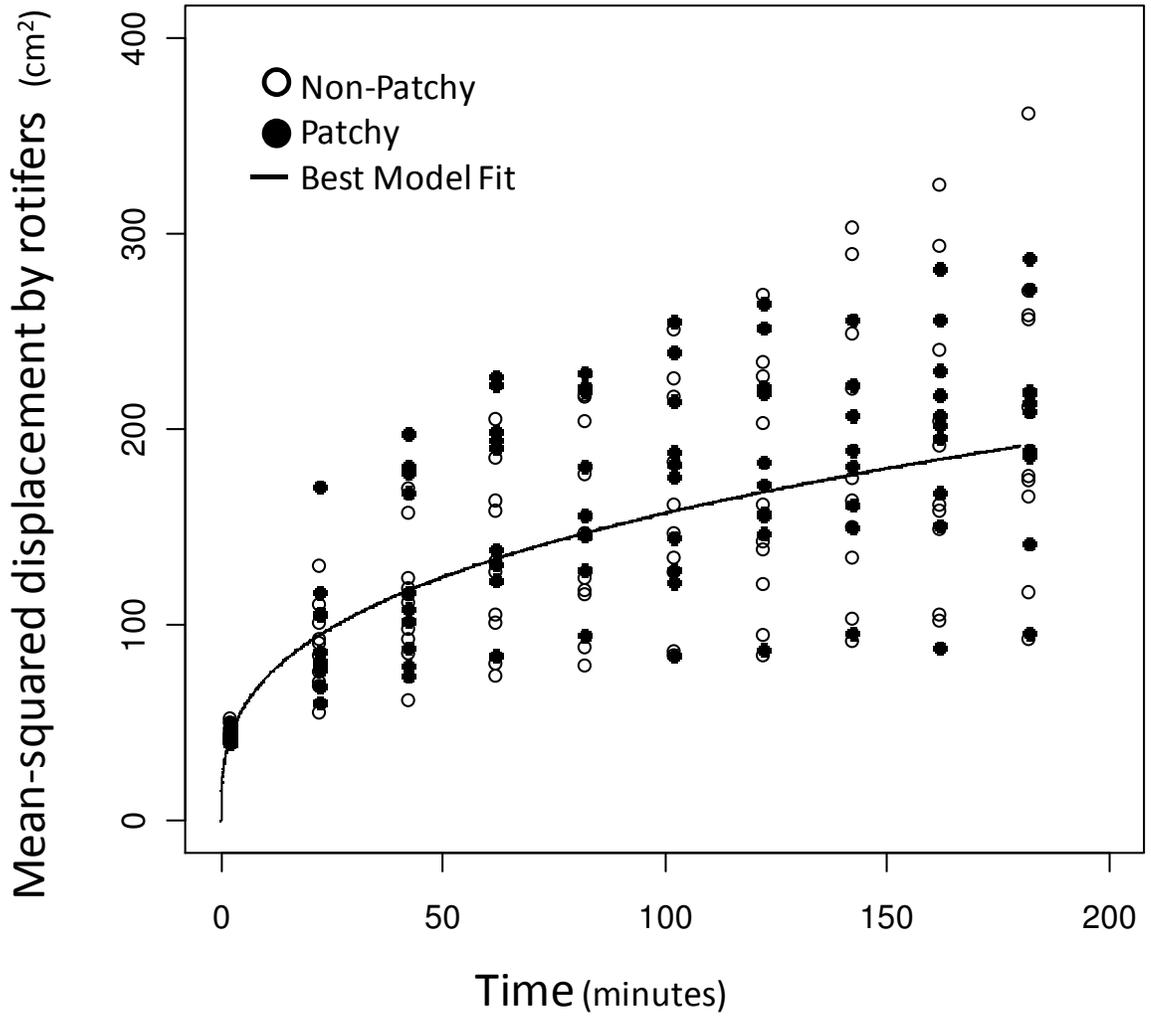


Figure 3



CONCLUSION

The primary goal of this research was to investigate the relative contribution of, and the interplay between, resources and conspecific competitors in driving consumer movement patterns across multiple scales. In Chapter One, I used experimental manipulations of conspecific and food densities to test their effects on the turn frequency and speed of individual consumers. In this chapter, displacement rates of individual rotifers were found to be lower in resource-rich environments primarily because of high rates of turning with little change in swimming speed. Displacement rates of individual rotifers were higher in conspecific-rich environments due to increases in swimming speeds, with little influence of turn frequency. In Chapter Two, I probed the degree to which these mechanistic processes were reflected in the behaviour of populations, by testing whether rates of population spread were sensitive to a wide range of resource and conspecific densities or the internal state of individuals in consumer populations. In this chapter, rates of spread were found to be negatively correlated with resource density, positively correlated with conspecific density, and to decline with starvation and predation risk. These experiments demonstrate empirically that resource- and- density dependent individual movement characteristics are translated, at the population level, to state-dependent diffusion and may thus play a crucial role in determining population redistribution patterns. In Chapter Three, I examined whether patterns of resource- or density- dependent population spread were detectable following point releases of populations into the center of two-dimensional microcosms with or

without resource patchiness. These experiments demonstrate that although individual rotifers show a preference for resource patches, the spatial configuration of resources on the landscape had no pronounced effect on overall rates of spread. At this micro-landscape scale, however, significant density-dependent factors were indicated by the observation of declining rates of spread as individuals spread out from their initial release point. In each of these chapters, resources and conspecifics show qualitatively similar effects on movement patterns but the underlying processes and the relative contribution of these two interacting components differed as the scale of observation shifted from individual to populations and from uniform to patchy environments.

Combined, these experiments demonstrate some of the common ground, and fundamental differences, in the relative contributions of local resource and conspecific densities towards generating animal movement patterns across multiple scales. In doing so, these experiments link these two distinct attributes of an individual's environment to local behavioural responses and subsequent patterns of population spread across heterogeneous landscapes. My hope is that these empirical demonstrations will serve future studies on consumer movement as a basis for disentangling these two important ecological variables. In doing so, studies may better distinguish the interplay between competitive, social, or other resource-competitor interactions and animal movement behaviours or distributional patterns. Lastly, my work serves to highlight the importance of taking a multi-scale and multi-process approach in movement ecology.