Eco-evolutionary feedbacks in self-organized ecosystems

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General Introduction

Monique de Jager

The simplicity of complex patterns

It is amazing how simple things in life can create immense complexity. With a few simple rules, complex patterns can arise from the interactions between individuals. When I was in Japan, I visited the world's most crowded crossing in Shibuya, Tokyo (Fig. 1.1A). Although it seemed impossible to cross the street in such a vast mass of people, I actually found it quite effortless to make it to the other side of the road. Looking back, I remember making a few simple decisions. I tried to find my way using a path of least resistance, which meant that I avoided collisions with fellow crossers and followed anyone walking before me that was going in the same direction as I was trying to go. After crossing the street, I climbed the stairs of one of the tall buildings right next to the crossing for a bird's eye view of the scramble that was taking place down below. At first I saw a complex mixture of pedestrians, but when I looked closer I could see patterns emerging during the crossover activity. I noticed that most people were using the same simple rules as I had earlier, and thereby they formed these large strings interlacing at the crossroad (Fig. 1.1B). Simply by crossing the street at a crowded location, we can see spatial patterns emerging from the straightforward actions of and interactions between individuals.

The most fascinating thing about the interactions responsible for the emergence of spatial patterns is how the success of one individual within the pattern depends on the actions of others. Just imagine that you are crossing a busy street, where cars turn into blazing menaces that will run you over once their light turns green. If you would be the sole pedestrian crossing this busy street, you simply cross at the sight of your green light and you will reach the other side in plenty of time. However, the situation becomes more complicated when the intersection is full of pedestrians. Those who are crossing in the same direction as you won't much affect your chances of reaching the other side in time, but the people traversing in the opposite direction might hamper your cross-over. The spatial pattern that is generated will affect the probability that you run into fellow crossers, and hence influences the ability of individuals to safely cross the street. Thus, spatial patterns that emerge from interactions between individuals will affect survival and fitness, and may thereby influence evolutionary processes.

Figure 1.1: Although the street-crossing behavior at Shibuya crossing, Tokyo, appears a pedestrian's pandemonium (**A**), spatial patterns emerge when we separate the people that are going in opposite directions (**B**), using a different color for those who are crossing to this side of the street (in blue) than for the those who are walking in the other direction (in yellow).

Surprisingly, evolutionary processes have seldom been investigated in studies on self-organized pattern formation (but see Hogeweg & Takeuchi, 2003; Kéfi *et al.*, 2008; Xavier *et al.*, 2009). Yet, a feedback between pattern formation and evolutionary adaptation of the pattern-generating traits likely exists. For instance, picture a fish population trying to arrive at their spawning grounds safely. Because individuals that try to stay close to conspecifics decrease their risk of being predated, more of these fish have a chance to reproduce than those who swim freely (Partridge 1982; Partridge *et al.*, 1983; Parrish *et al.*, 2002; Hemelrijk & Hildenbrandt, 2012). If schooling behavior is a heritable trait, the frequency of fish that school will be higher in the next generation, which generates a larger school and hence decreases predation risk even further for those fish that school together. This process repeats itself: schooling behavior again becomes more frequent in the next generation, producing an even larger, safer school, and so on. Here, the pattern-generating behavior – schooling – creates a spatial structure which influences the survival success of these individuals, thereby altering the pattern-generating behavior of the individuals in the next generation and, in turn, the emergent spatial structure. I believe that this feedback between ecology and evolution is of great importance for understanding both species traits and ecosystem functioning in natural systems with self-organized patterns.

The feedbacks between ecological pattern formation and evolutionary adaptation of self-organizing traits are not only of importance for street-crossing behavior or schooling of fish, but may also be vital in the wide prevalence of self-organized complexity throughout nature (Fig. 1.2). For instance, regular spatial patterns can emerge from individuals' self-organizing traits, such as movement, cooperation, and facilitation, in ecosystems as diverse as ribbon forests (Fig. 1.2C), coral reefs (Fig. 1.2D), arid bush lands, tidal wetlands, peat lands, and mussel beds (Klausmeier, 1999; Mistr & Bercovici, 2003; Rietkerk *et al.*, 2004a; Rietkerk *et al.*, 2004b; Van de Koppel *et al.*, 2005; Van de Koppel & Crain, 2006; Van de Koppel *et al.*, 2008; Eppinga *et al.*, 2009). In arid bush lands, for example, plants locally ameliorate their environment, which facilitates the settlement and survival of seedlings and thereby gives rise to spatially clustered patches of vegetation (Klausmeier, 1999). Another example involves mussels actively aggregating into
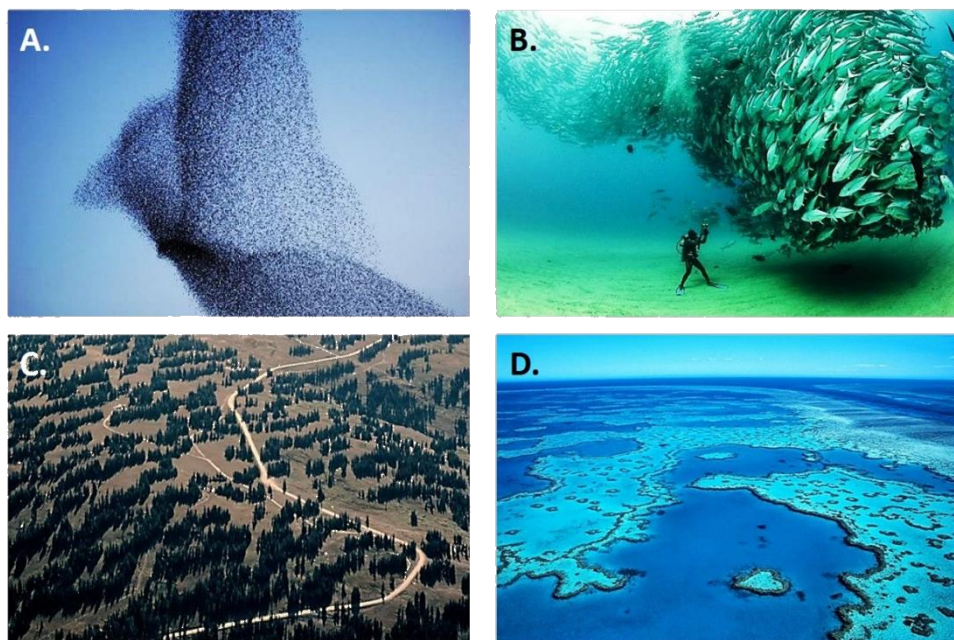
Figure 1.2: Self-organized spatial patterns are frequently observed in natural systems. For instance, spatial patterns arise in (**A**) bird flocks, (**B**) fish schools, (**C**) ribbon forests, and (**D**) coral reefs.

labyrinth-like patterns, which simultaneously decreases dislodgement risk and food competition (Van de Koppel *et al.*, 2008). The shared key feature in all self-organized systems is that structures larger than the organism develop from the local interactions between individuals, without any underlying templates or superior control. By means of self-organized pattern formation, organisms can strongly influence the ecosystem, thereby affecting environmental conditions as well, which in turn feeds back on the organisms' fitness. Although the ecology of self-organized pattern formation has been researched for a wide range of ecosystems, feedback between ecology and evolution has seldom been considered in these ecosystems (but see Kéfi *et al.*, 2008).

The apparent shortage of knowledge on eco-evolutionary feedbacks in self-organized ecosystems created a great opportunity for me to investigate this subject in my dissertation. In the past seven years, I have examined many aspects of self-organized patterning in young mussel beds, using both ecological experiments and eco-evolutionary models. With mussel beds as a model system, I will use the next five chapters to explore the dynamics and importance of eco-evolutionary

feedbacks in self-organized ecosystems. In the remainder of this introduction, I give more detail on self-organized pattern formation in mussel beds and the main traits responsible for self-organization in ecosystems – movement and cooperation.

Making the bed

Most of the work that I present in this thesis stems from mesocosm experiments, field experiments, and individual-based models that all involve mussel beds as a model system. These allow me to study the interaction between self-organization and evolutionary adaptation in spatially patterned ecosystems. When thinking about large-scale regular patterns in ecosystems, a mussel bed might not be the first habitat that comes to mind. Yet, mussel beds are an ideal system for studying self-organized complexity, as I will explain in the following paragraphs.

First, mussels actively move into a regular spatial pattern. Whereas self-organizing plant species are only dispersed as seeds before they settle, young mussels make use of their one foot and drag themselves along the sediment in search of conspecifics (Maas Geesteranus, 1942). They search for the perfect compromise between food availability and safety. On the one hand, mussels need sufficient algae on which to grow and live, yet on the other hand, they ought to be safely attached to neighboring mussels to decrease wave stress and predation risk (Van de Koppel *et al.*, 2005; Van de Koppel *et al.*, 2008). Aggregating into labyrinth-like patterns helps mussels to achieve this compromise and allows them to exist under conditions that would otherwise be lethal (Van de Koppel *et al.*, 2008). The movement of mussels into regularly patterned beds is an exciting self-organizing trait, which considerably affects the ecosystem's spatial structure.

Second, mussels cooperate with neighboring conspecifics, without any familiarity between them. Studies on cooperation in other self-organized ecosystems show that short-range dispersal is a prerequisite for local facilitation to evolve (Kéfi *et al.*, 2008). Whereas local dispersal is frequently regarded as a necessity for cooperation and facilitation, many cooperative organisms disperse over a wide range. Mussels, for example, settle down in a completely mixed mussel bed; yet they cooperate with others by attaching their byssus threads – a glue-like substance that can fasten two mussels together – to any random neighbor within

their well-mixed population. So far, the evolution of cooperation in spatially patterned populations with wide-ranging dispersal remains elusive, but mussel beds are a perfect model system to investigate this problem as well as its effect on self-organized patterning. Furthermore, the combination of aggregative movement and between-mussel attachment lends itself to a novel study of feedback between self-organization and the joint evolution of two traits (movement and cooperation).

Third, one of the most useful features of mussels is the ease at which they provide data. A simple camera is sufficient to take snapshots of individual-level pattern formation at the scale of meters. Mussels are not too particular on where they create patterns; they will even produce strings in a bucket. Using a seawater-filled tank and a webcam, we can follow mussel movement and pattern formation with little effort. Mussels create patterns within 8 hours, which is much faster than self-organization in most other ecosystems (for instance, self-organized pattern formation in arid systems takes decades; Barbier *et al.*, 2008). Data on between-mussel cooperation is also easily obtained using simple tools; the tweezers that are ideally suited for plucking eyebrows are also of great use when counting byssal attachments, nail polish does the trick when mussels are in need of individual identification, and cable ties are of good use for immobilizing mussels and preventing them from cooperating. Even the shape of a mussel – which is roughly oval – can be nicely approximated with circular individuals in agent-based models. In sum, the size and shape of the individuals and pattern, and the speed of pattern formation make mussel beds a great ecosystem to study the feedback between spatial pattern formation and the evolution of self-organizing traits.

A movement to aggregate

Active movement is frequently used by mobile organisms to aggregate with nearby conspecifics. For instance, birds fly into flocks of all shapes and sizes, fish swim close to each other to create dense schools, cockroaches move into aggregations, and ants carry their dead around and stock them onto massive ant piles (Theraulaz *et al.*, 2003; Jeanson *et al.*, 2005; Hemelrijk & Hildenbrandt, 2012). Similar to the strolling of pedestrians at a crowded crossing (Moussaïd *et al.*, 2009), the movement patterns of these aggregating animals also shape their large-scale spatial distribution and influence the organisms' efficiency and fitness. An individual can

improve its survival chances by adopting a movement strategy that allows it to move more rapidly to its preferred location. For example, being able to reach a group faster decreases predation risk, as aggregations provide cover, increase vigilance and information spreading, and can create a dilution effect (Treherne & Foster, 1981; Krause, 1994; Parrish & Edelstein-Keshet, 1999). Similar to the fish schooling example, the more effective movement types become increasingly frequent in the population and promote the generation of self-organized patterns.

The ability to aggregate into a patterned population initially requires that organisms are capable of finding each other. In the simplest case, conspecifics are within reach or viewing distance, which allows individuals to move in a straight line to join a neighbor and the crowd (as most natural populations are patchily distributed). However, finding others is far more complicated when the individual does not have any information about their neighbors' whereabouts. In this case, straight-line movement might not be efficient, since the individual may as well move in the wrong direction and miss the opportunity to turn and set another course. In this case, it might be advantageous to make random turns once in a while, allowing the individual to search in a closer range to its previous location. This arbitrary movement into random directions is what constitutes a random search strategy, where random steps and turning angles that are both drawn from particular frequency distributions can increase ones search efficiency when information about the environment is insufficient (Viswanathan *et al.*, 2000).

The classic example of such random movement is the Brownian walk, where the steps between random turns are of approximately the same length. Oddly enough, the main theory on Brownian motion finds its origin in the movement of pollen grains under a microscope. When Robert Brown struggled to examine pollen seeds in a petri dish, he initiated his investigation of the movements that impeded his original research. He discovered that these pollen grains randomly move around, with move lengths drawn from an exponential frequency distribution (Brown, 1828). Later on, Albert Einstein recommended research on Brownian motion and mathematically explained how colliding water particles actively changed the position of pollen grains. Using his study on Brownian motion, Einstein demonstrated that these collisions could describe the

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diffusion of dissolved particles (Einstein, 1905; Langevin, 1908). Following the wide applicability of diffusion in physics, movement patterns resembling Brownian motion were detected in the movement trajectories of many animal species. As Brownian motion is presumed to be an adequate, simple model, it has become the default template for describing animal movement (Skellam, 1951; Turchin, 1998; Okubo & Levin, 2002).

Recently, another random movement strategy – the Lévy walk – has been frequently observed in nature (Shlesinger & Klafter, 1986; Viswanathan *et al.*, 1996; Ramos-Fernandez *et al.*, 2004; De Knegt *et al.*, 2007; Sims *et al.*, 2008). A Lévy walk is a scale-free movement strategy that encompasses a long-tailed step length distribution, i.e. large steps occur more frequently than expected from Brownian movement (Clauset *et al.*, 2009). This movement strategy was named after Paul Pierre Lévy, a French mathematician who is famous for his discovery of the Lévy distribution (Mandelbrot, 1982). Lévy walks have been observed in myriad terrestrial and marine species, including ants, albatrosses, spider monkeys, goats, and marine predators (Shlesinger & Klafter, 1986; Viswanathan *et al.*, 1996; Ramos-Fernandez *et al.*, 2004; De Knegt *et al.*, 2007; Sims *et al.*, 2008).

Some random movement strategies exceed others in their effectiveness for finding resources, such as food, shelter, or mates; however, some may require greater intellect. Imagine searching for Easter eggs in a large field. When Easter eggs are scarce and difficult to find in the high grass, you must put effort into searching if you wish to indulge yourself with chocolate. There are a number of strategies you could follow. First, you could systematically search the field by browsing one row of grass after the other (Fig. 1.3A). Although this strategy will guarantee success, it does require that you remember exactly where you have been before and is therefore the most intellect-demanding strategy (Viswanathan *et al.*, 2011). A second strategy would be to start off in one direction and switch to a local search when you encounter an egg (the Easter bunny is likely to drop eggs in clusters, as is often the case with food items; Fig. 1.3B; Benhamou, 2007). After not finding anything for some time, you again switch to straight line movement until the next egg is found. Because this strategy requires an active shift between two random search modes, it is quite complex (Reynolds, 2008). A third strategy looks

fairly complicated; yet is the simplest of all. You move in one random direction for some time, then turn in another random direction and make a couple of steps, and so on (Fig. 1.3C). The trick here is to pick your step lengths from a power law frequency distribution, which is a step length distribution with a heavy tail that ensures you to make many small steps that are occasionally alternated by very long moves (in other words, a Lévy walk; Viswanathan *et al.*, 1999). The upside of this strategy is that you do not need to remember where you have been before, or how long it has been since you have encountered anything. However, for many ecologists, the strategy appears too simple (Benhamou, 2007; Jansen *et al.*, 2012).

As all search strategies have benefits and downsides, which movement strategy is most efficient under particular circumstances is much debated (James *et al.*, 2011; Jansen *et al.*, 2012). Especially in the case where organisms are searching in heterogeneous, patchy environments where food, shelter, or mates are scarce, ecologists tend to be divided in two opposing parties (Benhamou, 2007; Reynolds, 2008; Jansen *et al.*, 2012). Some ecologists consider Lévy walks to be most efficient and therefore most prominent in patchy environments (Viswanathan *et al.*, 1999; Bartumeus *et al*, 2002; de Jager *et al.*, 2011; de Jager *et al.*, 2014). Theoretical studies on search efficiency demonstrate that Lévy movement outcompetes simple Brownian movement in heterogeneous, patchy environments (Viswanathan *et al.*, 1996). Opposing this group are those who believe that organisms actively switch between two or more search modes using a Composite Brownian walk (Benhamou, 2007; Jansen *et al.*, 2012). A Composite Brownian walk comprises multiple Brownian walks with different mean step lengths into one movement strategy. Observed movement patterns that deviate from simple Brownian motion are often treated as either being the consequence of an interaction between Brownian movement and ecological encounters (Hastings *et al.*, 2005), or as multiple Brownian walks combined in a Composite Brownian walk (Benhamou, 2007; Jansen *et al.*, 2012). Although composite Brownian walks were found to give a better representation of movement patterns observed in nature than simple Lévy walks (Jansen *et al.*, 2012; De Jager *et al.*, 2012b), switching between multiple movement modes adds an extra level of complexity to the behavior. Presently, the debate continues.
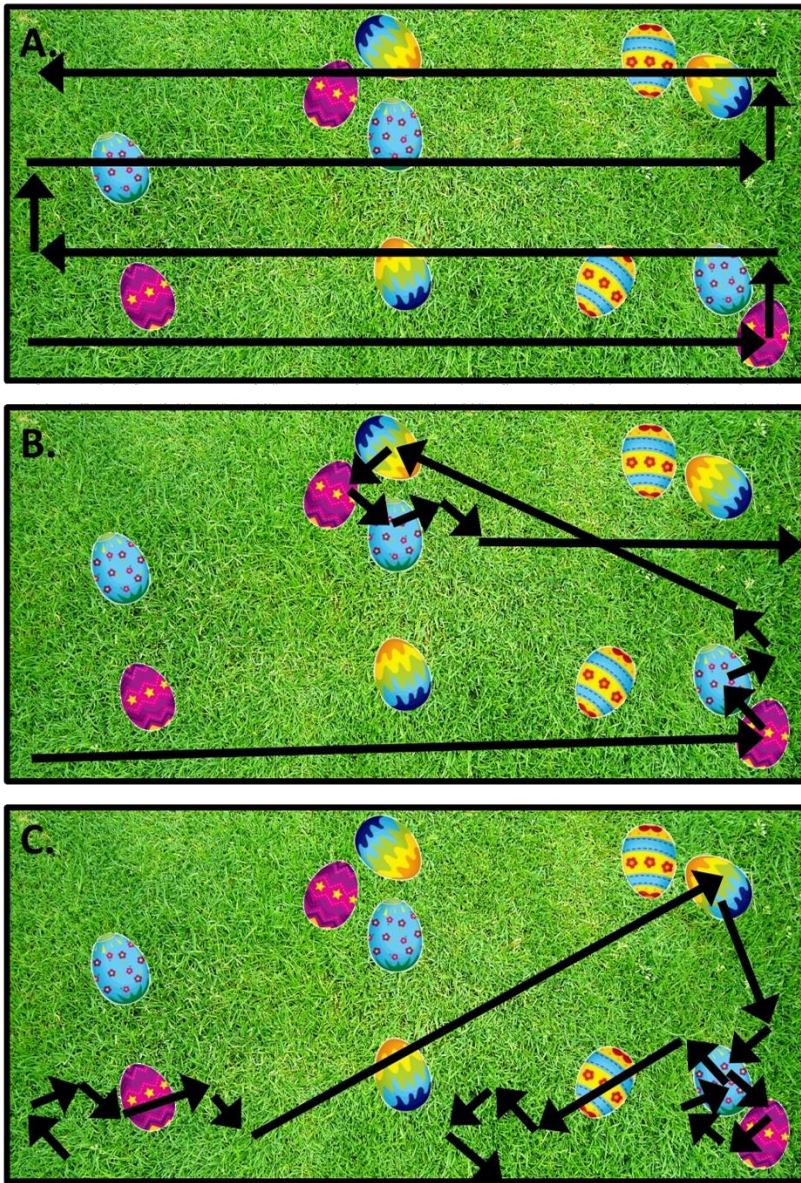
Figure 1.3: Three different methods to search for resources (such as Easter eggs). (**A**) Strategically browsing the area enables you to find all the Easter eggs; yet, it is also the most memory-demanding strategy. (**B**) Alternatively, one could switch between straight line movement until an egg is found and a local search at the site of the discovered egg. (**C**) A strategy that does not make use of your memory is to randomly draw step lengths from a certain step length frequency distribution. In between the steps, turns into random directions are made.

Optimizing ones random search strategy is not just a matter of finding the most efficient strategy to use in a certain environment, but also involves how this movement strategy in turn affects the environment. Whenever the environment affects an organism's behavior, the altered behavior can in turn influence that of others. Take for instance my example of the busy crossing. If one person moves a little to the left during his cross-over because he cannot move forward, others might have to adjust their walking direction to prevent a collision with this left-going individual. Certain movement strategies used by street-crossing pedestrians or other moving organisms can become less efficient due to the response of adjacent individuals on their crowded environment. Especially in self-organized systems, the movement of one individual affects the efficiency of the search strategy of others. As most of these interactions have not been considered in previous research, much remains unknown about the functioning of different movement strategies during self-organization. Furthermore, evolution of these movement strategies has been disregarded in earlier studies and, moreover, eco-evolutionary feedback with respect to movement strategies remains unstudied. Especially in self-organized ecosystems, the movement strategy used by individuals may have large implications for the development of the spatial population structure. As the emergent structure in turn affects the selection pressures for the individual organisms, evolutionary adaptation of movement behavior to self-generated conditions is expected to occur. In **Chapter 2** of this thesis, I investigate how Lévy walk movement strategies can evolve from the feedback between mussel movement and self-organized mussel bed formation.

An active response to environmental cues is not necessary for a change in an organism's movement pattern. For example, an intended step can be prematurely stopped because the organism can go no further due to a physical obstruction. In natural systems, organisms can interact with one another by consuming resources, predating each other, or simply encountering one another. These interactions can change an intended search strategy and generate a completely new movement pattern. A number of empirical studies have observed how the movement pattern of microzoöplankton, goats, marine predators, and albatrosses changed from Lévy-like movement in resource-poor environments to Brownian motion in denser locations (Bartumeus *et al.*, 2003; De Knegt *et al.*, 2007;

Humphries *et al.*, 2010; Humphries *et al.*, 2012). When we recall how Einstein (1905) demonstrated that Brownian motion of dissolved particles was caused by collisions between these particles and water molecules, we can easily imagine that observed Brownian patterns in the movement of organisms might also be the result of ecological 'collisions'. Until now, however, it is often hypothesized that the observed switch from Lévy-like to Brownian movement is an active response of an animal to changes in resource availability, because an active switch between Lévy and Brownian movement is assumed to increase the animal's search efficiency. In **Chapter 3** of my thesis, I experimentally demonstrate that observed Brownian movement patterns in dense mussel beds are the consequence of the interaction between an intrinsic Lévy walk and frequent collisions with neighboring conspecifics. I prove this principle with a simple argument and further show that actively switching between Lévy and Brownian motion does not improve one's ability to locate resources.

To settle the debate on whether organisms are using a Lévy walk or a Composite Brownian walk, I have been exploring ways to distinguish between these two movement strategies. I figured that environmental cues, such as the presence of food or other resources, might trigger the switch from one movement mode to another in a Composite Brownian walk. As resources are often patchily distributed, an efficient Composite Brownian walk would consist of a local search in the presence of resources and a straight-line leap between food patches. Lévy walks are not controlled by switches induced by environmental cues but are always fully random, despite the presence or absence of resources. Hence, one can imagine that with Lévy-like movement patterns, clusters of small steps are not only found near food patches but also in free space. In contrast, clusters of steps should be associated with resource distributions in Composite Brownian walks. We use this idea to investigate whether mud snails (*Hydrobia ulvae*) are making use of Lévy-like movement or a Composite Brownian walk, by examining clusters of steps on and off food patches in **Chapter 4** of this thesis.

Patterns of Cooperation

A crucial component of many forms of self-organization in ecosystems is local positive feedback, which is often generated by facilitative or cooperative

interactions between organisms. Moving into a self-organized pattern would be pointless if aggregation did not help you in any way. For instance, if mussels are not attached to their neighbors within the pattern, they risk becoming dislodged by wave action or predation (Hunt & Scheibling, 2001; Zardi *et al.*, 2006). Hence, creating a pattern without profiting from some sort of cooperation that the pattern offers is not advantageous. Both cooperation, where one individual helps another at its own expense, and facilitation, where the benefit to others is an accidental byproduct, aid in ameliorating the environment locally. In numerous species, cooperation between individuals is a common process; yet, understanding how cooperation has evolved remains a major challenge. For instance, I have seen young elephants helping one another by giving a little push on a climb up a steep slope, leaving the assisting youngster vulnerable on the dry river bed. Why did this elephant help the other? Assisting another might come at a great cost, and it remains uncertain whether the other will do anything in return. Evolutionarily speaking, cooperation can only evolve when cooperating individuals gain a fitness advantage over uncooperative conspecifics; therefore, cooperators should in the end benefit from their own generosity.

There is a Dutch saying that comes to mind when thinking of cooperation in spatially heterogeneous systems: 'better to have a good neighbor than a far friend'. This saying is quite true; since you will interact more frequently with those nearby than with distant individuals. Regularly cooperating with 'good neighbors' will be more profitable than the rare cooperation with a faraway friend. Without spatial segregation of cooperative interactions, everyone will randomly interact with each other, and this has been shown to result in the demise of cooperation in the first models of evolutionary game theory (Maynard-Smith, 1982; Axelrod, 1984). However, when individuals are placed within a spatial structure, cooperate only with close neighbors, and locally disperse their offspring, cooperation is able to evolve (Nowak & May, 1992; Skyrms & Pemantle, 2000; Ishibuchi & Namikawa, 2005; Kun *et al.*, 2006; Langer *et al.*, 2008; Szamado *et al.*, 2008). In these models of cooperation, staying close to related individuals increases ones chance that its relatives will assist it, provided that cooperation has a genetic basis. Furthermore, helping family members indirectly benefits an individual's fitness, as they share some of that individual's genes (Hamilton, 1963). This inclusive fitness concept is

habitually regarded as an essential and sufficient explanation for the evolution of cooperation.

Until now, research on the evolution of cooperation in spatially complex populations has overlooked at least two issues. First, many cooperative species disperse over a wide range and are therefore not interacting more frequently with relatives than with unrelated conspecifics. For example, various marine invertebrates that later in life interact with sessile neighbors have a suspended larval stage – where they can drift over large distances – before settling on a surface (Godfrey & Kerr, 2009). In most studies, the positive effect of spatial structure on the evolution of cooperation is attributable to the increased chance of cooperating with relatives; how this process works in populations with wide-ranging dispersal remains elusive. In **Chapter 5** of this thesis, I investigate the effect of spatial patterning on the evolution of between-mussel attachment in self-organized mussel beds, where mussels settle down in regular spatial patterns after being suspended during their larval stage.

The second neglected issue is that spatial structure can itself result from cooperation between organisms. For example, without the between-mussel cooperation of attaching byssus threads to neighbors, spatial patterns in mussel beds have little chance to persist. Moreover, the spatial structure that is generated by organisms and their interactions can lead to the formation of groups. When the ability to achieve a collective goal differs between these groups, group-level selection can occur (Van Boven & Weissing, 1999; Traulson & Nowak, 2006; Thompson 2000; Kohn, 2008; Burton *et al.*, 2012; Molleman *et al.*, 2013). For instance, picture a group of people in a rowing boat. To get across the sea and safely to land, one needs to cooperate with boat members. Whether the boat will return safely from the voyage depends on the paddling efforts of everyone on board. Hence, a group-level survival process is taking place; either everyone will return or nobody at all. At the same time, individual-level fitness differences between the boat members can arise when some people are putting more effort in rowing than others. Someone who rows too enthusiastically might die of a heart attack and thereby is eliminated by an individual-level selection process. By contrast, groups of lazy boatmen that all perish from hunger and thirst are killed

by a group-level selection process. When taken together, the group-level and individual-level processes will combine as multilevel selection (Wilson & Sober, 1994; Sober & Wilson, 1998; Thompson, 2000; Okasha, 2006; Wilson & Wilson, 2007; West *et al.*, 2008), where an individual's fitness depends on the paddling skills and efforts of the group and on that individual's own investment in rowing the boat. Hence, with the emergence of self-organized structures from the actions of and interactions between individuals, an additional level of selection may arise next to simple individual-level selection.

Self-organized ecosystems are likely to be influenced by multilevel selection. The additional level of selection that emerges from self-organization can create a feedback between pattern formation and the evolution of self-organizing traits. Yet, how multilevel selection affects the evolution of cooperation and thereby influences spatial pattern formation in self-organized ecosystems remains unknown. In **Chapter 6** of this thesis, I investigate the effect of multilevel selection on the joint evolution of aggregative movement and between-mussel cooperation in self-organized mussel beds. Subsequently, I examine how the feedback between multilevel selection and mussel bed formation will influence the development of spatial patterns in mussel populations.

The conclusions drawn from the studies considered in Chapters 2 to 6 are summarized in the **General Discussion**. In this final chapter, I discuss how the results of my research on animal movement, between-mussel cooperation, eco-evolutionary processes, and emergent spatial complexity can change our perspective on self-organized ecosystems. Specifically, I highlight the importance of investigating eco-evolutionary feedbacks within these systems, which is necessary for drawing reliable conclusions from models as well as from observations of natural processes.

2

Lévy walks evolve through interaction between movement and environmental complexity

Abstract

Ecological theory predicts that animal movement is shaped by its efficiency of resource acquisition. Focusing solely on efficiency, however, ignores that animal activity can impact resource availability and distribution. Here, we show that feedback between individual behavior and environmental complexity can explain movement strategies in mussels. Specifically, experiments show that mussels use a Lévy walk during the formation of spatially patterned beds and models reveal that this Lévy movement accelerates pattern formation. The emergent patterning in mussel beds, in turn, improves individual fitness. These results suggest that Lévy walks evolved due to the selective advantage conferred by autonomously generated, emergent, spatial patterns in mussel beds. Our results emphasize that an interaction between individual selection and habitat complexity shapes animal movement in natural systems.

Introduction

Animals must face the daunting complexity of the natural world when searching for food, shelter and other resources crucial for survival. To cope with the challenge to maximize the probability of resource encounters, many organisms adopt specialized search strategies (Bartumeus *et al.*, 2005; Sims *et al.,* 2008) that can be described by random walks. Brownian and Lévy walks are prominent examples of random walk strategies where both the direction and step length of the constituent moves are drawn from a probability distribution (Viswanathan *et al.*, 2000; Bartumeus *et al.*, 2005; Sims *et al.,* 2008; Bartumeus, 2009). These movement patterns differ in the distribution of step lengths, which are derived from an exponential distribution in the case of Brownian motion, but follow a power-law distribution in case of Lévy motion (See Appendix; Viswanathan *et al.*, 2000; Codling *et al.*, 2008; Viswanathan, 2010), where many short steps are occasionally alternated with a long step. Model simulations have shown that a Lévy walk provides faster dispersal (Bartumeus *et al.*, 2005; Bartumeus, 2009), more newly visited sites (Bartumeus *et al.*, 2005; Sims *et al.,* 2008), and less intra-specific competition than Brownian walks (Viswanathan *et al.*, 2000); it is therefore considered the most efficient random search strategy in resource-limited environments where food occurs patchily at locations unknown to the searcher (Bartumeus *et al.*, 2005; Sims *et al.,* 2008; Bartumeus, 2009) and, most importantly, where the resource distribution is largely unaffected by the activities of the searching animal (Viswanathan *et al.*, 1999; Reynolds & Bartumeus, 2009). Although shown to be optimal for only these specific conditions, Lévy walks are broadly found in nature (Ramos-Fernandez *et al.*, 2004; Reynolds *et al.*, 2007; Sims *et al.*, 2008; Humphries *et al.*, 2010), suggesting that they are actually adaptive over a wider range of conditions. We hypothesize that this wide occurrence is due to the fact that organisms themselves affect the availability and spatial distribution of the resources upon which they depend (Jones *et al.*, 1994). Consequently, the movement strategies of organisms can shape the environment.

On intertidal flats, the distribution of regularly-spaced clumps of mussels (*Mytilus edulis*) results from the interaction between local mussel density and the crawling movement of young mussels (See Appendix; Maas Geesteranus, 1942; Van de Koppel *et al.*, 2008). In particular, pattern formation in mussel beds is

attributable to two opposing mechanisms: cooperation and competition (Van de Koppel *et al.*, 2005). Through movement into cooperative aggregations, mussels increase their local density, which decreases wave stress and predation risk. Conversely, competition for algae, which occurs on a larger spatial scale than facilitation, prevents the formation of larger clumps by limiting the number of mussels within a long range. The interaction of local facilitation and long-range competition results in the emergence of a patchy distribution of individuals, which simultaneously reduces risk and minimizes competition for algae (Van de Koppel *et al.*, 2008). Hence, in this system, the distribution of suitable settling locations, an important resource for mussels, is determined by the existing distribution of mussels, which develops in response to the movement of its comprising individuals. Here, we investigate whether the interplay between movement strategy and habitat complexity results in the emergence of Lévy walks in these self-organizing mussel beds.

Methods & Results

We first tested the hypothesis that mussel movement is described by a Lévy walk (or a truncated Lévy walk) against alternative models reported in the literature, namely a Brownian walk and a composite Brownian walk (Nolet & Mooij, 2002; Benhamou, 2007; Reynolds & Rhodes, 2009). We observed the movements of 50 mussels during the process of pattern formation and of 12 mussels in solitary experiments in mesocosm tanks. Step lengths were estimated by the distance between two subsequent reorientation events (See Appendix). The resulting step length distribution was compared with the family of power-law distributions, $P(l) = Cl^{\mu}$, where $P(l)$ is the probability of a step of length l and C is a constant ensuring that the total probability equals one. The exponent μ defines the shape of the distribution and therefore determines the resulting movement strategy. If $1 < \mu < 3$, the movement pattern corresponds to a Lévy walk. When μ approaches 1, the movement is approximately ballistic, while it is approximately Brownian when μ approaches 3 (and for $\mu > 3$) (See Appendix; Fig. 2.5; Bartumeus *et al.*, 2005; Reynolds & Rhodes, 2009). The Lévy walks found in nature typically have an exponent μ of approximately 2 (Ramos-Fernandez *et al.*, 2004; Reynolds *et al.*, 2007; Sims *et al.*, 2008; Humphries *et al.*, 2010).
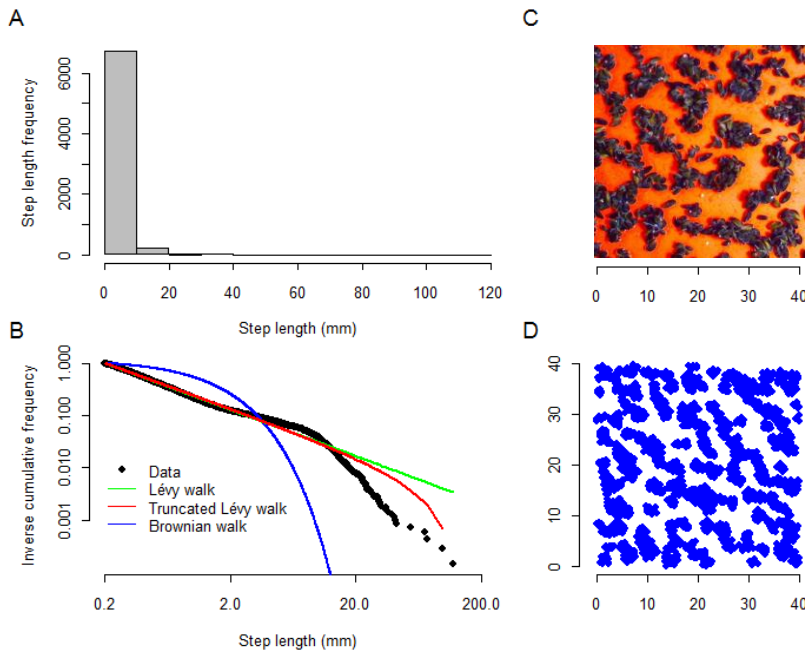
Figure 2.1: Experimental and model results showing that mussel movement, which is best described by a Lévy walk, generates patterns in mussel beds. (**A**) Frequency distribution of step lengths of all solitary mussels (18 mussels, 15,764 steps). (**B**) Inverse cumulative frequency distribution of the step lengths. (**C**) Pattern formation in an experimental mussel bed. (**D**) Pattern generated with our individual based model.

Our results show that mussels use a Lévy walk during the process of pattern formation. Based on maximum likelihood estimation and the derived Goodness-of-fit (G), Akaike Information Criterion (AIC) and the fraction of variance explained by the model (R2), we found that Lévy walk and truncated Lévy walk distributions, both with $\mu \approx 2$, provided the best fit to the data over a range of at least 2 orders of magnitude (See Appendix, Table 2.1; Fig. 2.1; Table 2.2). A possible alternative explanation is that mussel movement follows a composite Brownian walk, where movement speeds are adjusted to local environmental conditions (Nolet & Mooij, 2002; Benhamou, 2007; Reynolds, 2008; Benhamou, 2008; Reynolds & Rhodes, 2009). Such a strategy can have a similar step length distribution as a Lévy walk and is therefore often overlooked. However, when mussel movements were grouped by local mussel density (the density of mussels within a radius of 3.3 cm)

Table 2.1: Summary of the model fits to the step length data. Here, we only used the 'angle method' to calculate the step lengths from the movement data. The maximum likelihood estimation (ML) and the subsequent weighed Akaike Information Criterion (wAIC) show that a truncated Lévy walk with μ = 1.9 best (out of these three movement strategies) approximates the movement strategy of solitary mussels.

Model	ML	wAIC	Lévy exponent
Truncated Lévy walk	-165.9	1	1.9
Lévy walk	-3974.2	0	1.9
Brownian walk	-7238.0	0	-

and long-range density (the density of mussels within a radius of 22.5 cm) categories, step length distributions did not differ between the density categories and mussels were found to perform a Lévy walk with $\mu \approx 2$, irrespective of the local and long-range density (See Appendix, Table 2.3). Hence, we reject the hypotheses of Brownian walk and composite Brownian walk and conclude that mussel movement is best described by a Lévy walk.

To examine why mussels adopt a Lévy walk, we investigated the effect of movement strategy on the rate of pattern formation by designing an individual-based model (See Appendix). In this model, patterns arise by the mussels' decisions to stay at a location or move away from it. We used experimental data from a prior study to estimate the parameters of this stop-or-move behavior (See Appendix; Fig. 2.5; Van de Koppel *et al.*, 2008). Although step length distributions are unaffected by mussel density, we discovered that the probability that a mussel moves decreases with short-range density (the density of mussels within a radius of 3.3 cm) and increases with long-range density (the density of mussels within a radius of 22.5 cm). Based on these parameters, simulated mussels stay in places where they can aggregate with direct neighbors, but move away from crowded locations where food becomes limiting. If a simulated mussel moves, the movement distance is randomly drawn from the power law distribution that corresponds to its movement strategy. For a range of movement strategies ($1 < \mu \leq 3$), we observed the distance travelled until a pattern has formed. Operationally, we say that a pattern has formed when the density of simulated mussels within 3.3 cm distance is on
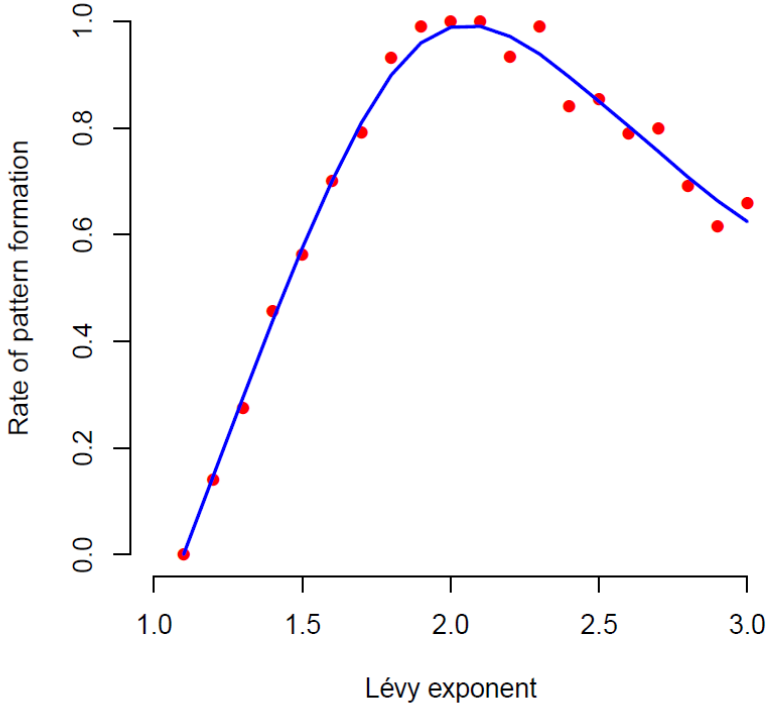
Figure 2.2: The rate of pattern formation for various movement strategies. As we assume that movement speed is constant, we can calculate the rate of patterning as the normalized inverse of the distance traversed until a pattern is formed. A Lévy walk with exponent $\mu \approx 2$ minimizes the time needed to form a pattern.

average 1.5 times as large as the density of mussels within 22.5 cm distance of an individual. Assuming that the movement speed is constant, the rate of pattern formation for each movement strategy is proportional to the inverse of the average distance traversed by the mussels until a pattern was formed (See Appendix).

Simulations reveal that movement strategies differ strongly in terms of the rate at which they create patterns (Fig. 2.2). A Lévy walk with exponent $\mu \approx 2$ generated a spatially heterogeneous pattern more rapidly than did either ballistic movement ($\mu \rightarrow 1$) or a Brownian walk ($\mu \rightarrow 3$). Specifically, the large steps associated with a small value of μ prevented quick formation of tight clusters, while a larger value of μ required many small steps to create clustering. A Lévy walk with

$\mu \approx 2$ seems to be the optimal trade-off between finding dispersed conspecifics and maintaining high local densities, thereby maximizing the rate of pattern development. Hence, our simulation results suggest that a Lévy strategy with $\mu \approx 2$ is optimal for pattern formation.

As pattern formation both improves mussel survival and decreases competition between mussels (Maas Geesteranus, 1942), the movement strategy of individual mussels is likely to be an important determinant of fitness. However, strategies that lead to a desirable outcome at the population level are often not evolutionarily stable, as they can be exploited by free-riding strategies (Reynolds & Rhodes, 2009). To determine the long-term outcome of selection acting on mussels differing in strategy (i.e. their exponent μ) we created a pairwise invasibility plot (PIP, Fig. 2.3) by performing an evolutionary invasibility analysis (See Appendix; Geritz *et al.*, 1998; Dercole & Rinaldi, 2008). The values along the x-axis of the PIP represent a broad range of hypothetical resident populations, each with a particular movement strategy characterized by an exponent μ_{res}. The y-axis represents the exponents μ_{mut} of potential mutant strategies. The colors indicate whether or not a mutant strategy μ_{mut} can successfully invade a resident strategy μ_{res}, i.e. whether or not mutant individuals have a higher fitness than resident individuals in the environment created by the resident population. Intersections between the lines separating the colored areas indicate the presence of an evolutionary attractor, thus predicting the outcome of selection on mussel movement strategies. Fitness was given by the product of mussel survival (which is proportional to short-range mussel density) and fecundity (which is inversely proportional to long-range mussel density and the energy invested in movement) (See Appendix).

The PIP reveals that a Lévy walk with $\mu \approx 2$ is the unique evolutionary attractor of the system (Fig. 2.3; Geritz *et al.*, 1998; Dercole & Rinaldi, 2008). Specifically, a succession of invasion events will lead to the establishment of a resident population with $\mu \approx 2$, and a resident population with $\mu \approx 2$ cannot be invaded by any other movement strategy. We conclude that the Lévy walk strategy observed in our experiments (Fig. 2.1) not only has a high patterning efficiency (Fig. 2.2) but is also an evolutionarily stable strategy (Fig. 2.3).
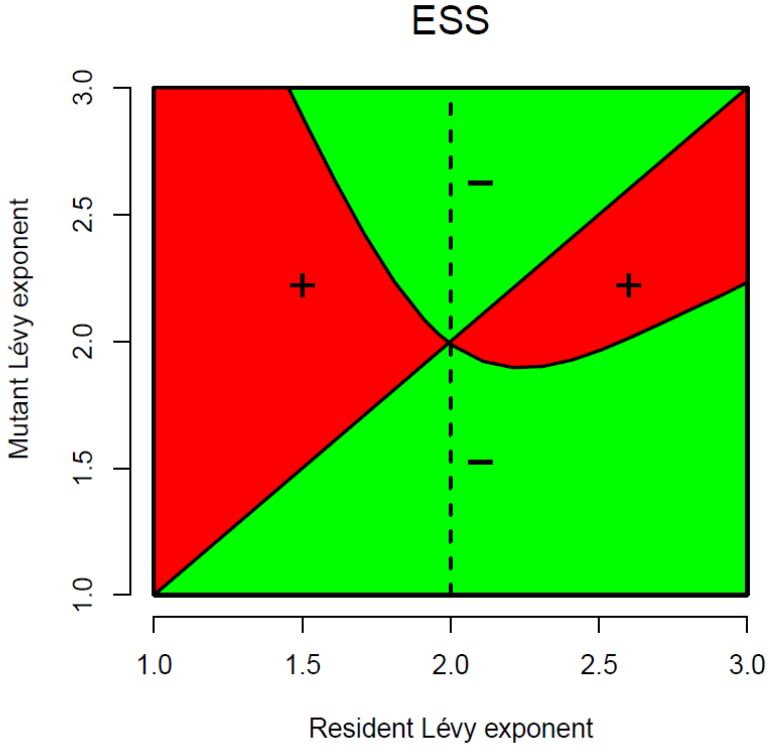
Figure 2.3: Pairwise invasibility plot (PIP) indicating that the movement strategy evolves towards a Lévy walk with $\mu \approx 2$. For a range of resident (x-axis) and mutant (y-axis) movement strategies, the PIP indicates whether a mutant has a higher (red) or a lower (green) fitness than the resident and, hence, whether or not a mutant can invade the resident population (Geritz *et al.*, 1998). Here, the PIP shows that a Lévy walk with $\mu \approx 2$ is the sole evolutionarily stable strategy (ESS).

Conclusion & Discussion

Our study demonstrates an evolutionary feedback between individual movement behavior and higher level complexity, and it provides a possible explanation for the evolution of Lévy walks in mussel beds. Rather than being a direct adaptation to an externally determined environment, Lévy movement in our study was found to result from feedback between animal behavior and mussel-generated environmental complexity. In essence, a Lévy walk with $\mu \approx 2$ creates a spatial environment in which just this movement strategy can flourish.

Although our study addresses a specific system, the assumption that search strategies can evolve through feedback between animal movement and environmental heterogeneity may be broadly applicable. Such feedbacks may exist not only in the search for conspecifics (as seen here in mussels) but also in the search for resources shared with conspecifics, as resource patterns reflect the movement patterns of their consumers. This applies, for instance, to the interaction between herbivores and vegetation, which shapes grasslands globally (Adler *et al.*, 2001). Additionally, feedback between movement strategy and habitat complexity may arise when the spatial distribution of a particular species depends on interactions with a searching organism (as in predator-prey relationships or animal-mediated seed dispersal [Boyer & Lopez-Corona, 2009]). We conclude that the interaction between animal movement and habitat complexity is a key component in understanding the evolution of animal movement strategies.

Appendix: Supplementary Materials & Methods

1. *Characteristics of mussel movement*

Although mussel movement becomes limited with increasing shell size, young mussels are good crawlers for many months after their metamorphosis (Maas Geesteranus, 1942). During this period, mussels are able to search for conspecifics and aggregate. Once arrived at a good quality location, with respect to the number of neighbors and food availability, a mussel stops moving and attaches itself to the bed. When conditions become less suitable, a young mussel can still detach itself and search for a better location. This movement and attachment behavior at individual level directly affects the habitat quality for others, thereby leading to spatial patterning in mussel beds.

2. *Extraction of mussel movement data*

Step lengths of young blue mussels (*Mytilus edulis*, 1.5-3 cm long) were obtained from experimental data of Van de Koppel *et al.* (2008). The blue mussels used in these experiments were obtained from wooden wave-breaker poles near Vlissingen, the Netherlands. Experiments were performed in a 120x80x8 cm containers filled with unfiltered seawater. Mussels were placed on a 60x80 cm red PVC sheet. To record mussel movement, a Logitech QuickCam 9000 Pro webcam, which was positioned about 60 cm above the water surface and attached to a computer, photographed the mussels at 1 minute intervals for several hours. In total, 68 mussels were used for the experiments, resulting in 19,401 steps. Tracks of 18 of these mussels (15,764 steps) were obtained from isolation experiments, preventing the mussels from finding conspecifics and creating clusters. To investigate density-dependence, the tracks of the other 50 mussels (7,000 steps) were obtained from pattern formation experiments (see Fig. 2.1B). In pattern formation experiments, mussels are initially evenly distributed over the red PVC sheet, after which the mussels start to move and create patterns.

The first method that we used for the extraction of step lengths was to simply calculate the distance between two subsequent points using a 60 seconds interval. This time interval was chosen since our observations revealed that time intervals
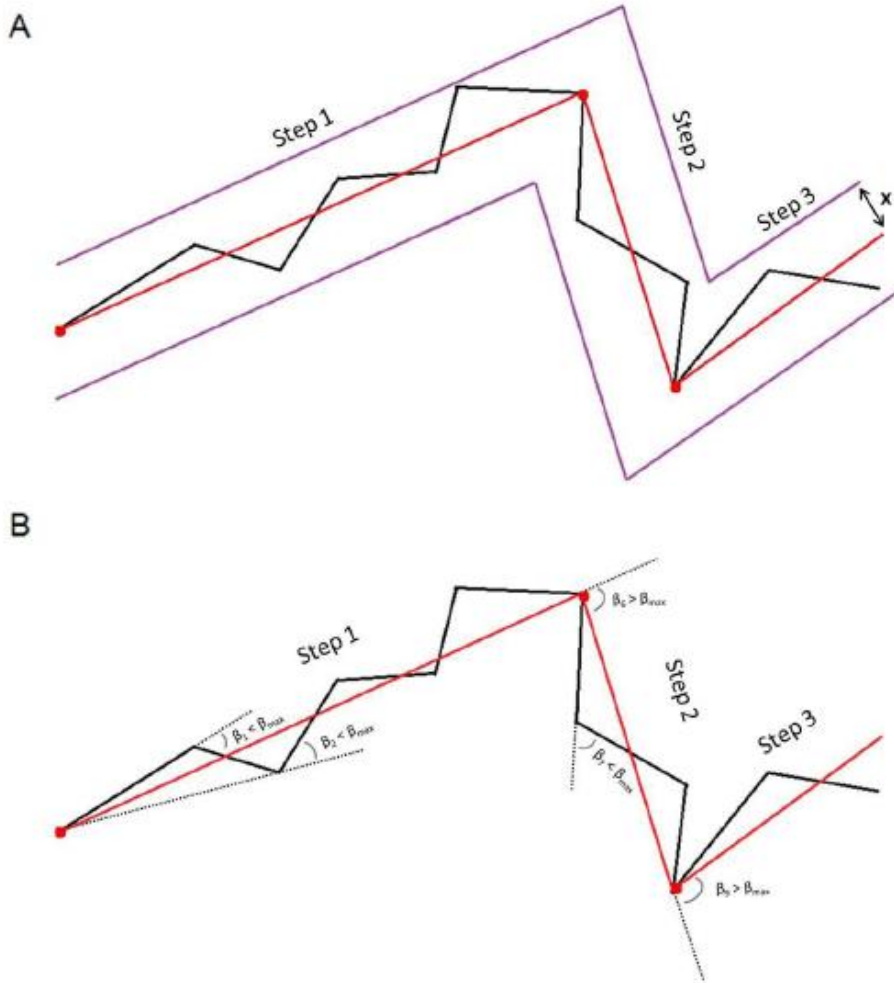
Figure 2.4: Step length calculation using the 'error radius method' (**A**) and the 'angle method' (**B**). In the first method (**A**), n steps are aggregated into one move if the n-1 intermediate spatial positions are no more than x units away from the line connecting the b beginning of the step to the end of it. The second method (**B**) is based on reorientation events; when the angle β (between the dotted black line and the solid black line) exceeds a certain threshold value, the corresponding point is the next new point (after Turchin, 1998).

between 40 and 80 seconds are most adequate for monitoring mussel movements in our experiments.

In addition, we extracted step length distributions by applying two step length extraction methods suggested by Turchin (1998). In the 'error radius method' (illustrated in Fig. 2.4a), the movements performed in n time intervals are aggregated into a single 'step' if the n-1 intermediate spatial positions are no more than a predefined distance x away from the line connecting the beginning of the movement to the end of it. When applying this method, the value of x was chosen by starting with a small value and then incrementing it iteratively until oversampling was minimized.

Turchin's 'angle method' (illustrated in Fig. 2.4b) concerns the angle between movements. The movements performed in n time intervals are aggregated into a single step if the angle between the starting position and the end position is smaller than a predefined value βmax. When this value is exceeded after the nth movement, the corresponding point becomes the starting point for the next step. The threshold value βmax was also chosen iteratively, starting with a small angle and gradually increasing it until oversampling was minimized ($\beta_{max} = 30°$).

As the method used for estimating step lengths does not affect our conclusions, we chose to calculate the step lengths using the 'angle method'. Without all steps smaller than the lower truncation boundary (0.2 mm), the step length data now contains 6996 data points.

3. *Fitting movement types to step length data*

The step length data of the mussel movements were used to create a step length frequency distribution (Fig. 2.1a). When plotted on a log-log scale, a power-law probability distribution $P(l)=Cl^{\mu}$ results in a straight line with slope $-\mu$. However, drawing conclusions from this kind of presentation can be deceptive (Sims *et al.*, 2007; Edwards *et al.*, 2007; White *et al.*, 2008). We therefore used a more robust method (Edwards *et al.*, 2007) and first determined the inverse cumulative frequency distribution of our data, which for each step length l gives the fraction of steps with lengths larger or equal to l. This cumulative distribution is plotted in Fig. 2.1b on a log-log scale. We compared this distribution with the cumulative probability distribution of three random movement strategies: Brownian walk, Lévy walk, and truncated Lévy walk.
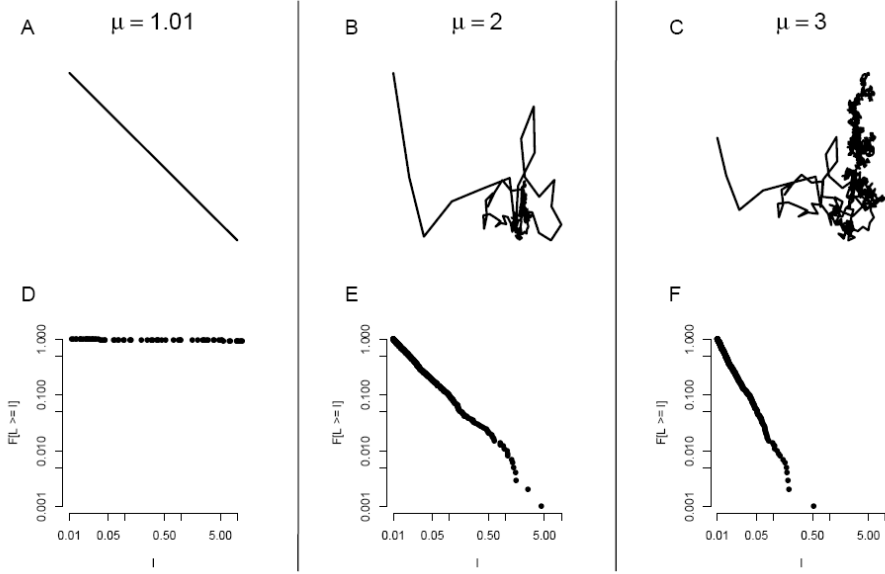
Figure 2.5: The Lévy exponent μ determines the shape of the step length distribution and thus the movement strategy. When μ is close to 1, the movement strategy resembles ballistic, straight-line motion (**A**, **D**), whereas the step length distribution is similar to that of a Brownian walk when µ approaches 3 (**C**, **F**). The movement strategy is referred to as a Lévy walk when $1 < \mu < 3$ (**B**, **E**). **A**, **B**, and **C** show movement trajectories obtained with $\mu = 1.01$, 2, and 3, respectively. The inverse cumulative step length frequency distributions (i.e. the fraction of steps that is larger than or equal to the displacement length (l) that is given on the x-axis) are given by **D**, **E**, and **F** for **µ** = 1.01, 2, and 3, respectively.

Brownian walk

Brownian walk is a random movement strategy that corresponds to normal diffusion. The step length distribution can be derived from an exponential distribution with $\lambda > 0$:

$$f(l) = \lambda e^{-\lambda(l - l_{min})}, \tag{2.1}$$

where l_{min} is the lower truncation boundary (l_{min} = 0.2 mm).

Lévy walk

The frequency distribution of step lengths that characterizes a Lévy walk has a heavy tail and is scale-free, i.e. the characteristic exponent of the distribution is independent of scale. To fit a Lévy walk to the data, a Pareto distribution (Clauset *et al.*, 2009) was used:

$$f(l) = C_\mu l^{-\mu}. \tag{2.2}$$

The shape parameter μ (which has to exceed 1) is known as the Lévy exponent or scaling exponent and determines the movement strategy (see Fig. 2.5). When μ is close to 1, the resulting movement strategy resembles ballistic, straight-line motion, as the probability to move a very large distance is equal to the chance of making a small displacement. A movement strategy is called a Lévy walk when the scaling exponent is between 1 and 3. When μ approaches 1, the movement is approximately ballistic, while it is approximately Brownian when μ approaches 3 (and for $\mu > 3$). The Lévy walks found in nature typically have an exponent μ of approximately 2 (Ramos-Fernandez *et al.*, 2004; Reynolds *et al.*, 2007; Sims *et al.*, 2007; Humphries *et al.*, 2010). C_μ is a normalization constant ensuring that the distribution *f(l)* has a total mass equal to 1, i.e. that all values of *f(l)* sum up to 1. If we impose the additional criterion that steps must have a minimum length l_{min} ($0 < l_{min} < l$), this constant is given by

$$C_\mu = (\mu - 1)l_{min}^{\mu-1}. \tag{2.3}$$

When fitting our data to a Lévy walk, we used the value of l_{min} that provided the most accurate movement data (without the small-scale measuring errors; $l_{min} = 0.2$ mm).

Truncated Lévy walk

A truncated Lévy walk differs from a standard Lévy walk in the tail section of the frequency distribution; a truncated Lévy walk has a maximum step size and, as a consequence, loses its infinite variance and scale-free character at large step sizes.

The truncated Lévy walk was represented by the truncated Pareto distribution, which can be described by the same function $f(l)$ as a standard Pareto distribution, but with different constant C_μ:

$$C_\mu = \frac{\mu - 1}{l_{min}^{1-\mu} - l_{max}^{1-\mu}}.$$

(2.4)

In a truncated Lévy walk, step lengths are constrained to the interval $l_{min} < l < l_{max}$. When fitting our data to a truncated Lévy walk, we used those values of l_{min} that provided the most accurate movement data (without the small-scale measuring errors; l_{min} = 0.2 mm). We used the maximum step length as the upper truncation boundary (l_{max}).

Goodness-of-fit and model selection

For the frequency distributions mentioned above, the fit to the step length data of solitary mussels was calculated using Maximum Likelihood (ML) estimation:

$$ML_{BW} = n \cdot \log(\lambda) - \lambda \cdot \sum(l - l_{min}),$$

(2.5)

$$ML_{LW} = n \cdot \log(\mu - 1) + n \cdot (\mu - 1) \cdot \log(l_{min}) - \sum \log(l),$$

(2.6)

$$ML_{TLW} = \frac{n}{\mu - 1} + \frac{n \cdot (l_{min}/l_{max})^{\mu-1} \cdot \log(l_{min}/l_{max})}{1 - (l_{min}/l_{max})^{\mu-1}} - \sum(\log(l) - \log(l_{min})),$$

(2.7)

where *n* is the number of data points. Subsequently, we calculated the AIC:

$$AIC_i = -2 \cdot ML_i + 2 \cdot K_i,$$

(2.8)

where *K* is the number of parameters of model *i*. Using the AIC's of the three movement strategies, we were able to calculate the weighed AIC (wAIC):

$$wAIC_i = \frac{e^{-0.5 \cdot (AIC_i - AIC_{min})}}{\sum e^{-0.5 \cdot (AIC_i - AIC_{min})}},$$

(2.9)

Table 2.2: Lévy exponent during pattern formation. The Lévy exponent (calculated with the 'angle method' step length data when n > 50) increases with local and long-range mussel density (df = 21, F = 15.46, r2 = 0.557, p < 0.001). This increase in μ with mussel density may be accounted for by collisions with conspecifics, which cause truncation of steps.

		Local mussel density									
		0.1	0.2	0.3	0.4	0.5	0.6	0.7	0.8	0.9	1
Long-range density	0.1	2	2.3	2.3	2.5	2.4	2.6	2.7			
	0.2	1.8	2.1			2.7	2.6	2.8	2.5	2.7	3
	0.3										
	0.4					2.2			2.7	2	2.3
	0.5							2	2.2	2.4	2.4
	0.6										

where AIC_{min} is the lowest AIC of the three movement strategies. The movement strategy with the highest weighed AIC provides the best fit to the mussel movement data (out of the three models). This method was used for the analysis of the movement strategies of the 12 solitary mussels (see Fig. 2.4). Additionally, step lengths obtained from pattern formation experiments were grouped for different combinations of local density (within a radius of 3.3 cm) and long-range density (within a radius of 22.5 cm). These groups of step lengths were used for determining the Lévy exponent at different densities, in order to observe whether a composite Brownian walk exists in mussel movement (see Table 2.2).

4. Computer Simulations

Individual based model

We developed an individual based model that describes pattern formation in mussels by relating the chance of movement to the short- and long-range densities of mussels, following Van de Koppel et al. (2008). Whereas they modeled pattern formation in mussel beds by adjusting the movement speed to the short- and long-range densities (Van de Koppel *et al.*, 2008), we extracted the stop and move behavior of the mussels from the experimental data. In our model, 2500 'mussels' (with a radius of 1.5 cm each) are initially spread homogeneously within a 150 cm by 150 cm arena. Each time step, the short-range (D_1) and long-range (D_2) densities

are determined for each individual, based on mussel densities within a radius of 3.3 cm and 22.5 cm, respectively. These radii correspond to the ranges in which we found significant correlations with the probability of moving in a multi-variate regression analysis of our experimental data (F = 77.17, p << 0.001, R^2 = 0.622, df = 136). The probability P_{move} that a mussel moves is negatively related to the short-range density D_1 and positively related to the long-range density D_2 (see Fig. 2.6), which causes mussels to stay in places where they can aggregate with direct neighbors, but move away from crowded locations where food becomes limiting. In the model, we used a linear relationship between P_{move} and the two densities:

$$P_{move} = a - bD_1 + cD_2,\qquad(2.10)$$

which was obtained by applying linear regression to our experimental data (a = 0.63, b = 1.26, and c = 1.05). If a mussel decided to move in our model, its step length l was chosen at random from a power law distribution (Newman, 2005) with a given Lévy exponent $\mu > 1$:

$$l = l_{min}(1 - x)^{-\frac{1}{\mu - 1}},\qquad(2.11)$$

where x is a random variable that is uniformly distributed over the unit interval ($0 \leq x \leq 1$), and l_{min} is the minimum distance traveled when moving (Clauset et $al.$, 2009), which we have set at 0.3 cm. Each simulation step, mussels move instantaneously from one location to another, though step lengths were truncated when a movement path was obstructed by another mussel. This truncation was calculated by determining the free movement path until collision, using a band width of 3 cm (the size of a mussel) around the line segment connecting the mussels' original location to its intended destination. When a conspecific was located within this band, the mussel stopped in front of this conspecific, thereby truncating its movement path. All movements occurred simultaneously and all individuals in a simulation used the same movement strategy.
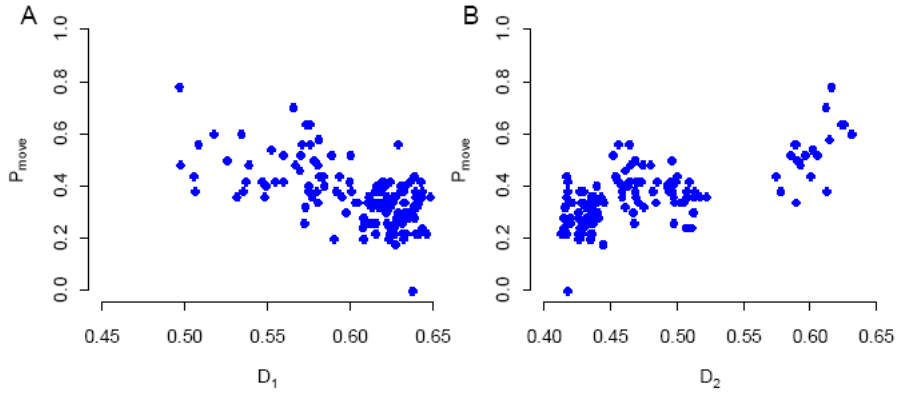
Figure 2.6: Experimental data shows that the probability of moving depends on short-range and long-range mussel densities. (**A**) Local mussel density decreases the probability of moving; mussels tend to stay in denser clumps. (**B**) The probability of moving positively correlates with long-range density; mussels move away from areas where competition is high.

As differences occur in the average distance covered per simulation step between the movement strategies (ballistic individuals move a larger distance per simulation step than Lévy or Brownian walkers) and assuming that movement speed is constant, more time is needed for a ballistic step than for a Brownian step. To avoid having Brownian movers switch more frequently between moving and stopping than ballistic movers, we updated the state of either moving or stopping not after each simulation step but after an average distance moved.

A simulation was finished when the average short-range density exceeded 1.5 times the mean long-range density. At that moment, the total distance travelled was recorded. As we assume that the movement speed is constant, the rate of patterning is proportional to the normalized inverse of the distance traversed until a pattern is formed. Simulations were run for a range of Lévy exponents ($1 < \mu \leq 3$), and for each value the rate of pattern formation was plotted as a function of μ. The model was implemented in Matlab version 7.9 (©1984-2009. The MathWorks, Inc.).

Evolutionary model

Evolutionary change was studied in a monomorphic resident population by investigating whether the fitness of rare mutants is higher than that of the residents, implying that the mutants can increase in frequency (Geritz *et al.*, 1998; Dercole & Rinaldi, 2008). After the mussels moved an equal distance, we recorded the short-range density, the long-range density, and the fraction of mussels that was still moving, for both the residents and the mutants. In a population with non-overlapping generations, fitness is given by the product of survival probability and fecundity. We assumed that survival probability is proportional to the local mussel density D_1 and that fecundity is inversely proportional to the long-range density D_2 (as this density affects food supply) and to the time X spent on moving (as energy spent on moving cannot be invested in offspring production). Dividing the fitness measures thus obtained for a mutant and a resident results in a measure for the relative fitness of the mutant strategy:

$$F_{mut} = \frac{D_{1,mut}}{D_{1,res}} * \frac{D_{2,res}}{D_{2,mut}} * \frac{X_{res}}{X_{mut}}. \tag{2.12}$$

Mutant strategies with a relative fitness value larger than one will invade and potentially take over the resident population. For any combination of resident and mutant movement strategy, the relative fitness of the mutants is depicted in a pairwise invasibility plot (Dercole & Rinaldi, 2008; see Fig. 2.3). In this plot, the color red indicates that the mutant has a higher fitness than the resident ($F_{mut} > 1$), while the color green indicates that the mutant cannot invade the resident population ($F_{mut} < 1$). The intersection of the line separating these two scenarios ($F_{mut} = 1$) with the main diagonal of the pairwise invasibility plot corresponds to an evolutionarily singular strategy (Geritz *et al.*, 1998; Dercole & Rinaldi, 2008).

I

Comment & Reply I:

Emergent properties of the Lévy walk are not adaptive strategies

Comment by: Frank van Langevelde, Willem F. de Boer, Hendrik J. de Knegt, Herbert H. T. Prins

Reply by: Monique de Jager, Franz J. Weissing, Peter M. J. Herman, Bart A. Nolet, Johan van de Koppel. *Science e-letter.*

Comment

M. de Jager *et al.*'s fascinating study on the interaction between animal movement and habitat complexity demonstrates that mussels move from random distributions to self-organized mussel beds (De Jager *et al.*, 2011). Mussel movements show properties of Lévy walks with the characteristic $\mu \approx 2$, which is the most efficient random search strategy (Sims *et al.*, 2008; Humphries *et al.*, 2010). De Jager *et al.* argue that mussels doing a Lévy walk with $\mu \approx 2$ create a spatial environment in which this strategy is evolutionarily stable. The conclusion that Lévy walks are selectively advantageous is important, as it could explain why animal movements are often superdiffusive (Viswanathan *et al.*, 1999; De Knegt *et al.*, 2007). Yet we contest that a Lévy walk is an adaptive strategy, and argue that it is merely an emergent property that arises through interaction with the environment.

Our simulations show that observed movement patterns differ from the innate movement strategy (Hengeveld *et al.*, 2007). The typical step-length distribution of Lévy walks ($\mu_{observed} \approx 2$) can be generated simply by truncations of long steps in walks with $\mu_{innate} < 2$: Finding targets decreases the step lengths and increases μ. Hence, $\mu_{observed}$ is larger than μ_{innate} (Fig. 2.7). With increasing target density, the deviation between $\mu_{observed}$ and μ_{innate} increases. The observed $\mu \approx 2$ in mussels can thus not be the innate μ that is selected to create mussel beds.

Consequently, we predict that μ_{innate}, measured using solitary mussels is smaller than $\mu_{observed}$ in mussel bed pattern formation. Secondly, we expect that $\mu_{observed}$ of the modeled mussels is larger than μ_{innate} used in the model, due to truncation of large steps by obstruction from conspecifics. Therefore, we challenge the evolutionarily stable strategy of $\mu \approx 2$, and predict that $\mu_{innate} < \mu_{observed}$, and hypothesize that the $\mu_{observed}$ at which the strategy is stable increases with mussel density (Viswanathan *et al.*, 1999; De Knegt *et al.*, 2007). More work is needed to understand how movement patterns are shaped by the interaction between the innate μ and habitat complexity.
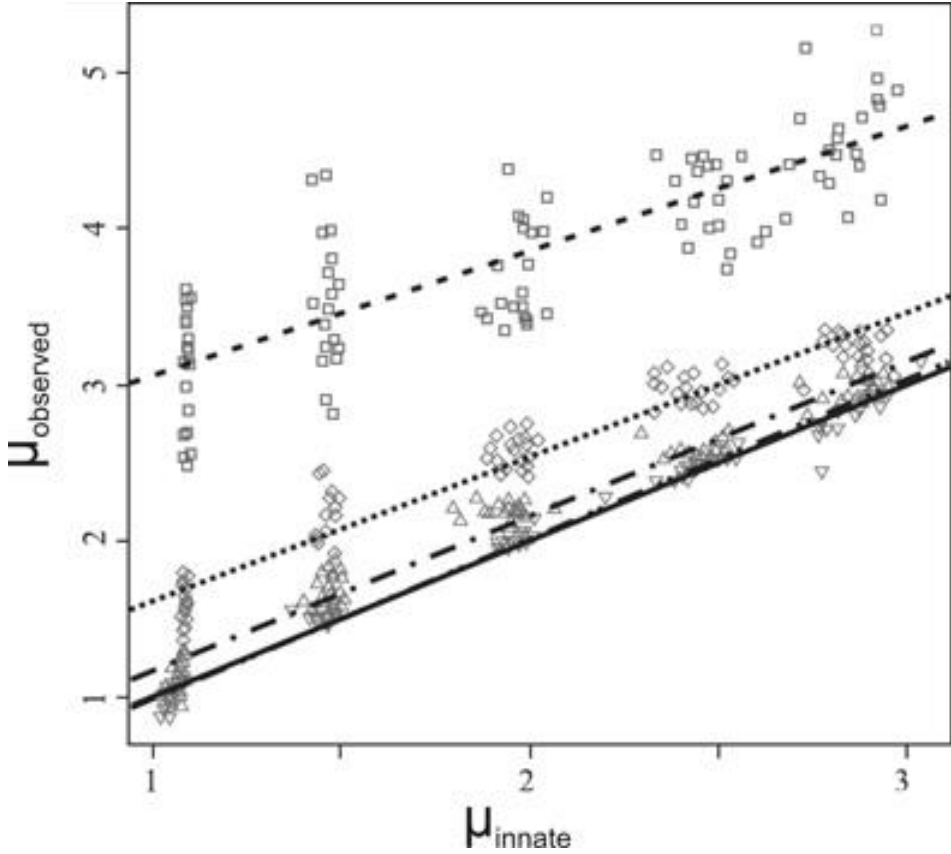
Figure 2.7: Observed $\mu_{observed}$ vs. innate μ_{innate} (Hengeveld *et al.*, 2007). The slopes of the downward part of the log-log frequency distribution of the observed flights ($\mu_{observed}$) are plotted against the slopes of the distribution of flight used to generate the paths (μ_{innate}). The relationship is plotted for 4 (triangle) resource densities (measured by the mean free path between targets δ): $\delta = 10$ (square), $\delta = 102$ ($\Diamond$), $\delta = 103$ (Δ), $\delta = 104$ ($\bullet$). The solid line is the reference line $\mu_{innate} = \mu_{observed}$.

Reply

F. van Langevelde *et al.* argue that the Lévy walks found in nature are not innate search strategies but rather emergent properties of the interplay between animal movement and environmental complexity. Their line of reasoning is that steps become truncated whenever an animal finds a target resource. Hence, they claim that the scaling exponent μ of the truncated Lévy walk that we observed in mussel movements should be larger than the μ of the innate search strategy, and that a Lévy walk therefore cannot be an adaptive strategy in dense mussel beds.

We agree with Van Langevelde *et al.* that the truncation of intended steps by resource encounter indeed can alter the movement pattern and increases the observed value of μ. However, the data that are presented in Figure 1B of our Report (de Jager *et al.*, 2011) are based on movements of solitary mussels, and therefore collisions with other mussels do not influence their movement. Hence, as Lévy movement is observed in the absence of conspecifics, it must reflect their innate strategy.

In the Supporting Online Material of our Report, however, we presented an analysis of the step size distribution of mussel movements in clumps of different densities, in which collisions do occur. Here, we concluded that the density of neighbors, the main determinant of the chances of a collision, did not affect the observed Lévy exponent μ, which was found to approximate a value of 2 for all. However, the results of our analysis reflected our choice to fit only a non-truncated power law to the data and to include samples of size $n < 50$. When we reanalyzed the data by fitting truncated Lévy walks, we found that μ indeed changes with mussel density: μ increases with local and long-range mussel density (Fig. 2.8; df = 21, F = 15.46, r^2 = 0.557, p <0.001).

This increase in μ with mussel density may be accounted for by collisions with conspecifics, which cause truncation of steps, supporting the hypothesis posed by Van Langevelde *et al.* (2011). Importantly, however, we do not concur with Van Langevelde *et al.* that these observations challenge our result that a μ close to 2 is the evolutionarily stable strategy. Collisions with conspecifics may indeed alter the observed μ, but selection acts on the innate movement strategy of organisms, rather than on the movements that we observe. The invasibility analysis presented in our Report (de Jager *et al.*, 2011) was based on the innate value of μ and not on the value of μ characterizing the observed movement pattern. Hence, we maintain our conclusion that a μ of approximately 2 is the evolutionarily stable strategy for mussels in self-organizing mussel beds, as is reflected by their innate strategy observed in the absence of conspecifics.
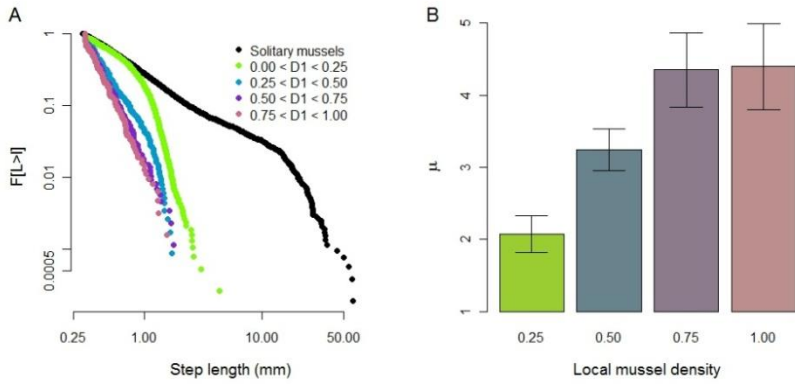
Figure 2.8: (**A**) The inverse cumulative step length frequency distributions (*F[L>l]*) of the mussel movements in clumps of different sizes diverges from that of the solitary mussels, resulting in a higher estimate of μ. D1 here indicates the mussel density within a radius of 3.3 cm. (**B**) When the steps are divided into groups based on the local and long-range mussel density, we find that the estimated μ of the fitted truncated Lévy walks increase with local mussel density

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II

Comment & Reply II:

Comment on 'Lévy walks evolve through interaction between movement and environmental complexity'

Comment by: Vincent A. A. Jansen, Alla Mashanova, Sergei Petrovskii.

Reply by: Monique de Jager, Franz J. Weissing, Peter M. J. Herman, Bart A. Nolet, Johan van de Koppel.

Comment

De Jager *et al.* (2011) concluded that mussels Lévy walk. We confronted a larger model set with these data and found that mussels do not Lévy walk: Their movement is best described by a composite Brownian walk. This shows how model selection based on an impoverished set of candidate models can lead to incorrect inferences.

A Lévy walk is a form of movement in which small steps are interspersed with very long ones, in such a manner that the step length distribution follows a power law. Movement characterized by a Lévy walk has no characteristic scale, and dispersal is superdiffusive so that individuals can cover distance much quicker than in standard diffusion models. De Jager et al. (2011) studied the movements of individual mussels and concluded that mussels move according to a Lévy walk.

The argument of De Jager *et al.* (2011) is based on model selection, a statistical methodology that compares a number of models — in this case, different step length distributions — and selects the model that describes the data best as the most likely model to explain the data (Burnham & Anderson, 2002). This methodology is used to infer types of movements of animals (Edwards *et al.*, 2007) and has led to a number of studies that claim Lévy walks are often encountered in the movement of animals. The methodology in De Jager *et al.* (2011) contrasts a power-law distribution, which is indicative of a Lévy walk, with an exponential distribution, which indicates a simple random walk. If one has to choose between these alternatives, the power-law distribution gives the best description. However, if a wider set of alternatives is considered, this conclusion does not follow.

Heterogeneity in individual movement behavior can create the impression of a power law (Benhamou, 2007; Petrovskii & Morozov, 2009; Petrovskii *et al.*, 2011). Mussels' movement is heterogeneous as they switch between moving very little or not at all, and moving much farther (De Jager *et al.*, 2011; Van de Koppel *et al.*, 2008). If mussels switch between different modes, and in each mode display Brownian motion, this suggests the use of a composite Brownian walk, which describes the movement as a sum of weighted exponential distributions. We confronted this plausible model with the mussel movement data.
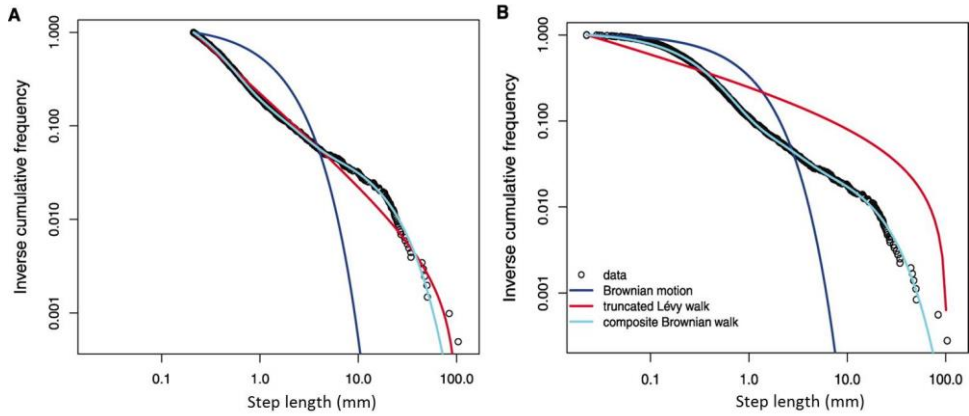
Figure 2.9: The step length distribution for mussel movement [as in De Jager *et al.* (2011)] and curves depicting some of the models. The circles represent the inverse cumulative frequency of step lengths; the curves represent Brownian motion (blue), a truncated power law (red), and a composite Brownian walk consisting of a mixture of three exponentials (blue-green). (**A**) Data as truncated in Fig. 1 in De Jager *et al.* (2011) (2029 steps). (**B**) The full untruncated data set (3584 steps).

Visual inspection of the data shows that the cumulative distribution of step lengths has a humped pattern that is indicative of a sum of exponentials (Fig. 2.9A). We applied a model selection procedure based on the Akaike information criterion (AIC) (Burnham & Anderson, 2002; Edwards *et al.*, 2007). We compared six different step length distributions: an exponential distribution, a power law, a truncated power law, and three hyperexponential distributions (a sum of two, three, or four exponentials to describe composite Brownian walks). We did this for the data truncated as in De Jager *et al.* (2011) (Fig. 2.9A) as well as all the full, untruncated data set (Fig. 2.9B). In both cases, we found that the composite Brownian walk consisting of the sum of three exponentials was the best model (Fig. 2.9 and Table 2.3). This convincingly shows that the mussels described in De Jager *et al.* (2011) do not do a Lévy walk. Only when we did not take the composite Brownian walk models into account did the truncated power law model perform best and could we reproduce the result in De Jager *et al.* (2011).

Mussel movement is best described by a composite Brownian walk with three modes of movement with different characteristic scales between which the

mussels switch. The mean movement in these modes is robust to truncation of the data set, in contrast to the parameters of the power law, which were sensitive to truncation [Table 2.3; also see supporting online material (SOM)]. This analysis does not tell us what these modes are, but we speculate that it relates to the stop-move behavior that mussels show, even in homogeneous environments (De Jager *et al.*, 2011). We speculate that the mode with the smallest average movement (~0.4 mm) is related to non-movement, combined with observational error. The next mode (average movement ~1.5 mm) is related to mussels moving their shells but not displacing, and the mode with the largest movements (on average 14 mm, about the size of a small mussel) is related to actual displacement. This suggests that in a homogeneous environment, mussels are mostly stationary, and if they move, they either wobble or move about randomly. Indeed, if we remove movements smaller than half the size of a small mussel (7.5 mm), the remaining data points are best described by Brownian motion. This shows that mussel movement is not scale invariant and not superdiffusive.

De Jager *et al.*'s analysis (2011) does show that mussels do not perform a simple random walk and that they intersperse relatively long displacements with virtually no displacement. However, one should not infer from that analysis that the movement distribution therefore follows a power law or that mussels move according to a Lévy walk, and there is no need to suggest that mussels must possess some form of memory to produce a power law–like distribution (Grünbaum, 2011). Having included the option of a composite Brownian walk, which was discussed in De Jager *et al.* (2011) but not included in the set of models tested, one finds that this describes mussels' movement extremely well.

Our analysis illustrates why one has to be cautious with inferring that animals move according to a Lévy walk based on too narrow a set of candidate models: If one has to choose between a power law and Brownian motion, often the power law is best, but this could simply reflect the absence of a better model. To make defensible inferences about animal movement, model selection should start with a set of carefully chosen models based on biologically relevant alternatives (Burnham & Anderson, 2002). Heterogeneous random movement often provides such an alternative and has the additional advantage that it can suggest a simple

Table 2.3: Model parameters and Akaike weights. The maximum likelihood parameter estimates, log maximum likelihoods (ML), AIC values, and Akaike weights are calculated for the data shown in Fig. 2.8, A and B. The Akaike weights without the composite Brownian walks are given in brackets. We analyzed the full data set (*) with x_{min} = 0.02236 mm, and the data set truncated as in De Jager *et al.* (2011) (†) with x_{min} = 0.21095 mm. For x_{max}, the longest observed step length (103.9mm) was used. The mix of four exponentials is not the best model according to the AIC weights. It gives a marginally, but not significantly, better fit and is overfitted.

Models	Formula	Parameters*	Parameters†	ML	AIC	Weight
Exponential (Brownian motion)	$P(X=x)=\lambda e^{-\lambda(x-x_{min})}$	$\lambda = 1.133$	$\lambda = 0.770$	−3136.89* −2558.67†	6275.78* 5119.37†	0 (0)* 0 (0)†
Power law (Lévy walk)	$P(X=x)=\frac{\mu-1}{x_{min}}x^{-\mu}$	$\mu = 1.397$	$\mu = 1.975$	−2290.10* −1002.32†	4582.20* 2006.64†	0 (0) * 0 (0.006)†
Truncated power law (Lévy walk)	$P(X=x)=\frac{\mu-1}{x_{min}^{1-\mu}-x_{max}^{1-\mu}}x^{-\mu}$	$\mu = 1.320$	$\mu = 1.960$	−2119.55* −997.29†	4241.10* 1996.58†	0 (1) * 0 (0.994)†
Mix of two exponentials (Composite Brownian walk)	$P(X=x)=\sum_{i=1}^{2}p_i\lambda_i e^{-\lambda_i(x-x_{min})}$ with $\sum_{i=1}^{2}p_i=1$	$p = 0.073,$ $\lambda_1 = 0.122,$ $\lambda_2 = 3.238$	$p = 0.127,$ $\lambda_1 = 0.123,$ $\lambda_2 = 3.275$	−906.15* −1022.44†	1818.31* 2050.87†	0* 0†
Mix of three exponentials (Composite Brownian walk)	$P(X=x)=\sum_{i=1}^{3}p_i\lambda_i e^{-\lambda_i(x-x_{min})}$ with $\sum_{i=1}^{3}p_i=1$	$p_1 = 0.034,$ $p_2 = 0.099,$ $\lambda_1 = 0.069,$ $\lambda_2 = 0.652,$ $\lambda_3 = 3.613$	$p_1 = 0.063,$ $p_2 = 0.210,$ $\lambda_1 = 0.072,$ $\lambda_2 = 0.832,$ $\lambda_3 = 4.309$	−861.55* −966.70†	1733.11* 1943.40†	0.881* 0.873†
Mix of four exponentials (Composite Brownian walk)	$P(X=x)=\sum_{i=1}^{4}p_i\lambda_i e^{-\lambda_i(x-x_{min})}$ with $\sum_{i=1}^{4}p_i=1$	$p_1 = 0.014,$ $p_2 = 0.034,$ $p_3 = 0.085,$ $\lambda_1 = 0.656,$ $\lambda_2 = 0.069,$ $\lambda_3 = 0.652,$ $\lambda_4 = 3.613$	$p_1 = 0.017,$ $p_2 = 0.060,$ $p_3 = 0.202,$ $\lambda_1 = 0.377,$ $\lambda_2 = 0.070,$ $\lambda_3 = 0.902,$ $\lambda_4 = 4.345$	−861.55* −966.63†	1737.11* 1947.26†	0.119* 0.127†

mechanism for the observed behavior.

Reply

We agree with Jansen *et al.* that a composite movement model provides a better statistical description of mussel movement than any simple movement strategy. This does not undermine the take-home message of our paper, which addresses the feedback between individual movement patterns and spatial complexity. Simple movement strategies provide more insight in the eco-evolutionary analysis and are therefore our model of choice.

The purpose of our paper (de Jager *et al.*, 2011; de Jager *et al.*, 2012a) was to demonstrate that movement strategies are shaped by the interaction between individual selection and the formation of spatial complexity on the population level. We showed that in a family of movement models ranging from ballistic motion, to Lévy walk, to Brownian motion, a Lévy walk with exponent $\mu \approx 2$ is the
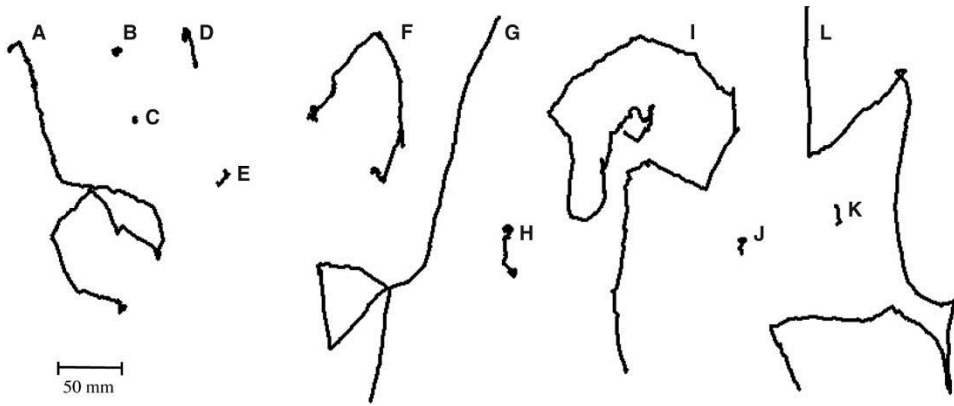
Figure 2.10: Movement trajectories of the 12 mussels on which we based the model fitting in our paper (de Jager *et al.*, 2011).

optimal strategy for mussels involved in pattern formation. Within this family of models, a single parameter (the scaling exponent μ) distinguishes between the different movement strategies. We intentionally chose a one-dimensional strategy space that can easily be used in pairwise invasibility analyses and the subsequent pairwise invasibility plots. It also keeps focus on the main differences in movement strategy, contrasting ballistic movement, Brownian diffusion, and long-tailed step length distributions, as in Lévy walks. As is often the case, the better fit of the complex model (i.e., composite Brownian walk) trades off with the elegance and clarity of the simpler model.

Nevertheless, it might be interesting to examine the mechanisms behind the composite Brownian walk that was observed in our mussel movement data by Jansen *et al.* (2012). Below, we investigate three possible causes of the observed movement pattern: (i) mussels switch between multiple movement modes because of changes in environmental conditions; (ii) the (collective) composite Brownian walk might be an ensemble of different individual Brownian walks; or (iii) internal switches between movement modes exist, with which mussels try to approximate a Lévy walk.

Table 2.4: Comparison of five movement models (Brownian walk BW, Lévy walk LW, truncated Lévy walk TLW, composite Brownian walk with two movement modes CBW2, composite Brownian walk with three movement modes CBW3) for the eight mussels for which sufficient data (n > 50) were available. For each mussel, the table presents the Akaike Information Criterion (AIC) and the Akaike weights (wAIC) for the five movement models. The minimal AIC value (corresponding to the best model) is shown in bold. The Akaike weights correspond to the relative likelihood of each model (Burnham & Anderson, 2002). For all model fits, we used a lower boundary (l_{min}) of 0.2 mm.

	BW		LW		TLW		CBW2		CBW3	
Mussel	**AIC**	**wAIC**	**AIC**	**wAIC**	**AIC**	**wAIC**	**AIC**	**wAIC**	**AIC**	**wAIC**
A	1917.4	0.000	1262.7	0.000	1236.6	0.000	1192.4	0.006	**1182.12**	**0.994**
B	**1293.2**	**0.867**	2030.8	0.000	1618.1	0.000	1297.2	0.117	1301.2	0.016
D	330.4	0.000	282.5	0.000	256.1	0.000	**209.1**	**0.502**	209.2	0.498
F	1101.7	0.000	642.3	0.000	628.9	0.054	638.8	0.000	**623.2**	**0.945**
G	1410.7	0.000	792.4	0.000	770.8	0.000	761.6	0.001	**748.5**	**0.998**
H	625.5	0.000	775.6	0.000	750.3	0.000	**519.9**	**0.881**	523.9	0.119
I	2177.2	0.000	1650.0	0.000	1592.5	0.003	**1582.1**	**0.620**	1583.1	0.376
L	1455.8	0.000	1179.0	0.000	1129.0	0.002	1123.2	0.033	**1116.4**	**0.966**

The first possible mechanism behind a composite Brownian walk is that mussels switch between movement modes in response to changes in environmental conditions. For example, a composite Brownian walk will result if animals switch between local Brownian search within a resource patch and straight-lined ballistic search between patches (Benhamou, 2007; Plank & James, 2008; Reynolds, 2009). Because the solitary mussels in our experiment were situated in a bare, homogeneous environment, repeated switches between movement strategies induced by changing environmental conditions do not provide a plausible explanation for the observed composite walk.

A second possible explanation for the observed composite Brownian walk could be that variation in individual movement behavior can explain the improved fit by the composite Brownian model (Petrovskii *et al.*, 2008) — for example, multiple different Brownian walks together make up the observed composite walk.
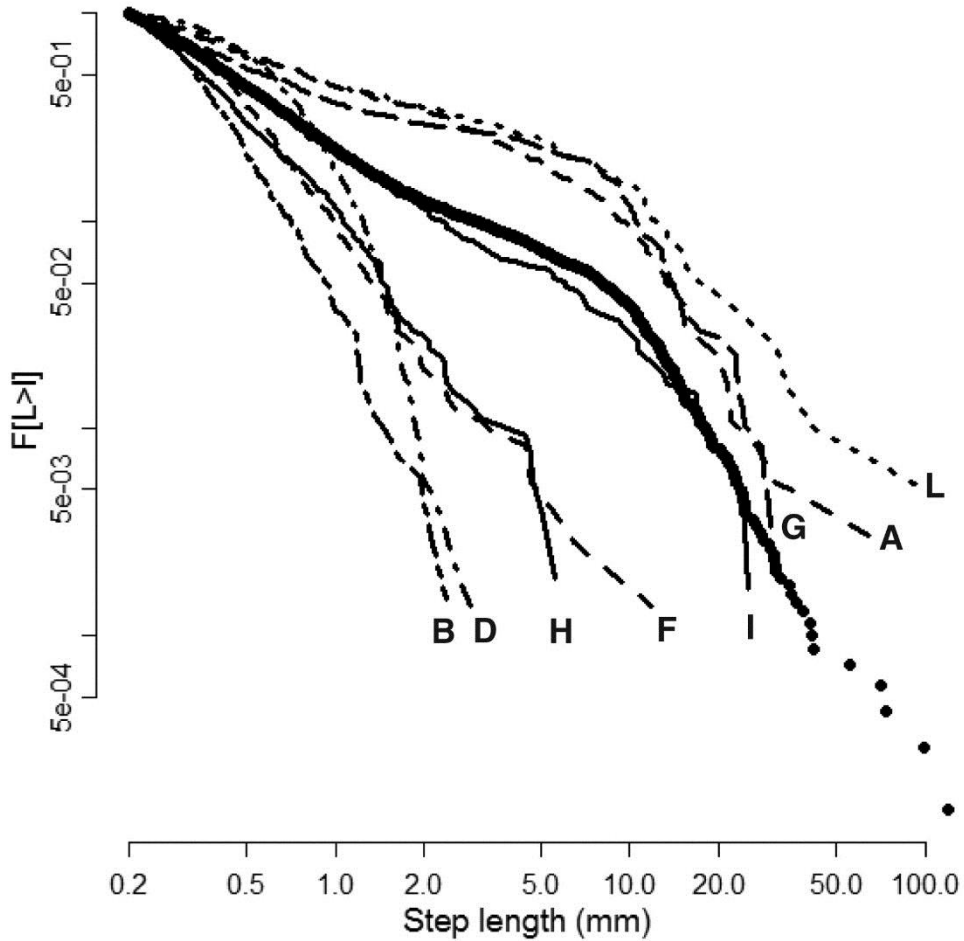
Figure 2.11: Inverse cumulative frequency distribution (e.g., the fraction of step lengths that is larger than or equal to a given step length) of the movement patterns of 12 individual mussels (thin dashed and dotted lines) and the combined data set (thick line and large dots).

To investigate this, we examined the individual movement tracks of the 12 mussels in our experiment. We indeed found a large variety of movement trajectories (Fig. 2.10); some mussels moved a large distance, whereas others stayed approximately at the original location. We fitted a Brownian walk, a Lévy walk, a truncated Lévy walk, and two composite Brownian walks to these individual movement trajectories, using the corrected data set and the analysis suggested by Jansen *et al.* (de Jager *et al.* 2012a, Jansen *et al.*, 2012). The analysis (Table 2.4 and Fig. 2.11) reveals that, in

most cases, a Brownian walk fitted very poorly to the data. A truncated Lévy walk provided large improvement over a Brownian walk, whereas a composite Brownian walk provided only small further improvement in fit, indicating that even at the individual level, composite behavior might underlie a long-tailed movement pattern.

A third possibility to mechanistically underpin the improved fit by a composite Brownian walk is that mussels use an internal switching rule to alternate between movement modes, independent from external triggers. Our study (de Jager *et al.*, 2011; de Jager *et al.*, 2012a) shows that a long-tailed step length distribution is a rewarding strategy for mussels living in, and contributing to, a spatially complex system. It is not obvious, however, how an animal should achieve such a step length distribution in practice. It is possible that animals approximate a Lévy walk by adopting an intrinsic composite movement strategy with different modes (which do not necessarily need to be Brownian). The observation by Jansen *et al.* (2012) that a composite walk yields a better fit to the observations thus suggests an interesting solution for this problem, which is worth further investigation. However, we think it most advisable to examine this switching behavior by means of temporal and spatial correlations of movement steps within animal tracks rather than fitting multimodal models to step size distributions. In our opinion, the observation by Jansen *et al.* (2012) does not change the overall conclusion of our paper (de Jager *et al.*, 2011), but it may contribute to a better understanding of the behavioral mechanisms by which animals achieve their optimal movement strategy.

3

How superdiffusion gets arrested:

Ecological encounters explain shift from Lévy to Brownian movement

Monique de Jager, Frederic Bartumeus, Andrea Kölzsch, Franz J. Weissing, Geerten M. Hengeveld, Bart A. Nolet, Peter M. J. Herman, Johan van de Koppel.

Abstract

Ecological theory uses Brownian motion as a default template for describing ecological movement, despite limited mechanistic underpinning. The generality of Brownian motion has recently been challenged by empirical studies that highlight alternative movement patterns of animals, especially when foraging in resource-poor environments. Yet, empirical studies reveal animals moving in a Brownian fashion when resources are abundant. We demonstrate that Einstein's original theory of collision-induced Brownian motion in physics provides a parsimonious, mechanistic explanation for these observations. Here, Brownian motion results from frequent encounters between organisms in dense environments. In density-controlled experiments, movement patterns of mussels shifted from Lévy towards Brownian motion with increasing density. When the analysis was restricted to moves not truncated by encounters, this shift did not occur. Using a theoretical argument, we explain that any movement pattern approximates Brownian motion at high resource densities, provided that movement is interrupted upon encounters. Hence, the observed shift to Brownian motion does not indicate a density-dependent change in movement strategy but rather results from frequent collisions. Our results emphasize the need for a more mechanistic use of Brownian motion in ecology, highlighting that especially in rich environments, Brownian motion emerges from ecological interactions, rather than being a default movement pattern.

Introduction

Traditionally, ecologists apply Brownian motion and diffusive dispersal as default models for animal movement (Skellam 1951; Kareiva & Shigesada 1983), both at individual and at population levels (Benhamou 2007; Sims *et al.* 2008; Edwards *et al.* 2012). Recently, however, empirical studies show that animal movement can strongly deviate from Brownian motion (Klafter & Sokolov 2005), revealing superdiffusive, Lévy-like movement in resource-poor environments, but standard Brownian motion when resource availability is high (Nolet & Mooij 2002; Bartumeus *et al.* 2003; De Knegt *et al.* 2007; Humphries *et al.* 2010; Humphries *et al.* 2012). Animal ecologists have explained this change from Lévy to Brownian motion by an active shift in individual movement strategy, reflecting the assumption that different movement strategies are optimal under different environmental conditions (Bell 1991; Humphries *et al.* 2010; Raposo *et al.* 2011; Humphries *et al.* 2012). In heterogeneous, resource-poor environments, Lévy movement will typically be more efficient than a Brownian walk since it provides faster dispersal and prevents revisiting the same sites (Bartumeus *et al.* 2002). In resource-rich environments, a Brownian walk may be equally or even more efficient as a Lévy walk, since large steps (which are the hallmark of Lévy movement) provide little benefit under these circumstances (Humphries *et al.* 2012).

Physical theory offers an alternative, more parsimonious explanation for the occurrence of Brownian motion in resource-rich environments. Einstein, followed by Langevin, theorized that Brownian motion in solutes results from collisions between particles (Einstein 1905; Langevin 1908). Likewise, Brownian motion in ecology might result from frequent "collisions" of animals with the resources they are searching for (food, shelter, or conspecifics) or with items that they are trying to avoid (e.g. territory boundaries; Giuggioli *et al.* 2012). Untangling whether the observed movement patterns in searching animals reflect adaptation of intrinsic movement strategies, or are the consequence of changing encounter (collision) rates with resources, is crucial both for sound mechanistic understanding of Brownian motion and for predicting animal movement patterns in ecosystems where resource availability varies in space or time.

Here we provide evidence that, as in physics, Brownian walks in animal movements can be caused by frequent encounters, rather than being the result of adaptation to high-density conditions. In density-controlled experiments with young mussels (*Mytilus edulis*), we were able to distinguish between intrinsic movement strategy and the effects of resource density by separating the movement steps that were truncated by encounters from those that were terminated spontaneously. Recently, it was shown that the individual movement of young mussels can be approximated by a simple Lévy walk (De Jager *et al.* 2011; or a more complex multi-scale walk, which provides an even better fit [Jansen *et al.* 2012; De Jager *et al.* 2012). The movement of individual mussels results in a self-organized mussel bed with a regular labyrinth-like pattern where local aggregation yields protection against wave stress and predation while it reduces competition for algal food resources (Hunt & Scheibling 2001; Hunt & Scheibling 2002; Van de Koppel *et al.* 2008). Since the movement of individual mussels can be experimentally studied in considerable detail, this experimental system offers a unique opportunity to provide a mechanistic basis for the appearance of Brownian motion in research-rich environments.

This paper is structured as follows. First, we describe movement of young mussels observed in density-controlled experiments, revealing that movement patterns are affected by changes in the density of mussels. By distinguishing between obstructed and unobstructed movement steps, we investigate the relation between intended and realized movement patterns. Second, we create an individual-based model of self-organized pattern formation in mussel beds to examine whether mussel density could cause a change in the efficiency of Brownian and Lévy walks, explaining a possible active shift in mussel movement strategy. Third, we use a general argument to demonstrate that the interplay between *any* intrinsic movement strategy and frequent ecological encounters will often result in Brownian motion.

Experiments

Methods

Using mesocosm experiments, we investigated how mussel movement patterns are affected by mussel density. Young blue mussels (*Mytilus edulis*) of approximately 1.5 cm in length were obtained from wooden wave-breaker poles on the beaches near Vlissingen, The Netherlands (51°46' N, 3°53' E). After careful separation and cleaning, the mussels were kept in containers and fed live cultures of diatoms (*Phaeodactylum tricornutum*) daily. Fresh, unfiltered seawater was supplied to the container at a rate of approximately one litre per minute; a constant water temperature of 16°C was maintained during the experiments. At the start of each experiment, mussels were spread homogeneously over an 80 x 60 cm red PVC sheet in a 120 x 80 x 30cm container. We used a red PVC sheet to provide a contrast-rich surface for later analysis and considered only the movements of the mussels within this 80 x 60 cm arena. The container was illuminated using fluorescent lamps. Mussel movement was recorded by photographing the mussels at a 1 minute interval for a duration of 300 minutes; we used a Logitech QuickCam 9000 Pro webcam (www.logitech.com), which was positioned about 60 cm above the water surface.

We derived the step lengths by calculating the distance between two reorientation events (e.g. where a mussel clearly changes its direction of movement) using Turchin's angle method (Turchin 1998; De Jager *et al.* 2011). With this method. First, the observed movement path is discretized into steps on basis of changes in the angle (α) of the movement path at observed position i using the prior (i-1) and the subsequent (i+1) observed locations as follows:

$$\alpha = \arccos[\frac{a^2 + b^2 - c^2}{2ac}], \hspace{3cm} (3.1)$$

where *a* is the length between position i and i+1, *b* is the length between position i-1 and i+1, and *c* is the length between positions i-1 and i. Whenever α was larger than a threshold angle α_T, a new step is considered to start. Following Turchin's approach (Turchin 1998), we used $\alpha_T = \pi/5$ for our step length calculations, as this

value minimized autocorrelation between subsequent turns. Using other threshold angles did not change our conclusions.

We studied the changes in the statistical properties of the observed movement pattern by recording 10 individual movement trajectories for 5 different density treatments each (0, 1.3, 2.0, 3.3, and 5.2 kg/m^2, approximately 1, 950, 1550, 2500, and 3850 mussels per square meter) during the initial 300 minutes of pattern formation (Van de Koppel *et al.* 2008). When a mussel encountered an obstacle, such as a conspecific, it was forced to truncate its step, which will likely alter the properties of the movement pattern. We used the complementary cumulative distribution function (*CCDF*) of the observed step lengths of each individual mussel in the five density treatments to illustrate the observed movement patterns. This *CCDF* is a preferred method for fitting power distributions as it provides a more reliable representation of movement patterns than other portraying methods (Benhamou 2007). For each step length *l*, the complementary cumulative distribution function *CCDF(l)* of the observed step lengths in each density treatment indicates the fraction of step lengths that were at least as long as *l*. Using maximum likelihood methods, we estimated the scaling exponent μ of a power-law step length distribution,

$$P(l) = (\mu - 1) \cdot l_{min}^{\mu-1} \cdot l^{-\mu}, \tag{3.2}$$

where *l* is the step length and l_{min} is the minimal step length of young mussels ($l_{min} \leq l$; Benhamou 2007; Edwards *et al.* 2007; Clauset *et al.* 2009; De Jager *et al.* 2011). The step length distribution corresponds to a Lévy walk for $1 < \mu < 3$ and it approximates a Brownian walk when $\mu > 3$ (Bartumeus *et al.* 2005). We apply a simple power-law model rather than a more complex composite model because we are interested in the change of general statistical properties with mussel density rather than in a detailed statistical description of mussel movement (De Jager *et al.* 2011; Jansen *et al.* 2012; De Jager *et al.* 2012). First, we kept the minimal step length constant at the fixed value l_{min} = 3 mm. Given l_{min}, the exponent μ can be estimated from the likelihood function (Edwards *et al.* 2007; Bertrand *et al.* 2007; Edwards 2008; Clauset *et al.* 2009):

$$L(\mu, l_1, \ldots, l_n) = \prod_i P(l_i) = (\mu - 1)^n \cdot l_{min}^{n \cdot (\mu - 1)} \cdot \left(\prod l_i\right)^{-\mu}, \tag{3.3}$$

where $\{l_i \ldots l_n\}$ are the observed step lengths. Taking the natural logarithm of L and maximizing with respect to µ yields the maximum-likelihood estimate:

$$\mu = 1 + n \cdot \left(\sum \ln(l_i) - \ln(l_{min})\right)^{-1}, \tag{3.4}$$

To check for the robustness of our results, we also fitted the observed step length distribution to a power law where the value of l_{min} was estimated separately for each individual trajectory (by equating l_{min} with the minimal observed step length). Our conclusions were not affected in any way.

By labelling steps as truncated whenever the step ended directly in front of another mussel, we were able to distinguish pure, non-truncated steps from those truncated by collisions with conspecifics. For the same 10 individuals in the 5 density treatments (50 mussels in total), we split the steps into truncated and non-truncated steps, examining the distributions separately.

Results

Our mesocosm experiments illustrate that the observed movement patterns are strongly affected by mussel density (Figures 3.1 and 3.2). Long steps occur less frequently with increasing mussel density (Figure 3.2a). The scaling exponent µ increases with mussel density from a value below 2.5 at low densities to values above 3.5 at high densities (Figure 3.2b). As a second test of our hypothesis that observed movement trajectories become more Brownian-like with increased resource density, we used the Akaike Information Criterion for deciding whether the individual trajectories in each density class were better fitted by a power law or by an exponential distribution (corresponding to a Brownian walk). In 83 percent of the movement trajectories in the lowest-density treatment, a Lévy walk provided a better fit to the step length data than a Brownian walk. In contrast, 75 percent of the tracks in the high-density treatment were better approximated by a Brownian walk than by a Lévy walk. Again, we conclude that movement trajectories become more Brownian-like with increasing mussel density.
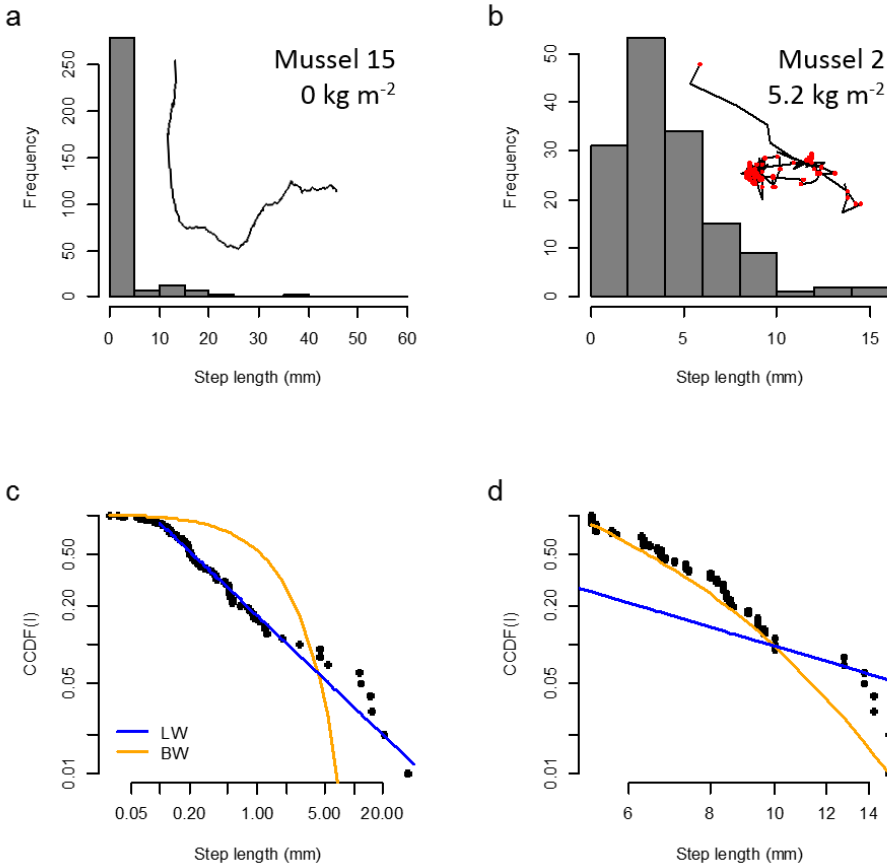
Figure 3.1: Step length distributions and model fits for movement trajectories at two mussel densities. Step length frequency distributions of mussel 15 in the 0 kg m^{-2} treatment (**a**) and mussel 2 in the 5.2 kg m^{-2} treatment (**b**), together with an illustration of the movement paths. The fitted lines to the complementary cumulative distribution functions (CCDF) of the step lengths of mussel 15 (**c**) and mussel 2 (**d**) indicate how well the movement trajectories are represented by a Lévy walk (LW) and a Brownian walk (BW).

Closer examination of the movement data indicates that the change of step length distribution with mussel density results from the frequent truncation of step lengths at high densities (Figure 3.2c-d). The fraction of truncated steps increases with mussel density (Figure 3.2c), presumably because the number of encounters leading to an interruption of the movement increases with density. When only considering non-truncated steps, mussel movement does not significantly differ between density treatments (Figure 3.2d). We conclude that the intrinsic movement
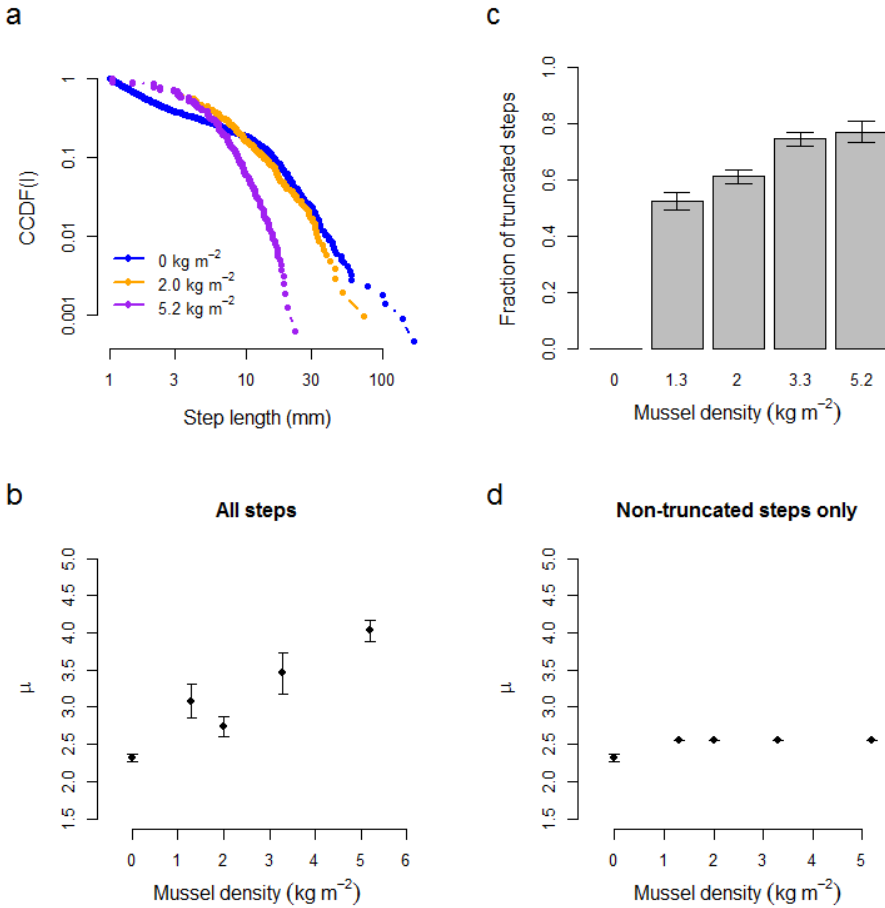
Figure 3.2: Effect of mussel density on individual movement trajectories. (**a**) Complementary cumulative distribution function (CCDF) of the pooled step lengths of moving mussels measured for three density treatments. With increasing mussel density, the fraction of long steps decreases. (**b**) Estimated scaling exponent μ as a function of mussel density; μ increases with mussel density (linear regression, $\beta_1 = 0.73$, $r = 0.46$, df $=46$, $P < 0.001$; bars indicate average μ per density group $\pm$ SE) and takes on values beyond 3 at high densities. (**c**) The fraction of steps that are truncated by collisions increases with mussel density (bars indicate means $\pm$ SE). (**d**) When considering the non-truncated steps only, the scaling exponent μ remains approximately constant (linear regression, $\beta_1 = 0.18$, $r = 0$, df $=26$, $P = 0.593$; bars indicate average μ per density group $\pm$ SE).

strategy of the mussels does not change with density and that the observed change from Lévy-like to Brownian-like movement results solely from the increased mussel encounter rates at high density.

A model of mussel movement

Methods

Using a well-established model for mussel movement (De Jager *et al.* 2011), we investigated whether an active switch from Lévy to Brownian movement at high densities is more efficient than the persistent use of Lévy movement. We ran individual-based computer simulations for a range of values of the scaling exponent μ and at various densities, where we repeated each simulation 10 times to account for stochasticity. Whenever a displacement was restricted by the presence of a conspecific, the step was truncated. In each simulation, we determined the sum D of all displacements required before the mussels settled in a stable pattern. The inverse of D can be viewed as a measure of the patterning efficiency of the movement strategy under consideration (De Jager *et al.* 2011; Viswanathan *et al.* 1999).

Results

Brownian movement is often assumed to be more efficient in dense environments; some researchers thus argue that animals switch from Lévy to Brownian movement when encountering areas of higher resource density. However, simulations with our individual-based model (De Jager *et al.* 2011) of mussel movement demonstrate that Lévy movement is at least as efficient as Brownian motion at all densities. At low densities, a Lévy walk with exponent $\mu \approx 2$ is the most efficient movement strategy (Figure 3.3). At higher densities, all movement strategies with $2 \le \mu \le 3$ lead to Brownian-like movement patterns and therefore have a similar patterning efficiency; hence, the simulations do not support the hypothesis that Brownian movement strategies lead to more efficient aggregation than Lévy movement strategies. This implies that there is no necessity to switch to a Brownian strategy with increasing density, and the mussels in our experiments do not behave suboptimally when using a Lévy walk at high densities (Figure 3.2d).
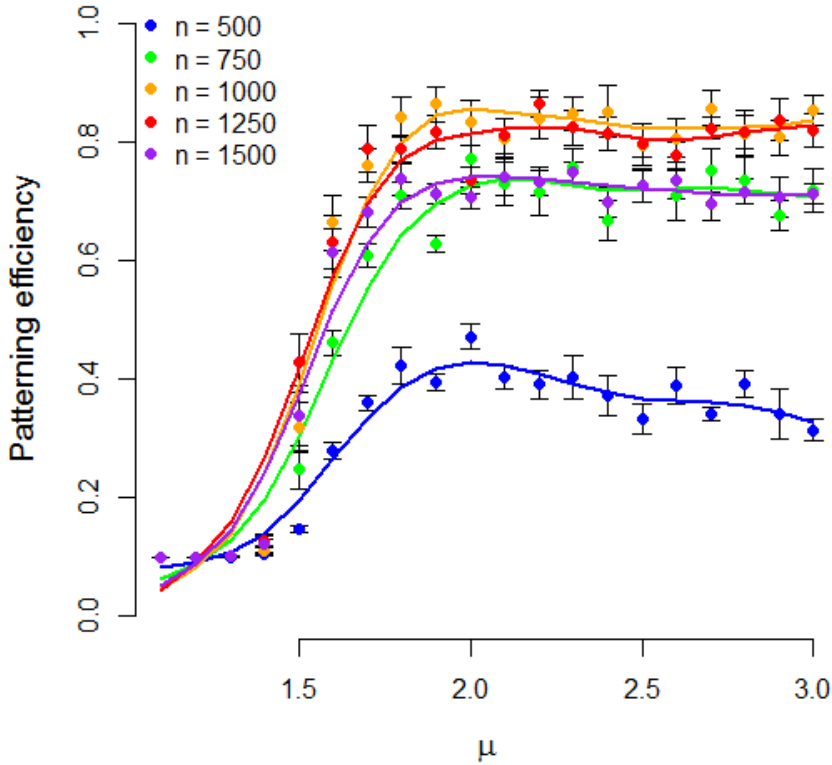
Figure 3.3: Patterning efficiency as a function of the scaling exponent μ in model simulations for five different mussel densities. At low mussel density (n=500), a Lévy walk with $\mu \approx 2$ has the highest patterning efficiency, i.e., this movement strategy creates a spatial pattern with a minimum of displacements. At higher densities, a Lévy walk with $\mu \approx 2$ still appears optimal, but most other movement strategies (including a Brownian walk) perform equally well. Bars indicate means of 10 simulations ± SD; lines illustrate cubic smoothing splines through the model results. Patterning efficiency, measured as the inverse of the distance D moved per mussel until a pattern was formed, was normalized by dividing by the largest efficiency found in all simulations.

A general argument

By means of a general argument, it can be seen that the transition from non-Brownian to Brownian motion at high densities is a general phenomenon and not restricted to mussel movement. Consider a population of animals where the individuals have a certain intrinsic movement strategy, such as a Lévy walk with a given exponent μ. If all individuals could complete their movement steps uninterrupted, this movement strategy would result in a step length distribution with a complementary cumulative distribution function $CCDF_{intended}(l)$ (as in Figure 3.2a, $CCDF(l)$ corresponds to the probability that a step is longer than or equal to l). Suppose now that an animal terminates its movement whenever it encounters its desired target, such as food or shelter. (The same arguments apply when moves are terminated due to encounters with obstacles or the presence of a potential danger, such as a predator or a rival.) If the encounters of the moving animals with the target objects is random, the probability that an intended step of length l will *not* be terminated is given by the zero term of a Poisson distribution: e^{-kAl}, where A is the density of target objects and k is a constant of proportionality that reflects aspects such as the search window of the animal or the size and visibility of the target objects. As a consequence, the complementary cumulative distribution function of the realized (and observed) step length distribution is given by

$$CCDF_{realized}(l) = CCDF_{intended}(l) \cdot e^{-kAl}. \quad\quad (3.5)$$

Since step lengths will become shorter due to the termination of steps by encounters, the realized step length distribution will have a different signature than the intended step length distribution. In particular, intended longer steps will be terminated more often than intended shorter steps, and the probability that a step is terminated will depend on the density of target objects. For large densities of the target object, the exponential term becomes dominant and forces the tail of the CCDF towards the exponential distribution that is characteristic of Brownian walks (Figure 3.4). For example, the CCDF of an intended Lévy walk with exponent $\mu_{intended} = 2$ results in a realized CCDF that, due to the termination of steps by encounters with the target object, resembles the CCDF of a Lévy walk with a larger
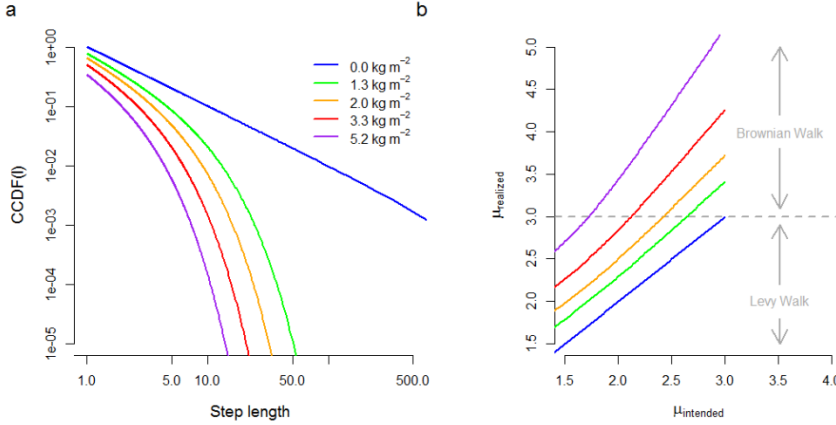
Figure 3.4: Difference between intended and realized step length distribution for various densities of the target object. (**a**) Complementary cumulative distribution functions (CCDF) of the realized step lengths of organisms using a Lévy walk with scaling exponent $\mu_{intended}$ = 2 as their intrinsic movement strategy. Only at zero density, the realized CCDF corresponds to the intended CCDF, while the fatness of the tail of the distribution strongly decreases at higher densities. The realized CCDF approximately correspond to the CCDF of a power law with scaling exponent $\mu_{realized}$ = 2.5, 2.9, 3.0, and 3.5 for the increasing densities, respectively. (**b**) Relationship between intrinsic scaling exponent $\mu_{intended}$ and realized scaling exponent $\mu_{realized}$ for various object densities. Movement patterns are often classified as a Lévy walk (LW) when the estimated value of μ is between 1 and 3 and as Brownian walk (BW) when μ > 3.

exponent $\mu_{realized}$ (Figure 3.4a). In more general terms, an intended movement strategy that is not Brownian at all takes on the signature of Brownian motion when intended movement steps are frequently terminated because of a high density of target objects (Figure 3.4b).

Discussion

Einstein demonstrated that Brownian motion of dissolved particles can be explained by heat-driven collisions of these particles with the molecules of the liquid (Einstein, 1905; Langevin, 1908). Despite obvious differences between movement in particles and organisms, our study shows that in analogy to physics, encounters between organisms result in Brownian motion, in particular when found in encounter-rich environments. We observed that under controlled, experimental conditions, mussel movement patterns shifted from Lévy to Brownian motion with increasing mussel density. By separating truncated from

non-truncated steps, we were able to show that this change in movement pattern is entirely the consequence of increased encounter rate, as we did not observe a shift in intrinsic movement strategy. We furthermore demonstrated the universality of this principle with a simple argument, showing that in general, encounters lead to Brownian motion in animal movement patterns.

The shift from Lévy-like to Brownian movement with increasing density has so far been explained as an adaptation to increased resource availability. Animals are considered to adapt to increased encounters with food items by refraining from large-scale movement steps, hence leading to adaptive Brownian walks (Bell, 1991; Frank, 2009). However, our study provides a different perspective on the observed shift from Levy-like to Brownian movement. When encounter rates are low, the observed movement pattern reflects the intrinsic search strategy, which can strongly deviate from Brownian movement. When encounter rates are high, the signature of the intrinsic search strategy is lost; large movement steps are frequently truncated by encounters and the movement pattern resembles Brownian motion irrespective of the underlying intrinsic strategy. This has important implications for ecological theory, as here Brownian motion is not a default, intrinsic movement mode that underlies animal dispersal, but emerges from ecological encounters between organisms, such as encounters with food items or interference with conspecifics, like the physical obstruction of mussel movement observed in our study.

The explanation of encounters driving Brownian motion can clarify observations from a number of terrestrial and marine studies. For instance, studies by Bartumeus *et al.* (2003), De Knegt *et al.* (2007), and Humphries *et al.* (2010, 2012) illustrate that microzooplankton, goats, marine predators, and albatrosses all exhibit Brownian motion in areas with high food density and Lévy-like movement in resource-poor environments. These studies highlight that an increased prevalence of Brownian motion in resource-rich environments is a general trend in ecological systems. Our explanation that encounters obscure the innate movement strategy into an observed movement pattern that closely resembles a Brownian walk rationalizes this universal trend. As a variety of ecological encounters, such as predator-prey interactions, mating, or aggregation, are prone to occur in real

ecosystems, observed animal movement patterns will always deviate from the employed intrinsic movement strategy. Especially in rich environments, resource encounters may alter the movement pattern extensively. Hence, our study not only illustrates the generality of this principle, but also highlights the importance of ecological interactions in shaping movement patterns of organisms throughout nature.

While density-dependence of demographic processes such as growth and predation forms the cornerstone of ecological theory, animal movement and dispersal are typically approximated by density-independent linear diffusion, based on the assumption of Brownian motion. This study, in combination with previous work (Nolet & Mooij 2002; Bartumeus *et al.* 2003; De Knegt *et al.* 2007; Humphries *et al.* 2010; Humphries *et al.* 2012; De Jager *et al.* 2011; Van de Koppel *et al.* 2008) shows that for many organisms, this assumption is not valid; both movement rates and movement characteristics may change as a function of the local density of food items or conspecifics, being either through ecological encounters as advocated in this paper, or through adaptation of movement (Humphries *et al,* 2010). As a consequence, movement characteristics at the population level may change with density, for instance from superdiffusive dispersal at low encounter rates, to more conservative linear diffusion at high encounter rates. This can have important consequences for, for instance, the rate of spread of infectious diseases and invasive species, or the formation of self-organized patterns. As the underlying movement strategy will often be masked under high-density conditions and organisms thus might behave differently under low-density conditions, one must be careful not to draw too far-reaching conclusions from movement patterns observed in dense environments. A more mechanistic understanding of ecological movement, facilitated by current improvements in techniques to monitor moving animals, will greatly expand our ability to examine, model, and comprehend animal movement patterns and their influence on other ecological processes.

Appendix A

Table 3.1: Best fits of exponential distributions (e.g. Brownian walks) and Pareto distributions (e.g. Lévy walks) to individual movement trajectories. The last column indicates whether a Brownian walk better represents the observed step length distribution than a Lévy walk (0 = LW fits better than BW; 1 = BW fits better than LW). Here, we used variable lower boundary estimates (lmin) and corrected for sample size in order to compare Akaike Information Criterions (AIC).

Density (kg m^{-2})	Mussel nr	Brownian walk			Lévy walk			Brownian walk fits best?
		l$_{min}$	lambda	AIC	l$_{min}$	mu	AIC	
0	1	0.10	1.57	113.29	0.10	1.83	19.93	0
0	2	0.10	0.58	313.33	0.10	1.56	217.65	0
0	3	0.05	0.59	309.22	0.10	1.57	208.16	0
0	4	0.95	6.99	-183.09	0.95	8.72	-187.19	0
0	5	0.05	0.89	226.23	0.05	1.55	88.24	0
0	6	0.15	8.66	-227.78	0.15	3.10	-228.12	0
0	7	0.10	5.33	-130.63	0.10	2.20	-126.66	1
0	8	0.15	5.53	-137.87	0.15	2.55	-133.99	1
0	9	0.05	3.88	-67.40	0.05	1.87	-139.78	0
0	10	0.20	1.52	120.85	0.20	1.98	90.12	0
0	11	0.10	11.09	-277.17	0.05	2.35	-307.42	0
0	12	0.05	1.23	162.13	0.05	1.77	-85.90	0
0	13	0.05	0.47	357.08	0.05	1.44	219.35	0
0	14	0.05	0.18	549.22	0.05	1.38	330.15	0
0	15	0.05	0.99	205.15	0.05	1.68	-24.44	0
0	16	0.05	20.17	-396.88	0.10	3.74	-385.31	1
0	17	0.10	11.60	-286.20	0.10	3.19	-322.56	0
0	18	0.05	1.28	154.34	0.05	1.59	45.46	0
Average	**18**	**0.13**	**4.59**	**44.66**	**0.14**	**2.45**	**-40.13**	**0.17**
1.3	1	1.05	0.37	404.29	2.10	2.64	374.86	0
1.3	2	2.65	0.46	357.43	2.65	3.12	340.23	0
1.3	3	3.70	0.71	268.58	3.70	4.76	251.28	0
1.3	4	0.50	0.43	373.52	1.05	2.11	374.15	1
1.3	5	3.15	0.77	252.67	3.15	4.15	264.69	1
1.3	6	2.65	0.80	246.31	2.65	3.99	244.23	0
1.3	7	2.10	1.02	198.75	2.10	4.06	192.39	0
1.3	9	2.35	0.40	388.00	2.65	2.92	373.05	0
1.3	10	2.10	0.43	373.62	2.10	2.87	334.09	0
Average	**9**	**2.25**	**0.60**	**318.13**	**2.46**	**3.40**	**305.44**	**0.22**

Density (kg m^{-2})	Mussel nr	Brownian walk			Lévy walk			Brownian walk fits best?
		l$_{min}$	lambda	AIC	l$_{min}$	mu	AIC	
2	1	0.75	0.33	427.68	1.05	1.98	422.09	0
2	2	2.15	0.44	369.44	2.15	2.68	372.77	1
2	3	2.65	0.53	327.30	2.65	3.29	317.86	0
2	4	2.85	0.26	469.67	2.40	2.28	481.10	1
2	7	2.10	0.48	348.91	2.10	2.70	359.88	1
2	8	3.10	0.37	400.85	3.10	2.93	397.65	0
2	10	1.05	0.35	416.77	1.50	2.26	397.66	0
Average	**7**	**2.09**	**0.39**	**394.37**	**2.14**	**2.59**	**392.72**	**0.43**
3.3	1	1.50	0.60	305.88	2.10	3.08	302.72	0
3.3	2	2.65	0.52	336.43	2.65	3.14	339.95	1
3.3	3	1.60	0.44	369.10	1.60	2.49	351.46	0
3.3	5	3.15	1.20	165.97	3.15	5.58	171.03	1
3.3	6	2.65	0.88	228.29	2.65	4.13	232.45	1
3.3	8	2.10	0.61	302.65	2.65	3.63	281.23	0
3.3	10	2.10	0.60	302.02	2.10	3.13	292.17	0
Average	**7**	**2.25**	**0.69**	**287.19**	**2.41**	**3.60**	**281.57**	**0.43**
5.2	1	1.05	1.25	157.25	1.05	3.18	148.01	0
5.2	2	2.10	0.88	228.71	2.10	3.63	234.94	1
5.2	3	3.00	0.89	227.34	3.00	4.53	227.91	1
5.2	4	3.15	0.76	257.64	3.15	4.19	261.18	1
5.2	5	3.70	1.12	180.00	3.70	5.99	182.54	1
5.2	7	3.15	0.78	251.06	3.15	4.28	254.33	1
5.2	9	3.70	1.00	201.04	3.70	5.60	201.87	1
5.2	10	2.65	0.75	261.99	2.65	3.86	258.35	0
Average	**8**	**2.81**	**0.93**	**220.63**	**2.81**	**4.41**	**221.14**	**0.75**

Appendix B
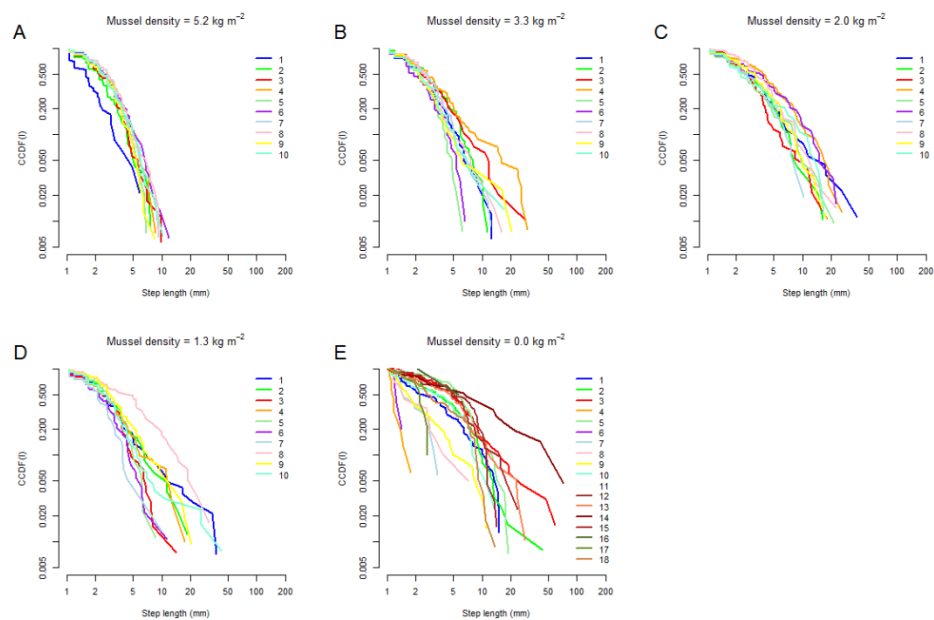
Figures 3.5 – 3.9: Individual movement trajectories of 10 mussels in different density treatments.

4

Experimental evidence for inherent Lévy search behaviour in foraging animals

Andrea Kölzsch, Adriana Alzate, Frederic Bartumeus, Monique de Jager, Ellen J. Weerman, Geerten M. Hengeveld, Marc Naguib, Bart A. Nolet, Johan van de Koppel

Abstract

Recently, Lévy walks have been put forward as a new paradigm for animal search and many cases have been made for its presence in nature. However, it remains debated whether Lévy walks are an inherent behavioural strategy or emerge from the animal reacting to its habitat. Here, we demonstrate signatures of Lévy behaviour in the search movement of mud snails (*Hydrobia ulvae*) based on a novel, direct assessment of movement properties in an experimental setup using different food distributions. Our experimental data uncovered clusters of small movement steps alternating with long moves independent of food encounter and landscape complexity. Moreover, size distributions of these clusters followed truncated powerlaws. These two findings are characteristic signatures of mechanisms underlying inherent Lévy-like movement. Thus, our study provides clear experimental evidence that such multi-scale movement is an inherent behaviour rather than resulting from the animal interacting with its environment.

Introduction

Many animal species move through differently structured landscapes searching for food. When food items are unperceivable, animals are assumed to follow specialised random search strategies in order to maximise foraging gain (Pyke, 1984; Zollner & Lima, 1999; Viswanathan *et al.*, 2000; Bartumeus *et al.*, 2002). Going beyond the classical approaches based on Brownian motion (Turchin, 1998), Lévy walks (Viswanathan *et al.*, 1996; Viswanathan *et al.*, 1999) have been put forward as a new movement paradigm for animals searching for rare, hard-to-find food items.

Lévy walks are a special case of multi-scale walks, composed of clusters of short movement steps and frequent turns (i.e. small-scale clusters of area-restricted search) alternating with long-distance displacements. The ratio of short vs. long steps is scale invariant in Lévy walks, described by the powerlaw probability density function $P(x\_i) \approx [\![x\_i]\!]^{\wedge}(-\mu)$, with x_i being the move length (displacement of consistent direction) and μ representing the powerlaw exponent, where $1 < \mu \leq 3$. To make a distinction between this mathematically strict Lévy foraging hypothesis and biological, Lévy-like movement that optimises search, we introduce for the latter the term "multi-scale search behaviour".

Initial scepticism against Lévy walks in natural systems (Boyer *et al.*, 2006; Reynolds & Bartumeus, 2009) and critics on methodology (Edwards, 2011; Edwards *et al.*, 2007; Viswanathan, Raposo & da Luz, 2008) have been overturned (Reynolds & Rhodes, 2009; Humphries & Sims, 2014), but see (Pyke, 2014), and many studies now show convincingly that Lévy-like, multi-scale search behaviour is not only present in a wide range of extant animals and humans (Ramos-Fernandez *et al.*, 2004; Sims *et al.*, 2008; Bartumeus *et al.*, 2010; Franks *et al.*, 2010; De Jager *et al.*, 2011; Humphries *et al.*, 2012; Raichlen *et al.*, 2014; Reynolds, Schultheiss & Cheng, 2014; Seuront & Stanley, 2014), but can even be found in trace fossil trails (Sims *et al.*, 2014).

The greatest challenge, however, is yet to discover and understand the mechanisms that underlie such multi-scale search patterns (Bartumeus, 2009;

Stumpf & Porter, 2012). On the one hand, it has been argued that the observed, long-tailed move length distributions that point to a Lévy walk can result from the interactions of animals with fractal-shaped landscape properties (Boyer *et al.*, 2006; Benhamou, 2007; Humphries *et al.*, 2010), obscuring underlying Brownian movement. This hypothesis, called the composite Brownian walk (Benhamou, 2007), presumes that area-restricted search (ARS) is triggered by encounter of food or food-rich patches. On the other hand, evidence is increasing that multi-scale, Lévy-like movement patterns are shaped by intrinsic behaviours, independent of environmental drivers (Maye *et al.*, 2007; Sims *et al.*, 2012; De Jager *et al.*, 2014).

Recent simulation studies and experiments have shown that multi-scale walks are optimal search (and foraging) strategies for a wide range of environmental conditions (Bartumeus *et al.*, 2014; De Jager *et al.*, 2014; Humphries & Sims, 2014; Raichlen *et al.*, 2014), including completely uniform, unstructured landscapes (Maye *et al.*, 2007; Reynolds, Lepretre & Bohan, 2013). Timing of spontaneous behaviours, like flight turns in Drosophila (Maye *et al.*, 2007), ambush waiting in marine predators (Wearmouth *et al.*, 2014) and activity dynamics of mice (Proekt *et al.*, 2012), as well as planned task cueing in humans (Barabasi, 2005) revealed Lévy walk characteristics without environmental feedback, indicating intrinsic control by the nervous system. In million-year old fossil tracks, Lévy walks were suggested to have emerged from simple self-avoiding trails, again suggesting an intrinsic mechanism that has evolved as a natural adaption (Sims *et al.*, 2014). A combination of intrinsic and extrinsic drivers of Lévy walk patterns was shown by copepods searching for mates (Seuront & Stanley, 2014). They exhibited intrinsic multi-scale search patterns in the absence of chemical cues as well as if pheromone was present, but with increased powerlaw exponents leading to more localised movement in the latter case. However, most of those examples are behaviours less complex than foraging, and a simple approach to test for the presence of intrinsic, multi-scale movement as foraging strategy still seems to be lacking (Reynolds, 2012).

To fill this gap, we followed an alternative approach and experimentally tested for the presence of intrinsic Lévy-like search behaviour using small animals, mud snails (Hydrobia ulvae), foraging within artificial landscapes of patches of

diatoms, their main food. After investigating the snails' cognitive performance, we determined their movement characteristics in artificial landscapes with different degrees of food heterogeneity. First, we evaluated the hypothesis, characteristic of Lévy foraging behaviour that ARS clusters would occur irrespective of the encounter of food. This hypothesis was contrasted against the alternative hypotheses that (i) ARS clusters would form only in response to food encounter, which is the premise underlying the composite Brownian walk, and that (ii) snails would move straight between food patches (ballistic search) (James, Plank & Brown, 2008; Plank & James, 2008). Second, we tested if the ARS clusters showed a long-tailed size distribution irrespective to the landscape configuration. This would indicate a complex alternation mechanism of intensive and extensive search behaviour (Méndez, Campos & Bartumeus, 2014) and point to intrinsic multi-scale search behaviour.

Methods & Results

Experiments

We collected sediment, benthic diatoms and mud snails at two different intertidal mud flats, the Kapellebank in the Westerschelde estuary (51.45°N, 3.97°E) and Dortsman in the Oosterschelde (51.52°N, 4.02°E; Netherlands). Before use in the laboratory, the muddy sediment was defaunated (freezing at 20°C for two days) and sieved (5mm) to remove coarse particles. Snails were kept in an aerated container with a thin layer of mud, filtered sea water and cultured diatoms for food.

To set up foraging landscapes, we isolated and cultivated motile epipelic diatoms (Round, 1981), one of the major components of mud snail diet (Haubois *et al.*, 2005). The filtered diatom suspension was applied on defaunated mud in 30 x 45 cm plastic containers, and food patch patterns were created by using a mesh template of 1.5 x 1.5 cm grids. Mesh cells were either filled with diatom suspension or filtered sea water. The food density in the patches was very high (approximately 100 µg chlorophyll-a per g sediment (Weerman, Herman & Van de Koppel, 2011)) to avoid depletion. To allow the diatoms to grow, the containers were placed below red and white LED light with a 12:12 h light-dark cycle and the temperature was set to 13°C.

After confirming the assumption of limited cognitive performance for our system (see Appendix), the main experiment was set up. We prepared containers of five different landscape types for the main experiments (performed 27/07 – 6/09 2010)). Two landscapes were homogeneous (bare mud or completely covered with diatoms) and three landscapes were prepared with 10% of its surface covered with diatoms in different levels of patchiness (see Appendix). The "regular" landscape was constructed by arranging mesh cells completely regularly, which allowed for frequent food encounter. The "random" landscape was created by placing the same amount of cells randomly. With the "fractal" landscape we intended to replicate the patchy character of the natural habitat of mud snails; it was created using the Midpoint displacement algorithm (Saupe, 1988).

Once the diatoms were well grown on the mud, the mesh cells were carefully taken off. The container was refilled with approximately 2 cm of filtered sea water, placed away from the LED lights under a webcam (Logitech QuickCam 9000 Pro) that was outlined by two fluorescent lights, providing homogeneous light conditions. Before each experiment, nine naïve snails (that had not been used for any experiment before) were starved for one hour and marked with a small dot of yellow nail polish for track recognition. All snails were treated in the same way, so the tracks in our experiment reflect comparable conditions apart from the experimental treatments. Furthermore, our conclusions are likely generalizable to unmarked snails, as the movements of a small sample of snails without nail polish were similar (see Appendix), and hence the nail polish seems not to notably have affected the snails' movements. Then, the snails were placed on the landscape in three rows and three columns at equal distances from each other, and the camera was set to take a picture each 10 s to record their movement paths for five hours. After this time the experiment was finished and the snails were removed.

The positions of each snail were digitised as x/y coordinates, additionally recording whether the position was on a food patch or not. For each landscape, we used four replicates. Each snail was only used once, so altogether we recorded the tracks of 180 individual snails. However, for one of the regular landscapes the experiment failed (landscape pattern destroyed), so that we used the tracks of 171 snails only. Furthermore, due to burrowing behaviour some snails did not move.

Others moved directly to the edges of the containers, where we truncated their tracks. For analysis we selected only individual tracks that contained >50 steps (N=116). The number of those tracks did not differ much between landscapes.

Data analysis

For each individual, the regularly sampled snail tracks were aggregated into sequences of moves, i.e. quasi-linear track segments at which the snail did not change direction. We used two segmentation methods: (i) a new approach that identifies direction reversals in single dimensions (1D method; (Humphries, Weimerskirch & Sims, 2014)) and (ii) a 2D technique extracting segments where the snail turns less than a certain threshold angle (Turchin, 1998). This threshold was selected to minimise the autocorrelation of stepwise directions (De Jager *et al.*, 2011), in our case 45 degrees. We determined and compared move length distributions of the two data sets, both for the tracks pooled by landscape and for each individual separately, forestalling that Lévy walks might be apparent from pooling the movement of animals that perform Brownian walks with typical move lengths of different sizes (Petrovskii, Mashanova & Jansen, 2011).

To additionally explore the influence of food encounter on move lengths, each of the two sets of distributions was split into moves (partly) within and (completely) outside of food patches. Each distribution was then fit to powerlaw, truncated powerlaw, exponential and hyperexponential (k=2 or k=3) distributions using maximum likelihood methods (Jansen, Mashanova & Petrovskii, 2012). We selected the best fit by means of Kolmogorov-Smirnov goodness of fit, G-Tests and Akaike weights (Clauset, Shalizi & Newman, 2009). From the 2D move lengths, characteristic scales s_i of hyperexponential distributions were calculated as $s_i = x_{min} + 1/\lambda_i$ (Jansen, Mashanova & Petrovskii, 2012) and compared to the mean free path (mean distance between two food patches) for each landscape type.

Before fitting, we determined the minimum and maximum value (x_{min}, x_{max}) for every set of move lengths. We calculated x_{min} by using a bilinear fit and selecting the change point, as has already been shown successfully (Franks *et al.*, 2010). For determining x_{max}, we applied statistical theory (Pueyo, 2003), depending on maximum likelihood estimation and confidence intervals.

For testing the inherent multi-scale walk concept that animals alternate small and large steps irrespective of the external environment, we calculated clusters of small steps (ARS clusters) from the original tracks and compared their properties between landscapes. We used the Brownian Bridge Kernel Method (BBKM) (Horne *et al.*, 2007; Sawyer & Kauffman, 2011), defining a regular grid for the landscapes (100 x 100 units, proportion of half arena size 300 mm to snail size 3 mm) in which the movement tracks were embedded and attributed a probability of animal presence to each cell (see Appendix). Each track was separated into positions within and outside of ARS clusters by selecting a cut-off probability outline (from the 25-80% outlines (Sawyer & Kauffman, 2011)) that maximised the difference between average turning angles in and outside of ARS clusters.

For each ARS cluster (shaped by ≥ 3 snail positions) we determined its maximum width (i.e. the maximum distance between any pair of two points of the cluster), area covered by the minimum convex polygon and time the snail spent in the cluster. The BBKM also detects clusters of slow, straight movement. To avoid considering these as ARS clusters, for any further analyses we excluded clusters for which the ratio of cluster area and cluster maximum width was below 0.2. Distributions of cluster sizes with and without encounter of food were fit to powerlaw, truncated powerlaw, exponential and hyperexponential distributions (similarly to move length distributions, see above).

To address the question whether mud snails alter their movement strategy at food encounter, we analysed their reorientation behaviour when they encountered and later left a food patch. We compared the distributions of turning angles of 2D moves between entry and exit of a food patch with randomly placed turns of similar temporal spacing.

Finally, we analysed the search efficiency of mud snails with a survival analysis (Kleinbaum & Klein, 2005) grouping the tracks of regular, random and fractal landscapes. The variable of interest was the estimated probability of encountering a food patch after leaving one; this was calculated as the inverse of time until food encounter. We only included encounters after a snail had the experience of food encounter to avoid bias due to different initial positions and
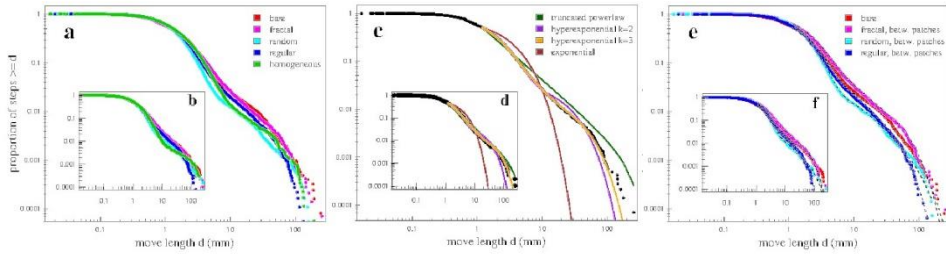
Figure 4.1: Cumulative move length distributions of mud snail tracks. From regularly sampled tracks, moves were determined as consecutive 2D track segments with turning angles of < 45° or as 1D direction reversals. (**a**) Pooled distributions of 2D move lengths and (**b**) 1D move lengths in x-axis direction (y-axis similar, not shown) of individuals foraging in five different landscapes, showing similar patterns. They point to an inherent multi-scale movement strategy, being only slightly modified by food encounters. (**c**) Pooled 2D and (**d**) 1D x-axis (y-axis similar, not shown) move length distribution of snails in the fractal landscape with maximum likelihood fits of exponential (simplest way of random movement), truncated powerlaw (indicating Lévy walks) and hyperexponential models (k = 2 and k = 3; recently proposed to stand for composite Brownian walks). The latter is favoured by AICs. (**e**) Pooled distributions of 2D and (**f**) 1D move lengths occurring only between food patches in four different landscapes. Dashed lines indicate the hyperexponential (k = 3) best fits to each of the distributions. Note that distributions did only slightly change shape compared to (**a**) and (**b**).

mean free paths in each of the landscapes. For each snail track we selected trajectory fragments that started when the snail had left a food patch and ended (i) at the subsequent encounter of either the same or another food patch, (ii) when the snail left the container, or (iii) when the experiment was terminated. The last fragment of each track is of type (ii) or (iii), therefore those segments were considered "censored data". This means that time until the next food encounter is assumed to be after leaving the container or after termination of the experiment, but unknown.

Results and Discussion

Fitting move length distributions

When accumulating the move lengths of all individual snails per landscape type, irrespective if obtained using the 1D or 2D method (summing to over 22,000 (1D) and 40,000 (2D) analysed displacements), move length distributions were similar between the landscapes (Fig. 4.1a, b) and clearly showed fat tails (i.e. a high

Table 4.1: Parameters and test statistics of (**a**) move length distributions (unit: mm) and (**b**) area sizes of ARS clusters outside of food patches (unit: mm^2), per landscape. x_{min} is the minimum move length/cluster size (obtained from a bilinear fit), w_{TPL} and w_{CBW3} are Akaike weights for the truncated powerlaw and hyperexponential fits with k=3. G and D are the goodness of fit statistics of the G-test and the Kolmogorov-Smirnov test; for the latter we provide a bootstrapped p-value. µ is the scaling exponent of the truncated powerlaw fit, OM is the order of magnitude over which this fit ranges, s_1, s_2 and s_3 are the characteristic scales of the exponential components of the hyperexponential distribution. Bold numbers indicate best fits; italics emphasize important scales and significant exponents. Fits to powerlaw, exponential and hyperexponential (k=2) distributions were included in the analysis, but not listed here, because of poor results.

	(a) Move length distributions				
	bare	**fractal**	**random**	**regular**	**complete**
x_{min}	1.1	1.1	1.2	1.3	1.2
w_{TPL}	0	0	0	0	0
G	-450	-494	-632	-575	-645
D (p)	0.099 (0)	0.097 (0)	0.080 (0)	0.089 (0)	0.099 (0)
µ	2.15	2.15	2.59	2.45	2.31
OM	2.44	2.44	2.51	2.09	2.31
w_{CBW3}	**1**	**1**	**1**	**1**	**1**
G	-63445	-69595	-89138	-80999	-90876
D (p)	0.011 (**0.10**)	0.014 (<0.01)	0.013 (<0.01)	0.030 (<0.01)	0.011 (<0.01)
scale 1	*2.63*	*2.59*	*2.25*	*2.53*	*2.59*
scale 2	13.89	6.87	10.69	7.14	5.94
scale 3	48.99	35.53	43.78	25.87	35.48
	(b) Cluster area size distributions				
x_{min}	2.4	32.9	6.9	6.1	
w_{TPL}	0.11	**0.96**	**0.8**	0	
G	-15	-1.3	-12.9	-11.7	
D (p)	0.099 (0)	0.091 (**0.19**)	0.073 (**0.09**)	0.122 (0)	
µ	1.5	*1.82*	*1.79*	1.63	
OM	4.22	2.16	3.31	2.4	
w_{CBW3}	**0.89**	0.02	0.1	**0.98**	
G	-5.04	-0.5	-5.79	-1646	
D (p)	0.028 (**0.64**)	0.042 (0.80)	0.031 (0.70)	0.029 (**0.87**)	
scale 1	*6.02*	67.22	11.93	*6.1*	
scale 2	*20.41*	172.12	28.19	*21.65*	
scale 3	759.19	2415.49	178.81	163.25	

frequency of long displacements), which is indicative for Lévy-like search behaviour. However, our statistical analyses showed that the composite movement model consisting of three exponentials (Fig. 4.1c-d, Tab. 4.1a) provided a superior fit over the other models, pointing at possible composite Brownian movement (Benhamou, 2007; Jansen, Mashanova & Petrovskii, 2012). Yet, very similar

composite exponential fits of the 2D move lengths, with similar characteristic scales (pairwise Wilcoxon-Tests p > 0.7; Tab. 4.1a) were obtained for both the patchy and homogeneous landscapes. This undermines the basic assumption of ARS models like composite Brownian walks that environmental triggers drive switches between alternate movement modes (Benhamou, 2007; Humphries *et al.*, 2010; Jansen, Mashanova & Petrovskii, 2012).

Moreover, the movement scales as obtained from the composite exponential fits (Tab. 4.1a) corresponded to snail size (2-3 mm), but did not match with any landscape features like the mean free path (regular: 78 mm, random: 88 mm, fractal: 155 mm). Thus, foraging strategies of mud snails seem to be inherently multi-scale and not solely determined by their environment. This goes into the direction of an earlier suggestion that multi-scale composite movement is an internal mechanism to approximate Lévy walks (De Jager *et al.*, 2012b; Reynolds, 2014).

Furthermore, if fitting truncated powerlaws to the data, powerlaw exponents were in the range typical for Lévy walks ($1.5 \leq \mu \leq 2.5$), irrespective of whether movement occurred on or outside of food patches (Tab. 4.1a, Fig. 4.1c-f; see Appendix). In the regular and random landscape, the scaling exponents were slightly larger ($2.4 \leq \mu \leq 2.6$), indicating that frequent food patch encounter truncated long moves (De Jager *et al.*, 2014). These results held true for both sets of move lengths distributions and also when we took individual variation in movement characteristics into account, i.e. analysed individual tracks separately (see Appendix). If contrasting exponentials with (truncated) powerlaws, the majority of individual tracks were best fit by a (truncated) powerlaw, but only for 45.7% of the individuals did the fit range over more than 1.5 orders of magnitude, allowing doubt about this method to infer strict Lévy search properties. Hence, the results of classical statistical analysis of move length distributions remained inconclusive and are open to different explanations, similar to what is found in other studies in animal search theory (Edwards, 2011; Jansen, Mashanova & Petrovskii, 2012).
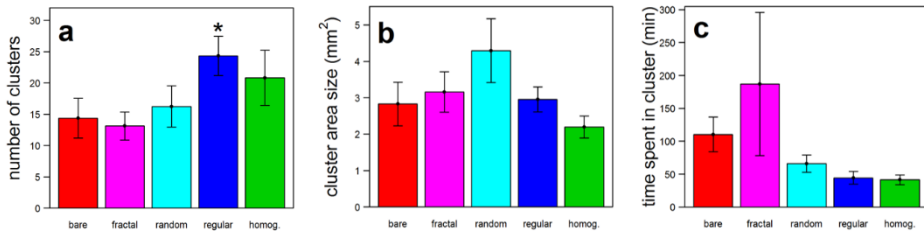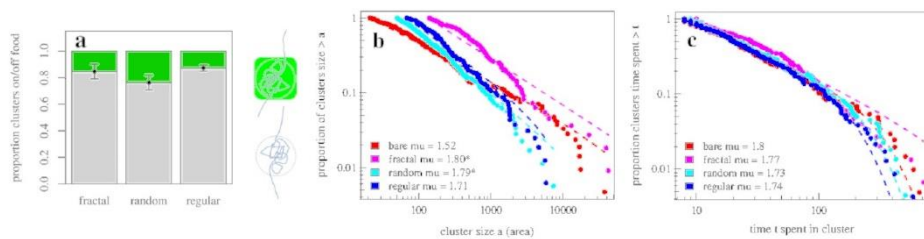
Figure 4.2: Cluster analysis results compared among the five experimental landscapes. (**a**) The average number of ARS clusters of individual tracks (±SE) is significantly larger for the regular landscape (Wilcoxon Tests, p < 0.05). In all other landscapes, snails produced similar numbers of ARS clusters, indicating that ARS cluster movement was not only initiated by food encounter. (**b**) Average cluster area sizes and (**c**) time intervals spent in the clusters for each individual (±SE) reveal no significant differences among the landscapes.

Area restricted search clustering

Comparisons of the average degree of clustering between the homogeneous and patterned experimental landscapes revealed only minor differences in the number of ARS clusters and no differences in the size of these clusters and the time spent within them (Fig. 4.2), indicating that animals alternate intensive-extensive search behaviour irrespective of landscape features.

Strikingly, we found strong ARS clustering behaviour in both the homogeneous landscapes and in the bare areas of the patterned landscapes (Fig. 4.3a), strongly suggesting that the observed alternation reflects inherent behaviour of the snails, and therefore providing indications for intrinsic multi-scale search behaviour. On average, as much as 87-89% of ARS clusters in the random, regular and fractal landscapes were observed outside of food patches. Numbers are similar for time spent in search clusters outside of food (68-76%). Moreover, in the fractal and random landscapes, the size distribution of the ARS clusters outside of food patches was well described by a powerlaw ($\mu = 1.8$; Fig. 4.3b, Tab. 4.1b), which is again a clear signature of Lévy-like search behaviour (Mandelbrodt, 1983). Also time spent in ARS clusters without food encounter was distributed with heavy tails in all landscapes (Fig 4.3c), providing a direct parallel to earlier studies on intrinsic, multi-scale timing of search tasks (Maye *et al.*, 2007). Hence, we observed a large number of size- and time-diverse ARS clusters away from food patches, providing

Figure 4.3: Cluster analysis results in relation to food encounter. (**a**) Proportion of ARS clusters on bare mud (grey) and food patches (green); see examples of search clusters on the right. Error bars are standard errors of the proportion of clusters on bare mud. (**b**) Cumulative inter-patch (i.e. off-food) cluster size distributions (tail) grouped by landscape type. Dashed lines indicate the best fit to each data set; hyperexponential (k = 3) for the bare and regular landscapes and truncated powerlaw for the fractal and random landscapes. (**c**) Cumulative distributions (tail) of time spent in inter-patch ARS clusters grouped by landscape. Dashed lines are best fit hyperexponentials (k = 3) for all landscapes. Powerlaw scaling exponents are provided for all distributions; asterisks (only in **b**) indicate distributions for which powerlaw fits were superior to hyperexponentials.

clear experimental evidence that the observed movement behaviour is inherent behaviour for our snails.

Reaction to food encounter

Our observations that snails form search clusters away from food prompts the question whether they at all change their movement behaviour when encountering food patches. Despite of the prominence of ARS clusters outside of food patches, we found that > 90% of the encounters with food coincided with the start of an ARS cluster, clearly suggesting behavioural changes when animals encounter a food patch. Thus, snails seem to initiate local search both in the absence of food and in response to food encounter.

Additional analyses of patch arrival and departure directions showed that snails also often change search direction after exploiting food patches (Fig. 4.4). Turning angles between entry and exit of a food patch were centred on 180°, indicating that snails often reverse search direction within a food patch, exiting at a position not far from its entry point. On the contrary, turning angles (with an absolute value) below 90° appeared less frequently than at random, suggesting that at food encounter the previous course is lost. By strong turning behaviour, snails
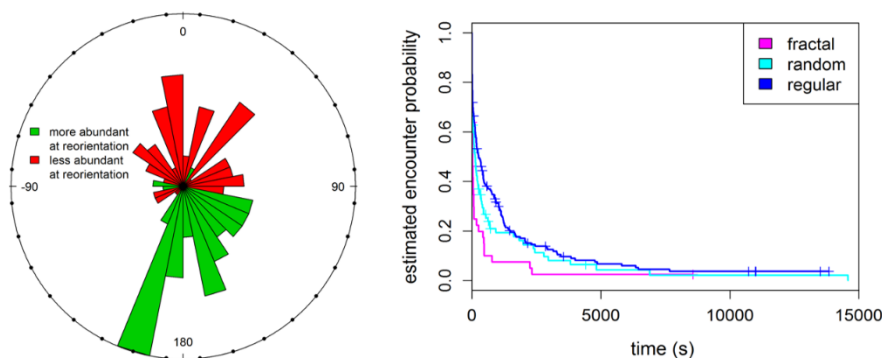
Figures 4.4 (left): Reorientation at food encounter. Differences of abundances of turning angles between directions at food patch entry and exit and random turning angles of similar time lags. Green indicates that at food encounter the respective turning angles are more abundant than random, whereas red indicates that at the encounter of food patches the angles are less abundant than random. This distribution differs significantly from a uniform distribution (Kolmogorov-Smirnov-Test, D=0.51, p<0.001).

Figure 4.5 (right): Survival curves representing the estimated proportion of individuals that have not encountered a food patch, yet, for the regular (green), random (blue) and fractal (black) landscapes. Landscape type significantly affects time to first encounter (Cox's proportional hazards model with covariates, LR=13.4, p=0.001).

may try to exploit the food patch they just found (Bell, 1991). These results indicate that snails, similarly to many other animals (Weimerskirch *et al.*, 2007), react to the presence of food patches by initiating area-restricted search, obviously trying to exploit them (Turchin, 1998). Thus, our results indicate that encounters with food - characteristic of the composite Brownian walks hypothesis - as well as internal triggers – characteristic of intrinsic multi-scale search behaviour - can initiate local, area-restricted search in the mud snails. The relative importance of each process depends on the density and spatial distribution of food patches.

Search efficiency

Ecological theory proposes that Lévy walks are an evolutionary adaption of naïve foragers to optimise food encounter in specific target heterogeneous conditions (Bartumeus *et al.*, 2002; Humphries *et al.*, 2010). Our test of this hypothesis by using empirical survival functions of search efficiency (Fig. 4.5) showed that the time it took a snail to find food was affected by the food distribution, i.e. landscape

type (Cox's proportional hazards model with covariates, likelihood ratio = 13.4, df = 2, N = 334, p = 0.0012, Bonferroni corrected threshold p < 0.016). Snails moving on fractally distributed food encountered patches faster than snails searching for regularly distributed food patches (z = 3.8, p < 0.016), revealing that the search efficiency of snails was highest in the experimental landscape most closely resembling their natural habitat (Seuront & Spilmont, 2002). Hence, our results suggest that multi-scale movement is not only the inherent search strategy for mud snails, but also the most efficient for finding food in the snails' native habitat configuration.

General Discussion

In this work, we have put forward and applied a new experimental approach to test for the presence of inherent Lévy-like, multi-scale search behaviour, using mud snails that move as uninformed searchers in artificial landscapes and exposing them to different types of spatial food distributions. In all of our experiments, even in homogeneous landscapes, composite models consisting of multiple exponentials provided the best fit to the overall movement, being superior to the fits provided by (truncated) Lévy walks. At first glance, this result supports the composite Brownian walk hypothesis (Benhamou, 2007), which explains long-tailed movement patterns by an alternation of Brownian movement modes triggered by external cues, such as food encounter or other environmental heterogeneity (Boyer *et al.*, 2006; Humphries *et al.*, 2010). However, the general insensitivity of estimated parameters to the differing landscape features, in combination with the observation of clusters of area-restricted search in homogeneous landscapes, contradicts this explanation. Close inspection of the search characteristics of mud snails in controlled landscapes revealed clear signatures of Lévy search behaviour: clusters of area-restricted search were found in the (controlled) absence of food encounter, and the clusters followed a powerlaw size distribution. Thus, mud snails inherently switched between long-distance movement and area restricted search, which reflects a multi-scale search strategy that is not solely triggered by the landscape.

Our finding of inherent complex movement strategies in mud snails is an important addition to the recent set of studies that aim at understanding the processes underlying multi-scale search patterns (Hays *et al.*, 2006; Maye *et al.*,

2007; Proekt *et al.*, 2012; Sims *et al.*, 2012; Stumpf & Porter, 2012; Seuront & Stanley, 2014). Similar to most of those studies, the timing of ARS clustering in mud snails showed multi-scale search behaviour also in a homogeneous environment, implying intrinsic behavioural control (Maye *et al.*, 2007; Proekt *et al.*, 2012; Reynolds, Lepretre & Bohan, 2013). Because of our novel experimental setup we could also demonstrate spatial multi-scale foraging behaviour in the absence of food encounter (Pyke, 2014). Hence, and in accordance with other studies on search movement patterns in the absence of chemical cues (Seuront & Stanley, 2014), Lévy or more general multi-scale movement can be an intrinsic strategy of searching animals, and does not require landscape heterogeneity or other external triggers as explanation.

Still, our results do not contradict the classical perspective on movement ecology where animals respond to environmental cues to make foraging decisions (Pyke, 1984). Search strategies are per definition affected by encounters, as was shown in our study by the high percentage of food encounters coinciding with ARS clusters. Thus, observed movement patterns were modified by step truncation and increased turning. Analogously, we observed that in the regular and random landscapes, where encounter rates were highest, the Lévy exponent was increased relative to the bare and fractal landscapes to approach values that are more akin to Brownian motion. Thus, our findings contradict the hypothesis that long-tailed move length distributions are solely explained by animals adjusting their movement in response to food encounter or changing habitat characteristics (Boyer *et al.*, 2006; Benhamou, 2007; Humphries *et al.*, 2010). Instead, we find support for the earlier stated opposite hypothesis that Brownian motion may emerge from the interplay between inherent Lévy search behaviour and ecological encounters, such as consumption or interference, that lead to step truncations, especially in resource rich or dense communities where ecological encounters are plenty (De Jager *et al.*, 2014; Reynolds, 2014).

The result that mud snails were most efficient in finding food in fractal landscapes concurs well with the insight that diatoms are fractally distributed in the natural habitat of our mud snails (Seuront & Spilmont., 2002; Weerman *et al.*, 2012). However, still the animals were performing the same strategy in the other

landscapes. Thus, these animals seem to have inherently followed a search strategy that is adapted to their environment, but likely robust enough to cope with other conditions, where e.g. food is distributed more homogeneously (Bartumeus & Levin, 2008; Raposo *et al.*, 2011; De Jager *et al.*, 2014). This insight supports the notion that Lévy and other multi-scale walks might be an evolutionary adaptation that provides a survival advantage if the environment is highly diverse (Raichlen *et al.*, 2014) or changes (Sims *et al.*, 2014).

One of our most striking findings is that the sizes of clusters of area-restricted search can be described by powerlaws. To make sure that this is a valid conclusion for our data we simulated tracks from truncated Lévy walks as well as composite Brownian motion and determined their cluster size distribution (see Appendix). The outcomes confirmed that powerlaw cluster size distributions are characteristic of Lévy walks. Cluster size distributions of composite Brownian motion were, on the contrary, best fitted by hyperexponentials. When disregarding fit quality, it was striking to see that we could fit any of the two simulated distributions (where parameters of our data set had been used) with either a powerlaw or a composite Brownian model with similar parameters: (i) scaling exponents (μ = 1.68 for the simulated Lévy and μ = 1.71 for the simulated composite Brownian motion) and (ii) hyperexponential parameters (s_1 = 52 mm^2, s_2=128 mm^2 and s_3 =503 mm^2 for the simulated Lévy and s_1 = 36 mm^2, s_2 = 91 mm^2 and s_3 = 538 mm^2 for the simulated composite Brownian motion). This indicates how very similar Lévy walks and composite Brownian walks are in supporting the concept of general multi-scale search behaviour, especially if composite Brownian walk parameters are carefully tuned (Reynolds, 2013). Thus, we must be especially careful to not only fit distributions but, like we attempted, to find other means to test movement behavioural hypotheses (Stumpf & Porter, 2012; Reynolds, 2012).

Our investigation does not allow to directly address the question about the underlying inherent process producing the multi-scale behaviour we found in our snails. The animals might follow an internal mechanism that approximates a theoretically ideal, random search process (e.g. the Lévy walk) (Reynolds, 2005; Reynolds & Bartumeus, 2009; De Jager *et al.*, 2011; De Jager *et al.*, 2012b; Raichlen

et al., 2014) and that was carefully fine-tuned (see also simulations above) as an adaptation to optimise search strategies (Reynolds, 2013; Reynolds, 2014). It was suggested that nonlinear processes in the brain might provide such a movement mechanism (Maye *et al.*, 2007) and that inherent, characteristic macroscopic scales might govern them (Proekt *et al.*, 2012). The latter is likely to exist for mud snails, because characteristic scales of the composite Brownian fits were similar for all landscapes; one scale even related to average snail body size. Another suggested mechanism, self-avoidance by inherent cueing (Sims *et al.*, 2014), seems not to apply here, as tracks often overlapped, especially in ARS clusters.

The mud snails in this study alternated long moves with clusters of short moves and frequent turns even in the absence of external triggers such as food encounters. Alternations between movement modes of different scales in the absence of external triggers can be considered as a signature for inherent Lévy type search strategies. Here we view multi-scale search behaviour as a general movement strategy where the animal intrinsically alternates movement steps of different sizes, not in the mathematical sense of an observed precise power-law movement step distribution. To make a distinction between strict Lévy walks and biological implementations of Lévy-like patterns that are generated with different types of heavy-tailed distributions (Pyke, 2014; Bartumeus *et al.*, 2014) and capable to optimise search, we propose for the latter to use the term "multi-scale search behaviour". In conclusion, our experiments provide an intriguing perspective on the behavioural processes that underlie search in foraging animals and shows new routes to explore the search problem combining adequate experimental setups with simple quantitative approaches.

Appendix: Supplementary Methods & Figures

Cognitive performance

Before the main set of experiments, we tested the assumption of limited cognitive performance for our system, examining how much information about their surroundings mud snails use. In a container with mud we regularly placed 9 mesh cells with diatoms. As antennae are the snails' main sensory organ (Haubois *et al.*, 2005), we placed snails at four different distances to a food patch based on antenna size (2 - 3 mm): 1, 3, 5 and 10 mm (see Fig. 4.6). Then, we observed the snails for one hour, determining how many of them found the food patch and how directed their movement was. We used three replicate containers, in total observing 80 snails (20 per initial distance), and computed the proportion of snails hitting the patch with the direction they originally chose. Each snail was starved for one hour before the
experiment.

Numbers of snails that encountered the food patch within the hour were compared to a random model that relied on simple geometrics and assumed that snails either encounter the food patch in a straight line or not. The expected proportion of snails finding food was $v = \arctan(7.5 / d) / \pi$, with d being the distance the snail was placed from the food patch.

The experiments revealed that mud snails acted as uninformed searchers. We found that the probability of finding a food patch strongly decreased with distance (Proportions test, $\chi^2 = 16.6$, df = 4, p=0.002). When splitting the data by distance, the proportions test showed significant differences from random encounter for d=1 mm (80% success, p=0.004) and d=3 mm (65% success, p=0.023), but not for d=5 mm (40% success, p=0.55) and d=10 mm (25% success, p=0.06). This suggests that the snails' response to food is within 3 and 5 mm, possibly related to the antenna size (~3 mm). The limited response range of the mud snails underlines their suitability for our experiments on random search behaviour.
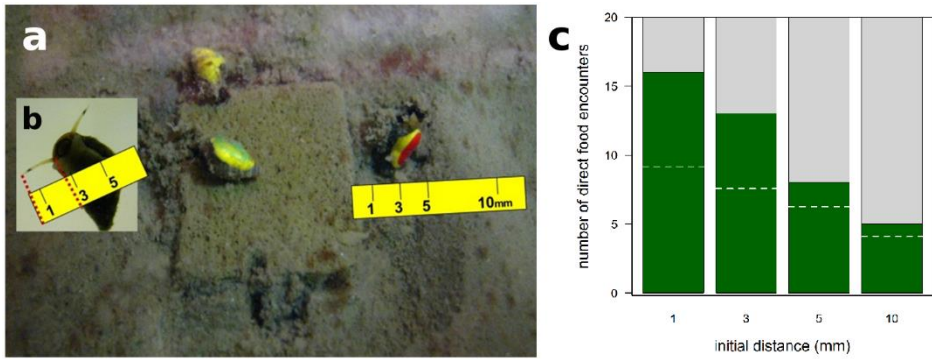
Figure 4.6: Setup and results of the cognitive performance experiment. (**a**) On each side of a square food patch snails were placed in a distance of 1, 3, 5, or 10 mm, respectively. (**b**) A mud snail and its antennae length. (**c**) Number of snails out of the 20 snails per initial distance that reached the food patch directly (green bars). The white, dotted lines are the expected numbers of the random model (see main text).
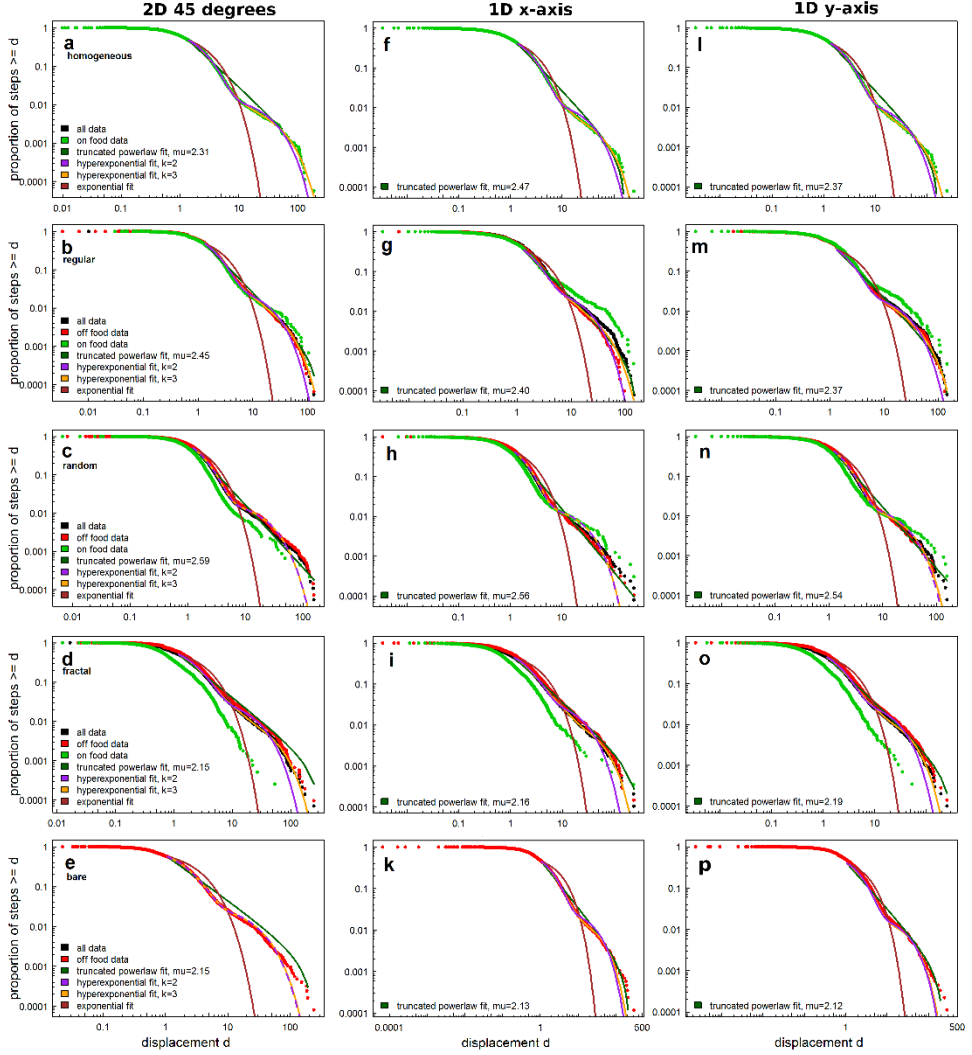
Experimental landscapes
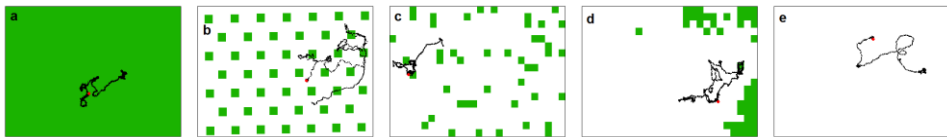
Figure 4.7: Different landscape patterns with the track of one snail. The red dot indicates the starting position. (**a**) Sediment fully covered with diatoms, (**b**) "regular" landscape, (**c**) "random" landscape, (**d**) "fractal" landscape, (**e**) bare mud.

Pooled distribution fits

Figure 4.8: Pooled move length distributions (in mm; black dots) for (**a-e**) the 2D segmentation method with 45 degree threshold, (**f-k**) the x-axis displacements and (**l-p**) the y-axis displacements of the 1D segmentation method (see main text). The displacements are of tracks in the homogeneous (**a,f,l**), regular (**b,g,m**), random (**c,h,n**), fractal (**d.i.o**) and bare (**e,k,p**) landscape. The dark green, purple, yellow and brown lines indicate the truncated power law, hyperexponential (k = 2), hyperexponential (k = 3) and exponential fits. Powerlaw exponents are provided, even if hyperexponential (k = 3) is the best fit for all distributions. Note also the distributions of lengths of moves within (green dots) and outside of foot patches (red dots) that overlay the black dots in the bare and homogeneous landscapes.

Individual distribution fits

It can be argued that pooled move length distributions might appear as power laws due to individual variation in movement characteristics. We tested for this possibility by analysing each individual track separately, again using the 2D and 1D segmentation methods in parallel to determine moves (see main text). However, we considered it not sensible to fit hyperexponential distributions here, because of the small amount of data. Therefore, we compared (truncated) power law and exponential fits.

Independently of the segmentation method, the majority of tracks (54-87%) were most compliant with truncated Lévy walks, especially in the fractal landscape (see Table 4.2). Thus, individual mud snail movement can clearly be long tailed (i.e. contains many long distance displacements) and multi-scale. Note that the move distributions extracted with the 2D method is more conservative than the 1D method, as more tracks are fitted by exponentials.

Tracks that were best fit by a (truncated) power law showed similar exponents, the mean power law exponents corresponding to those of the fits to the pooled data sets. Individual variation in exponents, however, is great and a considerable proportion of snail trajectories are best fit by exponential move length distributions (100 - %PLbest fit, see Table 4.2b). For each landscape We provide a selection of tracks and their move length distributions (Fig. 4.9); the individuals were selected for longer, robust tracks (track length was not related to the fit) and a variability of fits as present in the whole data set.

Table 4.2: Properties of the pooled move length distributions for each landscape. (**a**) Numbers of individual tracks used for each landscape (# idv tracks) and number of moves (# moves) pooled over those 116 longer individual tracks in the respective landscape. We provide the minimum and maximum move length (all in mm), x_{min} and x_{max}, obtained by optimisation and used for the fits. $\tilde{x}$ is the median move length. (**b**) $\bar{\mu}_{idv}$ indicates the mean (truncated) power law exponent of move length distributions of individual tracks per landscape. The percentage of individual tracks for which the truncated power law was the best fit is given by *% TPL best fit.* These values can be compared with Table 4.1 in the main text.

Landscape	Bare	Fractal	Random	Regular	Homogeneous
(a) # idv tracks	22	24	26	24	20
# moves	6741	7815	9281	8703	9957
x_{min}	1.1	1.2	1.2	1.3	1.4
x_{max}	230.5	335.5	1539.9	165.3	168.3
median x	2.2	2.3	2.0	2.3	2.4
(b) mean μ	2.26	2.45	2.61	2.65	2.45
% TPL best fit	59.1	66.7	65.4	54.2	45.0

Table 4.3: Comparison results of individual best fits of move length distributions extracted with the 1D method (x-axis as well as y-axis) and 2D method (threshold 45 degrees). (**a**) Numbers of tracks that show the same best fit model for the x-axis and y-axis distribution of the 1D method. Theoretical results have shown earlier that they should be identical (Humphries *et al.* 2014). This is the case in 83.6% of the cases. (**b**) and (**c**) show a comparison of the number of individual tracks with the same best fit for the 2D method and one of the 1D method distributions. They coincide in 72.4% and 83.6% of the cases, respectively. Note that for most cases with different results, the 2D method is more conservative, showing exponential fits rather than powerlaws.

a		1D y-axis	
		Powerlaw	Exponential
1D x-axis	Powerlaw	76	13
	Exponential	6	21
b		**2D 45 degree**	
		Powerlaw	Exponential
1D x-axis	Powerlaw	64	25
	Exponential	7	20
c		**2D 45 degree**	
		Powerlaw	Exponential
1D y-axis	Powerlaw	67	15
	Exponential	4	30
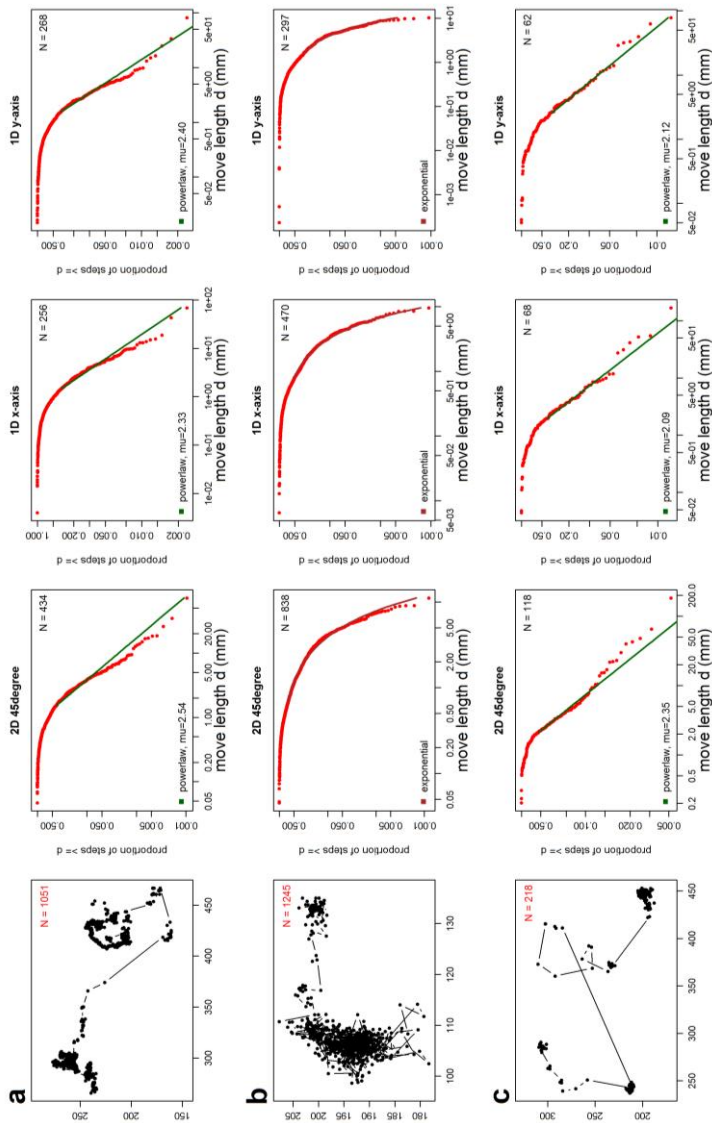
Figure 4.9: Movement tracks (left) and move length distributions (in mm; right, black dots) of three single individuals each in the five different landscapes: bare (**a-c**), fractal (**d-f**), random (**g-i**), regular (**k-m**) and homogeneous (**n-p**). In the movement tracks food encounters are noted as green dots. For each presented track we show the 2D move distribution as well as the 1D x-axis and y-axis distributions (see main text); note their similarity. In each distribution we provide the best fit (exponential or (truncated) powerlaw), and add the distribution of moves on food (green dots) and away from food patches (red dots).
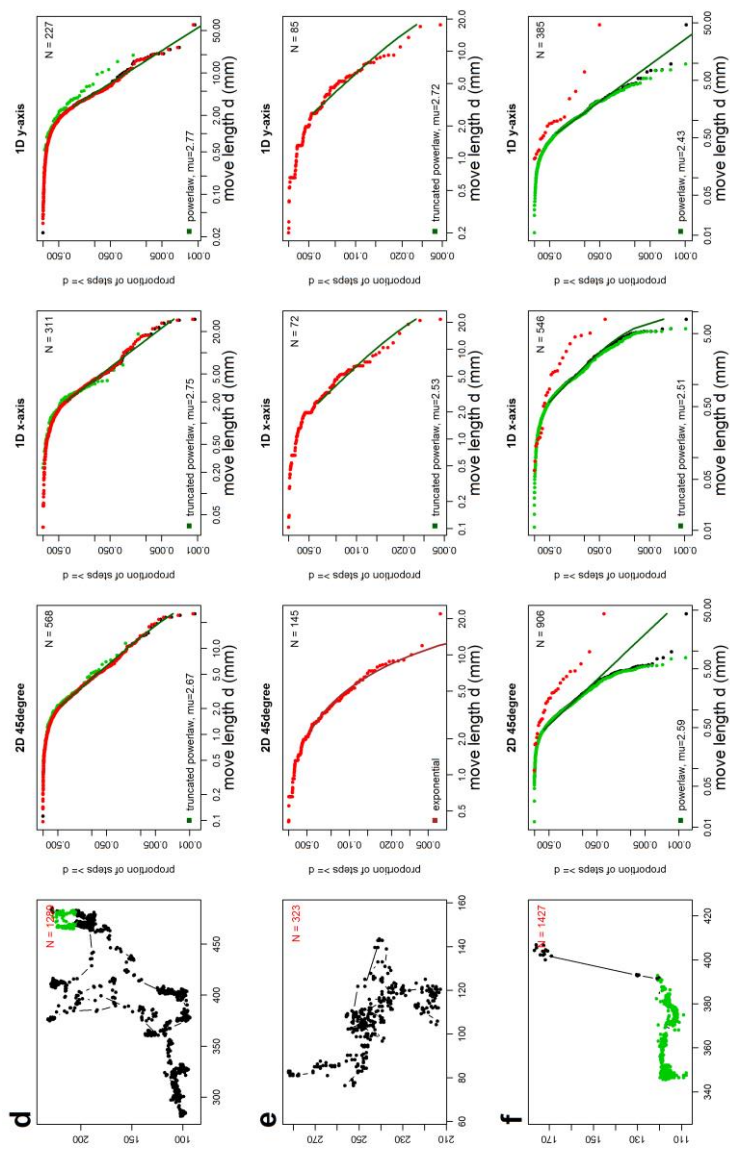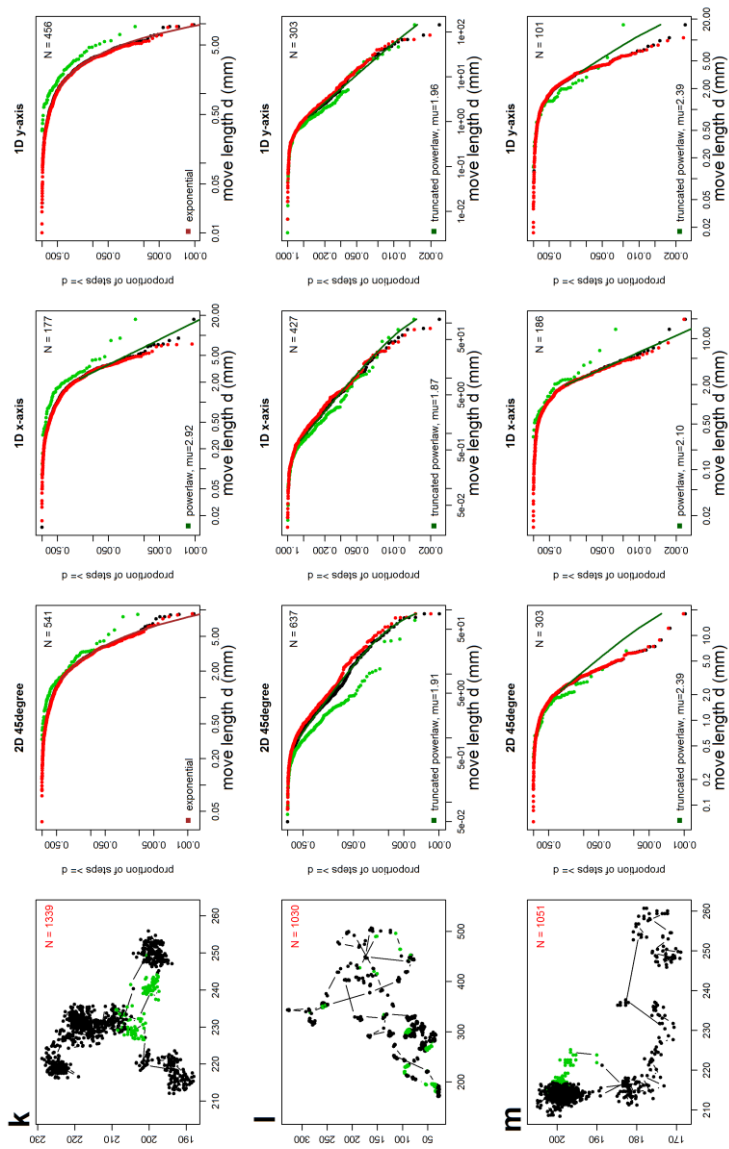
Figure 4.9 contiunued.
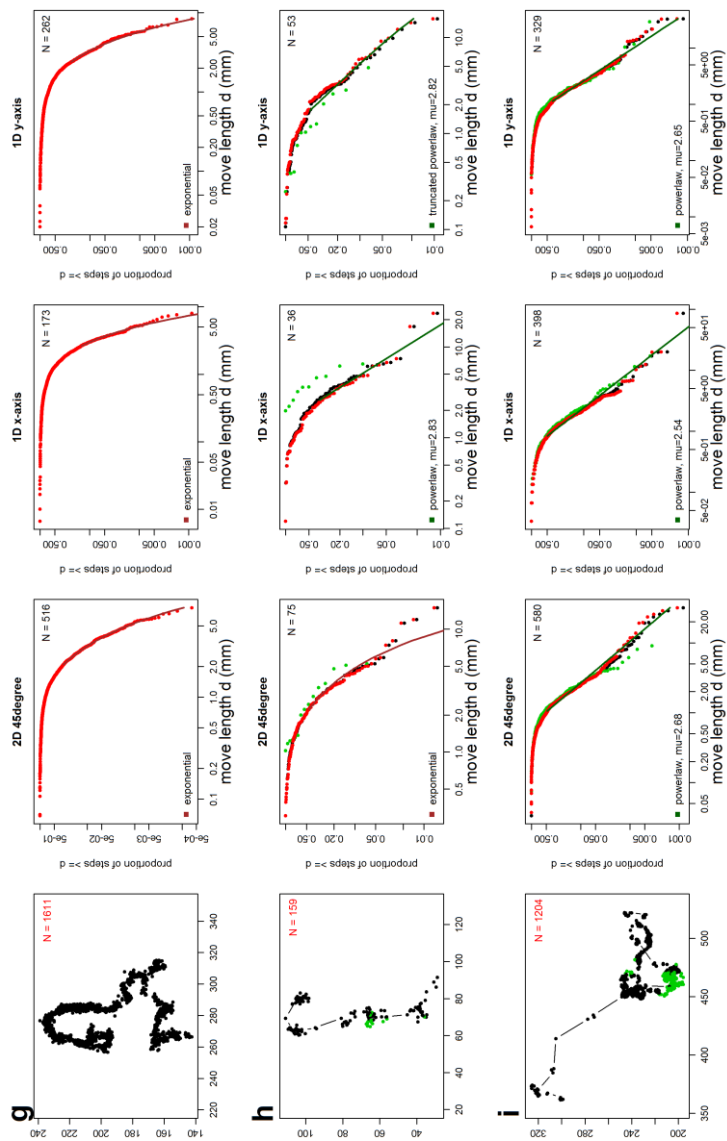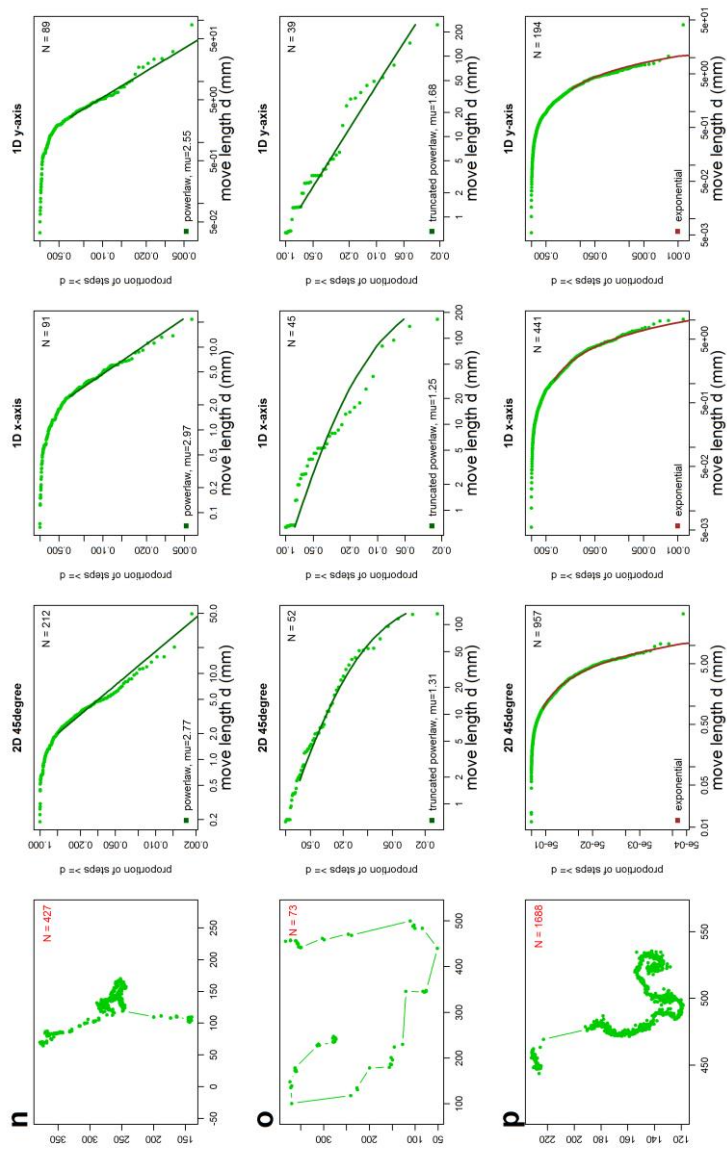
Figure 4.9 continued.

Figure 4.9 continued.

Figure 4.9 continued.

Tracks of unpainted snails

In a preliminary analysis we have followed three snails without paint (nail polish) marking, to get an idea of a possible effect of the paint on snail movement patterns. Their tracks and move length distributions (see Fig. 4.10) indicate that the snails with and without paint treatment move similarly. We did not perform a comparative test, because the power of the test would be low (i.e., large probability for a type II error); in other words, failure to reject the null hypothesis (of no difference in movement patterns between painted and unpainted snails) would anyhow not convincingly indicate that it was valid. However, all the snails in our main trials are treated similarly and are thus comparable. How far their behaviour is generalizable to wild snails is not the main point here and remains to be further analyzed in a follow-up study.
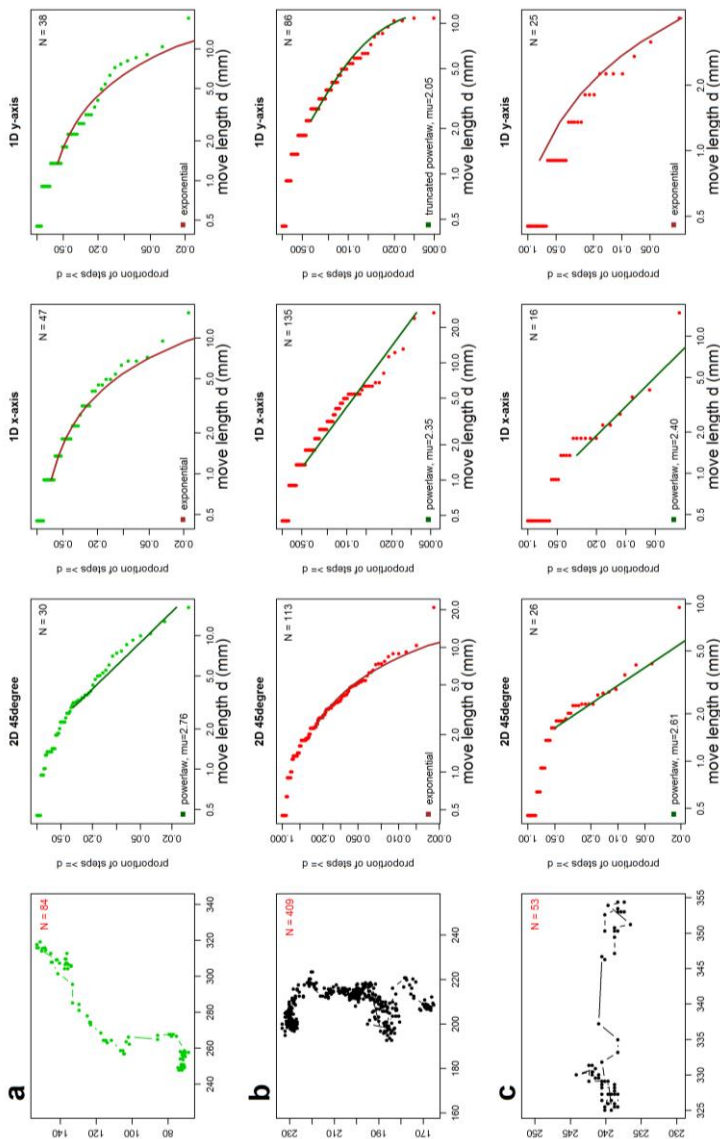
Figure 4.10: Movement tracks (left) and move length distributions (in mm; right, black dots) of three single individuals without paint in the homogeneous landscapes: homogeneous (**a**) and bare (**b,c**). In the movement tracks food encounters are noted as green dots. For each presented track we show the 2D move distribution as well as the 1D x-axis and y-axis distributions (see main text); note their similarity. In each distribution we provide the best fit (exponential or (truncated) powerlaw), and add the distribution of moves on food (green dots) and away from food patches (red dots). Compare with Figure 4.9.

Figure 4.11: Concept of the determination of local search clusters with the Brownian Bridge Kernel Method. (**a**) Movement track of one snail. (**b**) Brownian Bridge probability/density of the track (red-yellow-white gradient: high - low density, grey: zero density) and the selected 68% region of local search clusters. (**c**) Snail positions derived to local search (green dots) and global search (blue dots).

Clusters of simulated tracks

To confirm that cluster size distributions created by our BBKM algorithm (in line with the "Levy dust" concept) indeed are an indicator for Lévy walks and how they differ from composite Brownian walks, we evaluated the algorithm.

Using the Lévy exponent that was fit to the move length distribution of steps outside of food patches on the fractal landscape (µ =2.19) we simulated 100 walks, each of length 2000 (according to our data) with random turning angles. To test if cluster sizes deviate if created by a composite Brownian walk, we simulated 100 such walks using the parameters that had been fit to the moves without food encounter on the fractal landscape.

From both sets of tracks we calculated local search cluster size areas (see above). Results revealed that local search cluster size distributions of the simulated truncated Lévy walks are best fit by a truncated power law (Figure 4.12a; w_{TPL} = 1). This is in accordance with conclusions from data analysis and the "Lévy dust" idea. The power law exponent is only somewhat smaller than that estimated from the data set.

On the other hand, the cluster size distribution of the simulated Composite Brownian walks follows a hyperexponential distribution (Figure 4.12b; w_{CBW3} = 1). This is not in accordance to the data, but indicates how very similar Lévy walks and
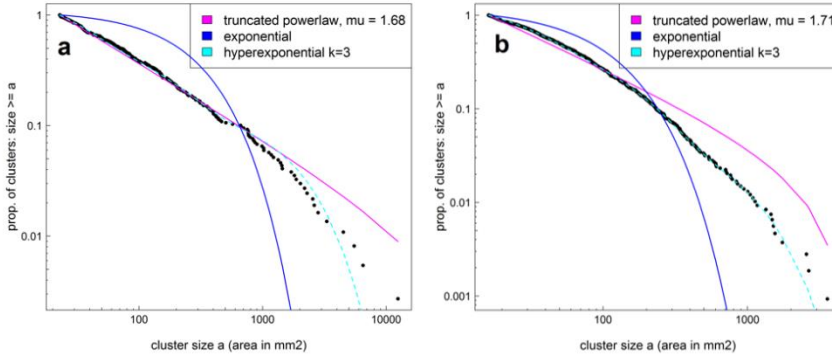
Figure 4.12: Cluster results of data simulated using parameters as fit to the distribution of move lengths that do not incorporate food encounter in the fractal landscape. (**a**) Cumulative distribution of cluster sizes (in mm²; black dots) in terms of minimum convex polygon area, determined from data simulated from a truncated powerlaw with $\mu = 2.19$. Lines indicate exponential (blue line), truncated power law (pink) and hyperexponential with three terms (light blue) fits. In terms of maximum likelihood, the truncated powerlaw is the best fit. (**b**) Distribution of cluster sizes calculated from sample data set determined from a hyperexponential distribution with parameters: $p_1=0.119$, $p_2=0.035$, $\lambda_1=0.471$, $\lambda_2=0.085$, $\lambda_3=1.955$. In this case a hyperexponential is the best fit.

composite Brownian walks are. Thus, the concept of multi-scale search behaviour to approximate the optimal Lévy search is supported.

It is striking that both simulated data sets' cluster size distributions are fit with (i) truncated power laws of similar scaling exponents (see Figure 4.11) and (ii) hyperexponentials of almost the same scales (s_1=38 mm², s_2=120mm² and s_3=1000mm₂). The first scale s_1 may be related to snail size or turning behaviour, but the others have no connection to measures of the experiment. Thus, we propose them to be intrinsic scales that are optimal for the given landscape conditions.

5

Why mussels stick together:

self-organization affects the evolution of cooperation

Monique de Jager, Franz J. Weissing & Johan van de Koppel

Abstract

Cooperation is an important driver for the persistence of populations in stressful environments. Yet, when neighbouring individuals provide sufficient help, less cooperative individuals may profit from their behavior and invade in the population. Using self-organizing mussels as our model template, we show that active aggregation into spatially structured populations can affect the evolution of cooperativeness. Using an individual-based model of mussel bed pattern formation, we demonstrate that active movement into the labyrinth-like patterns that we observe in natural mussel beds results in populations where individuals have an intermediate number of neighbours within cooperation distance. With an evolutionary model we then show that this intermediate number of neighbours can maximize the investment in between-mussel attachments in the population. Our results suggest that active movement of organisms into spatially structured populations can affect the evolution of cooperativeness.

Introduction

Cooperation between neighbouring individuals is often essential for survival in stressful environments (Bertness & Callaway, 1994; Callaway & Walker 1997; Holmgren et al., 1997; Stachowicz, 2001). Organisms ameliorate their environment locally, for instance by providing shade or by drawing moisture and nutrients towards themselves and close neighbours (Schlesinger et al., 1996; Aguiar & Sala, 1999), which allows others to survive in an otherwise hostile world. To what extent cooperation evolves in a population seems to depend on the nature and intensity of interactions between individuals (Doebeli & Hauert, 2005; West, Griffin, & Gardner, 2007; Van Dyken & Wade, 2012). When cooperation is costly and the recipients can reap the benefits of cooperation without helping others in return, cooperation by neighbouring organisms can be exploited by less cooperative individuals; an individual that profits from its neighbours' cooperative behaviour can afford to invest less in cooperation itself. The number of cooperating neighbours an individual has likely determines the effectiveness of its cooperation strategy and may affect the degree of cooperativeness that evolves within a population (Vainstein & Arenzon, 2001; Zhang et al., 2005; Ohtsuki et al., 2006; Hui & McGeoch, 2007).

Systems as diverse as mussel beds, coral reefs, marsh tussocks, tidal wetlands, peat lands, arid ecosystems, and ribbon forests are highly structured in space due to the interplay between local facilitation and long-range inhibition, for instance by depletion of nutrients (Klausmeier, 1999; Mistr & Bercovici, 2003; Rietkerk et al., 2004a; Rietkerk et al., 2004b; Van de Koppel et al., 2005; Van de Koppel & Crain, 2006; Rietkerk & Van de Koppel, 2008; Van de Koppel et al., 2008; Eppinga et al., 2009). In these systems, the number of potentially cooperating neighbours depends on the spatial scale and distribution pattern of the population. In many systems, the spatial pattern results from the active movement of organisms (Theraulaz et al., 2003; Jeanson et al., 2005; Hemelrijk & Hildenbrandt, 2012; Van de Koppel et al., 2008; De Jager et al., 2011). Accordingly, the movement strategies of these organisms can indirectly affect the number of neighbours an individual will encounter. In situations where costs and benefits of facilitation depend on the availability and density of local neighbours, the movement strategy

therefore affects the evolution of facilitation. It is, however, unknown under what circumstances movement promotes or hampers the evolution of cooperation.

An example of active pattern formation can be found in intertidal mussel beds. Mussels self-organize into large-scale labyrinth-like patterns (Van de Koppel et al., 2005; Van de Koppel et al., 2008). They use their foot to aggregate into a group of conspecifics after wide dispersion by the currents during the larval stage (Maas Geesteranus, 1942). When aggregated, mussels facilitate each other by attaching byssus threads (a glue-like substance) to the shells of conspecifics that are within reach. These attachments decrease dislodgement chance and predation risk for both the attaching mussel and the one receiving the byssus thread (Hunt & Scheibling 2001; Hunt & Scheibling 2002). Mussels that are sufficiently affixed by neighbours do not need to create attachments themselves and can therefore profit from having a lower level of cooperativeness. Through active aggregation into mussel clumps with various densities, mussels can modify the number of neighbours within their attachment range. By self-organizing into the labyrinth-like patterns that are characteristic for intertidal mussel beds, mussels attain an intermediate number of neighbours, which lies between the few neighbours within attachment distance in scattered distributions and many neighbours in dense mussel clumps.

In this paper, three questions regarding cooperation in mussel beds will be addressed. First, we investigate how the aggregation strategy of mussels affects the spatial pattern and, in particular, the number of neighbours available for cooperation. Aggregation in mussels typically leads to the formation of a spatial pattern consisting of regularly spaced strings and clumps (Van de Koppel *et al.*, 2005; Van de Koppel *et al.*, 2008). This self-organized pattern is likely related to the number of neighbours that mussels experience, ranging from few neighbours in scattered distributions to many neighbours in dense clumps. We tested this hypothesis using an individual-based model (IBM; de Jager *et al.*, 2011; de Jager *et al.*, 2014). Second, we examine how the number of neighbours affects the evolutionarily stable degree of cooperativeness with an adaptive dynamics approach (Geritz et al., 1998). Here, cooperativeness corresponds to the tendency of attaching byssus threads to neighbours (e.g. the 'attachment tendency'). Building

on the fundamental assumption that the spatial pattern relates to the average number of neighbours that a mussel can attach its byssus threads to, investigating how the number of neighbours affects the evolution of the attachment tendency of mussels gives us insight into whether and how aggregation strategies promote or hamper cooperation. Third, we study the effect of harshness of the environment, which is likely to influence the results of our evolutionary model. How well a mussel is attached to its neighbours influences its survival under stressful conditions. We examine the evolution of between-mussel cooperation over a range of environmental conditions. Furthermore, we take into account that environmental stress likely differs substantially between generations, which may further affect evolutionary processes.

Methods

An individual-based model of self-organized patterning

We modelled the effect of individual aggregation strategies (the 'settlement threshold') on the formation of mussel beds with an individual-based model (IBM). The self-organized pattern in mussel beds is a compromise between reducing wave stress and predation risk (requiring dense aggregations) on the one hand and minimizing food competition (requiring low densities on a larger spatial scale) on the other (Van de Koppel *et al.*, 2005; Van de Koppel *et al.*, 2008). Hence, mussels move around until they find a location where the number of neighbours within attachment distance is high enough to decrease dislodgement risk while the mussel density over a longer range is sufficiently low to decrease competition for algae. We developed an individual based model that describes pattern formation in mussels by relating the chance of movement to the short- and long-range densities of mussels, following De Jager *et al.* (2011). We consider 1600 circular individuals with a diameter of 1 cm that are initially spread homogeneously on a 25 x 25 cm surface. In each of the 500 time steps within a simulation, all individuals get a chance to move in random order. Whether a mussel moves or not depends on the density of mussels within the local attachment range of 1.1 cm Ø (i.e. the 'local density') and the density of mussels within the larger, 3.3 cm Ø competition range (i.e. the 'long-range density'); a mussel moves when the local density is lower than a certain settlement threshold (which we will vary below) and/or when the long-

range density is higher than 0.7 individuals/cm². These parameter values were estimated using a regression analysis of experimental data (Van de Koppel *et al.*, 2008; De Jager *et al.*, 2011). We modelled movement of individuals to correspond to natural mussel movements, using a heavy-tailed step length distribution (a Lévy walk with $\mu = 2$; De Jager *et al.*, 2011), where steps are made in random directions and their lengths are drawn from a power law distribution. A mussel ends its step prematurely when it encounters a conspecific (De Jager *et al.*, 2014). In our model, mussels cooperate after pattern formation (and not during); therefore the attachment of byssus threads does not impair mussel movement. To examine the relation between the number of neighbours within the facilitation range and the spatial structure that emerges in the self-organized mussel bed, we vary the settlement threshold, e.g. the minimum mussel density required for local aggregation. We simulated mussel bed formation for a range of settlement thresholds and plotted the emerged spatial patterns. We calculated the average number of neighbours ± SE within attachment range for each simulation.

A model of the evolution of between-mussel cooperation

To investigate the evolution of cooperation, we make two plausible assumptions on how the survival probability and the fecundity of a mussel is affected by its attachment tendency A and on the number n of neighbours within attachment distance. The attachment tendency A $(0 \leq A \leq 1)$ corresponds to the probability of attaching a byssus thread to any given neighbour. Hence, a mussel with attachment tendency A and n neighbors attaches itself on average to $n \cdot A$ of its neighbours. Mussels, however, do not only make attachments themselves, but also receive attachments from other mussels. Hence, the total number of attached neighbours N depends on both a mussel's own production of byssus threads ($n \cdot A$) and on the number of attachments produced by its neighbours. A mussel can be attached to a neighbour by its own byssus thread, by the byssal attachment of its neighbour, or by both; it stays disconnected from the neighbour if both do not attach to one another. Thus, we can calculate the probability that two mussels are attached as 1 minus the probability that they remain disconnected. Given that a mussel has n neighbours, an attachment tendency A, and neighbours with an attachment tendency A', the expected total number of attached neighbours is given by:
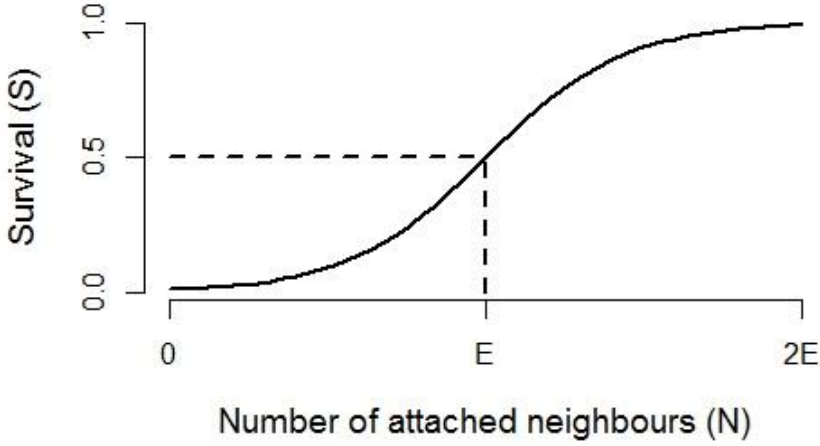
Figure 5.1: We assume that survival is a sigmoid function of the number of attached neighbours. The parameter E corresponds to that value of N for which the survival probability is 0.5. Intuitively, E may be viewed as a measure of the harshness of the environment: under mild conditions (small E), survival is already high for small values of N, while under harsh conditions (large E) survival is low unless mussels are attached to a large number of neighbours.

$$N(A, A') = n * [1 - (1 - A') \cdot (1 - A)]. \tag{5.1}$$

We consider this total number of attached neigbours to be an important determinant of an individual's survival probability. We assume that survival is high when a mussel is attached to many neighbours and is much lower when a mussel has only few attached neighbours:

$$S(A, A') = [1 + e^{-\lambda(N(A,A')-E)}]^{-1}. \tag{5.2}$$

Here, E is the number of attached neighbours needed for the survival chance to be 50 percent and λ determines the steepness of the logistic, S-shaped function (Fig. 5.1). Throughout, we will assume that survival for mussels attached to zero

neighbours is 1% ($S_0(0) = 0.01$). This imposes a constraint on the parameters λ and E, essentially reducing the number of parameters to one.

We further assume that the production and attachment of byssus threads has fecundity costs and consider a linear relation between fecundity and the average number of byssus threads produced:

$$F(A) = 1 - c \cdot n \cdot A. \tag{5.3}$$

Here, c denotes the costs per cooperation with a neighbour (Nicastro et al., 2009).

To study the evolution of the attachment tendency, we use an adaptive dynamics approach (Geritz *et al.*, 1998). To this end, consider a monomorphic resident population with attachment tendency A', in which a mutant with strategy A arises. Whether this mutant invades the resident population depends on its relative fitness (W). For simplicity, individuals in the model are semelparous. We assume that fitness relates to the expected lifetime reproductive success, which corresponds to the product of the probability to survive (S) until reproduction and expected fecundity (F). Hence, the relative fitness of a mutant with attachment tendency A is given by:

$$W(A, A') = \frac{S(A, A') \cdot F(A, A')}{S(A', A') \cdot F(A', A')}. \tag{5.4}$$

If $W(A,A') > 1$, the mutant genotype has larger fitness than the resident genotype and can increase in relative frequency. Assuming asexual reproduction and mutations of small effect, the invasion of a mutant when rare typically guarantees that the mutant will spread to fixation, hence replacing the former resident (Geritz *et al.*, 1998). Through a series of consecutive gene-substitution events, the attachment tendency will evolve to an Evolutionarily Singular Strategy A^* (Dercole & Rinaldi, 2008). Such a strategy is evolutionarily stable if no mutant strategy can invade a population of individuals using strategy A^*. An Evolutionarily Singular Strategy A^* is convergence stable if those mutants successfully invade a given resident strategy A' that is closer to A^* (Geritz *et al.*, 1998).

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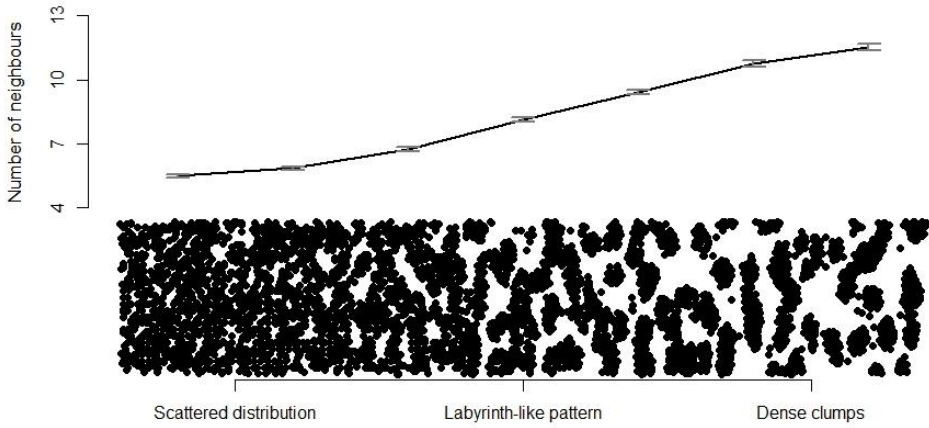
Figure 5.2: Spatial patterns and neighborhood sizes generated by the individual-based simulation model. (Bottom) By increasing the settlement threshold in the model from low (left) to high (right) values, the spatial distribution of mussels changes gradually from scattered to labyrinth-like to clumped. (Top) In line with pattern formation, the average number of neighbors in the attachment range increases as well (bars indicate SE).

The parameter E in eq. 5.3 represents environmental conditions, such as wave stress and predation risk. In harsh environments, E will take on a larger value than in benign environments. We will examine the evolution of attachment for a range of environmental conditions. Furthermore, environmental conditions are likely to vary between generations. Hence, we will also investigate the effect of alternating environments on the evolution of cooperation.

Results

Spatial patterning relates to number of neighbours

As a first step, we demonstrate that the aggregation strategy of mussels strongly affects their spatial distribution as well as the number of neighbours a mussel can interact with. To this end, we systematically changed the settlement threshold of the mussels in a population. Our individual-based simulations reveal that a scattered distribution results when the settlement threshold is low, that a labyrinth-like pattern emerges when the settlement threshold is intermediate, and that dense clumps are formed when the settlement threshold is high (Fig. 5.2 Bottom). The
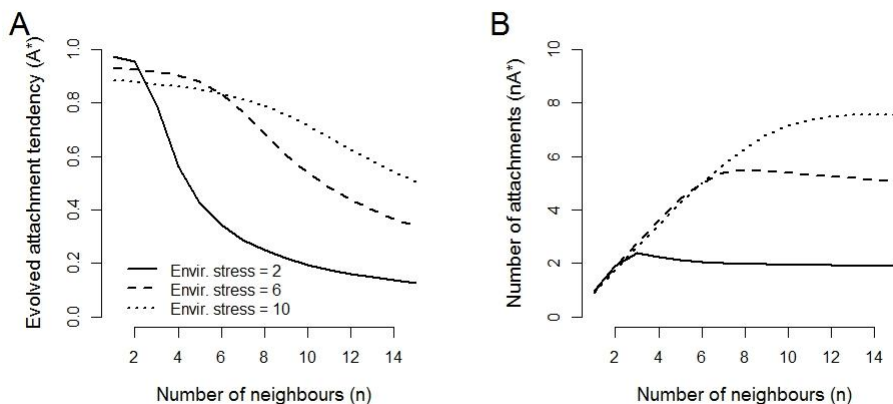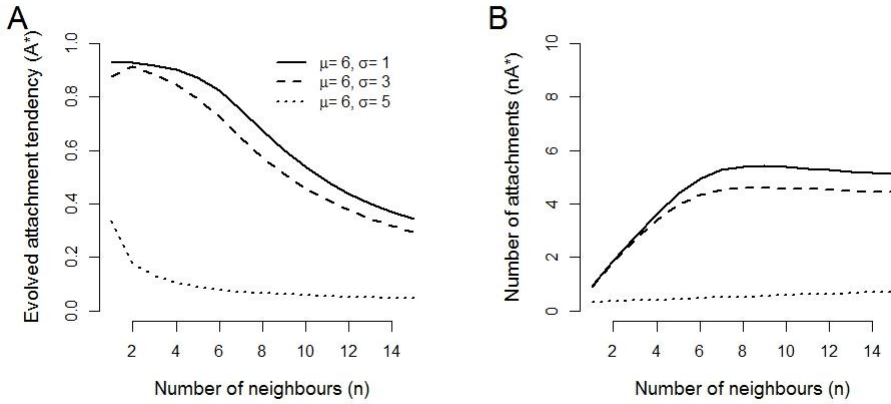
Figure 5.3: (**A**) Evolution of the attachment tendency is influenced by the number of neighbours within attachment distance and the level of environmental stress. (**B**) Investment in the number of attachments created to neighbouring individuals is hump-shaped and is for moderate stress levels maximized in the labyrinth-like patterns that we observe in nature ($n = 8$).

average number of neighbours increases with the degree of aggregation (Fig. 5.2 Top). For the remainder of this paper, we will use the following neighbourhood sizes (n) to represent the different spatial structures: $n = 6$ for scattered distributions, $n = 8$ for labyrinth-like patterns, and $n = 12$ for dense mussel clumps. Because natural mussel beds are often labyrinth-like, we specifically concentrate on how an intermediate number of neighbours ($n = 8$) affects the evolution of the attachment tendency A.

Evolution of the attachment tendency A

By actively aggregating into spatially structured mussel beds, mussels are able to modify the number of neighbours they can cooperate with and may thereby also affect the level of cooperativeness that evolves in the population. For three different environmental conditions (benign ($E = 2$), moderate ($E = 6$), and stressful ($E = 10$)), Figure 5.3A shows how the evolutionarily stable attachment strategy A^* depends on the neighbourhood size n. In all three cases, the evolved level of attachment tendency decreases when increasing the number of neighbours. The differences in how the number of neighbours affects the evolution of the

Figure 5.4: Evolution of attachment tendency when environmental conditions differ between generations and vary according to a normal distribution. (**A**) The evolved attachment tendency and (**B**) the number of attachments created per individual for a range of numbers of neighbours, given three different variances of the stress level distribution. The solid line indicates the case where environmental stress is normally distributed with little variance ($\mu = 6$, $\sigma = 1$); variance is increased for the two dashed lines ($\sigma = 3$ and $\sigma = 5$, respectively).

attachment tendency in Figure 5.3A illustrates that environmental conditions are of key importance in this evolutionary process. Especially in benign environments, active aggregation into spatially structured populations can have substantial effects on the attachment tendency that evolves.

Interestingly, the number of attachments created when cooperating at the evolved level A^* is maximized at intermediate numbers of neighbours ($n = 8$) for intermediate levels of environmental stress (Figure 5.3B). Though the attachment tendency provides us with a measure of cooperativeness, the costs and benefits of cooperation are better represented by the average number of attachments made to neighbouring individuals ($n \cdot A^*$). Investment in attachment peaks at different numbers of neighbours for different levels of environmental stress. In moderate environments, self-organization into a labyrinth-like pattern, which is characterized by intermediate numbers of neighbours ($n = 8$), can yield an evolved attachment tendency that maximizes the number of attachments made. Note that the number of attachments created can never be larger than n. Interestingly, $A \cdot n$ in Figure 5.3B

first increases more or less linearly with *n* before levelling off. Given the constraints of the system, the maximal number of attachments is realized for low numbers of neighbours. In that sense, cooperativeness is maximized at low values of *n*. Nevertheless, investment in attachments is maximized in labyrinth-like patterns or dense mussel clumps, depending on environmental conditions.

Changing environmental stress levels

Because mussels disperse over a wide range as larvae before settling on a mussel bed, environmental conditions are most likely different between generations. Adaptation of between-mussel cooperation to a particular stress level is therefore difficult and evolution of cooperation becomes more challenging than described above. In Figure 5.4, we considered the three situations where the environmental stress level a generation encounters is drawn from a random distribution ($\mu = 6$) with low ($\sigma = 1$), intermediate ($\sigma = 3$), and high ($\sigma = 5$) variation in stress, but the results below are also valid for stress level distributions with higher or lower μ. When variation in *E* is high, the evolutionarily stable attachment tendency is very low for all *n* (Fig. 5.4A), as is the number of attachments created (Fig. 5.4B). Highest levels of between-mussel cooperation evolve when mussels have few neighbours and variation in environmental stress is low. With a mean stress level μ = 6, little variation in environmental stress gives rise to a hump-shaped relation between the number of neighbours and the average number of attachments a mussel produces, which is quite similar to the situation without variation in environmental conditions between generations (Figure 5.3). Increased variation in environmental stress between generations causes lower attachment tendencies to evolve than when conditions are more stable.

Inter-generational variation in environmental stress implies that the attachment tendency that evolves when environmental stress differs between generations is either lower or higher than the attachment tendency that would evolve when conditions throughout all generations remains constant. For instance, when stress follows a normal distribution with $\mu = 6$ and $\sigma = 1$, the evolved attachment tendency is approximately 0.82, 0.69, and 0.43 in scattered distributions (*n* = 6), labyrinth-like patterns (*n* = 8), and dense clumps (*n* = 12), respectively, regardless of the environment met by the current generation. When a mussel bed
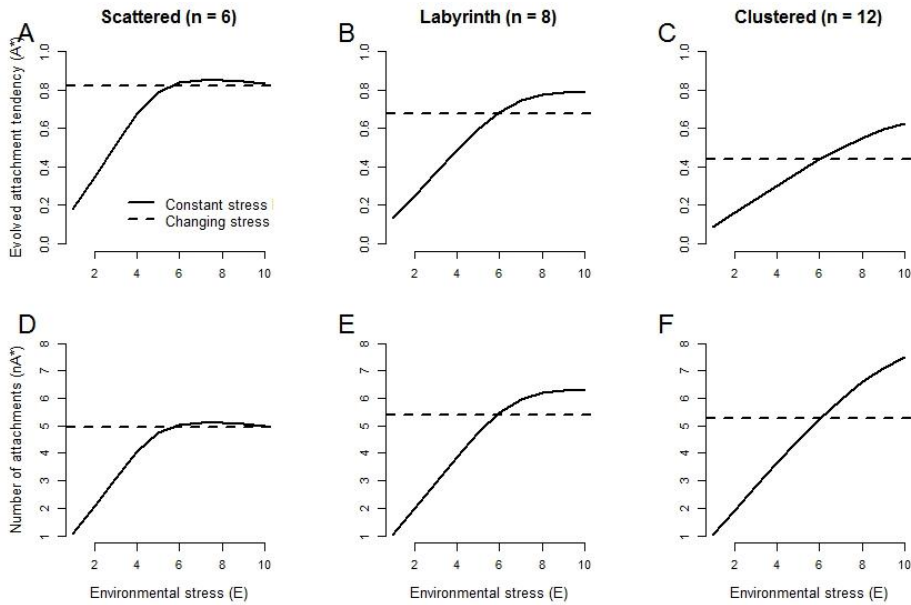
Figure 5.5: Evolution of between-mussel cooperation for three spatial population distributions and a range of environments, when environmental stress differs between generations (dashed lines) or remains constant (solid lines). The attachment tendencies that evolved in both constant and changing environments in scattered beds (**A**), labyrinth-like patterns (**B**), and dense clumps (**C**). (**D-F**) The average number of attachments created by an individual per spatial pattern and stress level. Here, we used the normally distributed stress levels ($\mu = 6$, $\sigma = 1$) to model evolution of between-mussel cooperation in inter-generational variation in environmental stress.

emerges in a benign environment, the mussels are attached to more neighbours than minimally needed for survival (Fig. 5.5D-F). However, mussel beds in harsh environments can easily get dislodged, as the evolved attachment tendency results in too few attachments than required for adequate mussel survival. Especially in dense clumps, the attachment tendency that would have evolved if all generations had experienced high environmental stress is substantially higher than the attachment tendency that evolves when generations experience different stress levels (Fig. 5.5C). In this sense, dense clumps are more risk-prone than scattered distributions. Overall, the level of cooperativeness that evolves in self-organized mussel beds appears to depend on the range and frequency of occurrence of environmental conditions and on the spatial pattern that is generated within the mussel bed.

Discussion

Cooperation is often a necessity for survival in harsh environments and is therefore found in many species. Organisms utilize a multitude of supporting traits and behaviours, such as local dispersal, reciprocity, and punishment, to maintain high levels of cooperation (West *et al.*, 2007). Here, we demonstrate a new behaviour that can promote the evolution of cooperation: active movement into spatial patterns. Though earlier studies have highlighted the importance of spatial structure in locally dispersing populations to improve relatedness amongst cooperating individuals (Ohtsuki et al., 2006; Santos et al., 2006; Masuda 2007), we demonstrate that spatial patterning can also promote cooperation in the absence of kinship between neighbours. Our theoretical analysis reveals that in intertidal mussels – where individuals disperse over a wide range – aggregation into spatial patterns stimulates the evolution of cooperation, despite of a complete absence of relatedness among the cooperating conspecifics. Yet, because mussels benefit from any attachment of byssus threads with neighbouring individuals, some degree of between-mussel cooperation evolves in any type of mussel bed, irrespective of the spatial pattern. Our analysis, however, shows that cooperative interactions by formation of byssal attachments can be maximized when the mussels form a self-organized, labyrinth-shaped pattern, where they interact with an intermediate number of neighbours. From this study and others (Ohtsuki et al., 2006; Santos et al., 2006; Masuda 2007), we can conclude that spatial patterning can substantially influence the degree of cooperativeness that evolves in a population, both in species with local and long-range dispersal.

From a game-theoretical point of view, spatial population structure is generally thought of as the consequence of local dispersal of offspring (Nowak & May, 1992). As local dispersal initiates spatial heterogeneity in a population, related individuals cooperate more amongst themselves than in mixed populations. Because of the advantages of cooperating with kin (i.e. inclusive fitness), cooperativeness can readily evolve in viscous populations where offspring remains local. Spatial population structure, however, is not necessarily the consequence of local dispersal; other factors, such as habitat suitability, predation, and food availability, might affect spatial population structure, also in populations with wide-ranging offspring dispersal. Recent studies have let go of the assumed link between

local dispersal and spatial structuring, but yet maintain using local dispersal in their models of cooperation in network-structured populations (Santos & Pacheco, 2005; Ohtsuki et al., 2006; Santos et al., 2006; Masuda 2007). Our work suggests that this assumption is not essential. We demonstrate that, despite of offspring dispersing over a wide range, spatial population structure can substantially increase the amount of cooperativeness that evolves in a population, depending on environmental conditions. Our work corroborates with a number of studies stressing that cooperative species exist that have spatially structured populations, but are genetically well-mixed (Godfrey & Kerr, 2009) and which act out of an innate cooperative strategy. Hence, our study highlights the importance of spatial structure and active aggregation for the evolution of cooperation even in populations where dispersal is not localized.

Self-organized ecosystems are known for their characteristic large-scale spatial patterns, including spots, stripes, labyrinths, and gaps, which are partly caused by local cooperation (Rietkerk & Van de Koppel, 2008). Kéfi *et al.* (2008) showed that cooperation in self-organized arid ecosystems can only be sustained when plants disperse locally. If these plants would disperse over a wide range, uncooperative individuals could invade in the population, causing the entire system to collapse. In our paper, we show that this conclusion may not be general for all self-organizing populations. In mussel beds, local dispersal is not necessary for the evolution of cooperation. Although cooperation in self-organized arid systems and mussel beds show similarities – for instance, cooperation in both systems resembles a Snowdrift Game (Doebeli & Hauert, 2005) – the main difference lies in the mobility of the individuals. In arid systems, plants cannot move around, and hence have to accept the neighbourhood they encounter, as they are dependent on the location to which their seeds disperse. When plant density drops because of a decrease in cooperativeness, plants have fewer neighbours to cooperate with. As life with less neighbours is even tougher, less individuals produce offspring, causing the eventual collapse of the system. In mussel beds, a similar number of neighbours can be maintained throughout generations, despite fluctuations in mussel density. Hence, because of their mobility, mussel populations can be maintained at low levels of cooperation, which would cause evolutionary suicide in arid systems. This suggests that cooperation can more easily

be sustained in ecosystems with actively aggregating organisms, where local neighbourhood size is to a certain extent independent from population density.

Variability in environmental conditions can have substantial consequences for how well a population is adapted to its environment. The level of cooperativeness that evolves when environmental conditions are continually changing between generations can be too little in highly stressful environments, resulting in the dislodgement of entire mussel beds after settlement in the wrong locations. In most intertidal ecosystems, an extensive range of environmental conditions can be encountered at any time, from very benign habitats that also provide little food, to very harsh conditions where food is often abundant. Moreover, mussel offspring is likely to reach all of these habitats, as is witnessed by the high availability of mussel spat on artificial settlement structures. This implies that the offspring of any mussels can spread itself over different habitats where a harsher environment implies a better food supply. For simplicity, we did not take this correlation between environmental stress and food availability into account; further research may show whether the inclusion of this relationship will give different results. It is likely that the levels of cooperation that are found in real-world mussels reflects an adaptation to the habitat where they can generate the highest number of offspring, taking into account the availability of the habitat in the overall area.

For the sake of simplicity, we adopted a number of simplifying assumptions that do not agree with the conditions that mussels, or any real-world organism, would encounter. In our model, we used semelparous individuals, whereas real mussels can survive for many years and reproduce at least once a year. In mussels, reproductive output per unit of biomass increases with age, as growth takes an ever smaller part of energy. Under most circumstances, our simplification has little consequences, yet it might become important in temporally variable environments. We assumed a fixed self-organizing behavior within each and throughout generations; in each simulation of our IBM, all individuals used the same set of rules, including the settlement threshold, to move into a spatial pattern. This is an unrealistic assumption for several reasons. For example, generations are likely to differ in initial overall density; a scattered population in a

dense mussel bed will result in a higher number of neighbours within attachment distance than in less dense but patterned beds. Especially for small and large settlement thresholds, a stable population structure may not be reached due to too high or too low overall mortality rates, respectively, hence creating differences in mussel densities. Furthermore, individuals might differ in their self-organizing strategy; though some are aggregating in dense clumps, others may be strategically moving away from dense mussel clusters. The settlement threshold used in our IBM may be a trait that is under evolutionary selection itself and might even jointly evolve with cooperation. Because we were interested in how spatial patterning affects the evolution of cooperation, we stayed with our assumption of a fixed aggregation behavior within and between generations.

Our study demonstrates that active self-organization can have substantial consequences for the degree of cooperation that evolves in a population. Inversely, self-organized spatial patterns have been described in a wide range of ecosystems, and many of these studies highlight the importance of cooperative interactions for the formation of these spatial patterns. In patterned arid bush lands, for instance, plants promote the infiltration of water into the soil, facilitating other plants (Klausmeier, 1999). This highlights the potential importance of feedback interaction between pattern formation processes on the one hand, and cooperation on the other. Yet, so far, the evolution of cooperation and the pattern forming characteristics of organisms, such as their aggregative behavior, have been studied in isolation. The joint evolution of pattern forming properties and cooperative behavior is, for this reason, an interesting subject for further investigation.

6

Patterning in mussel beds explained by the interplay of multilevel selection and spatial self-organization

Monique de Jager, Johan van de Koppel, Ellen J. Weerman, & Franz J. Weissing

Abstract

Cooperation, ubiquitous in nature, is yet difficult to explain from an evolutionary perspective. Many modelling studies strive to resolve this challenge, but their simplifying assumptions on the population and interaction structure are rarely met in ecological settings. Here we use a modelling approach that includes more ecological detail to investigate the evolution of cooperation in spatially self-organized mussel beds, where mussels aggregate and attach byssus threads to neighbouring conspecifics in order to decrease losses to predation and wave stress. We develop a mechanistic, individual-based model of spatial self-organization where individual strategies of movement and attachment generate spatial patterns, which in turn determine the fitness consequences of these strategies. By combining an individual-based simulation approach for studying spatial self-organization within generations with an analytical adaptive dynamics approach that studies selection pressures across generations, we are able to predict how the evolutionary outcome is affected by environmental conditions. When selection pressures on cooperation and movement are only governed by local interactions, that is, the attachment of individuals to their neighbours, evolution does typically not result in the labyrinth-like spatial patterns that are characteristic for mussel beds. However, when we include a second level of selection by considering the additional protection provided by the formation of mussel clumps, evolutionarily stable movement and attachment strategies lead to labyrinth-like patterns under a wide range of conditions.

Introduction

Fighting the elements is a challenging task that is frequently best achieved by cooperation. Under harsh environmental conditions, many organisms join forces to reduce predation risk, locate resources, or build shelters. Although cooperative behaviour is widespread throughout nature, cooperation can potentially be exploited by free-riders that benefit but do not contribute (e.g. West *et al.,* 2007; Van Dyken & Wade, 2012). This 'paradox of cooperation' has fascinated theoreticians and empirical biologists alike, making the evolutionary emergence and stability of cooperation one of the most intensely studied questions in biology (Lehman & Keller, 2006; West *et al.,* 2007 & 2008). Theoretical and empirical studies demonstrate that the evolution of cooperation has many interesting facets, and that a multitude of factors (such as spatial structure, relatedness, reciprocity, and punishment) are of potential relevance for resolving the paradox of cooperation (Dugatkin, 1997; Nowak & Sigmund, 2005; Foster & Wenseleers, 2006; Lion & Van Baalen, 2008; Clutton-Brock, 2009; Archetti *et al.,* 2011; Bourke, 2011; Raihani *et al.,* 2012).

In view of the intricacy of the problem, it is not surprising that most theoretical studies are centred around 'toy models,' that is on models that are based on an abstract, cartoon-like representation of real-world interactions. Although such studies have been extremely useful in furthering our conceptual understanding of cooperation, the empirical relevance of their findings is not self-evident. Cooperation in natural systems is typically taking place in much more ambiguous settings than depicted by toy models, and standard concepts of cooperation theory (such as 'cooperation', 'defection', and 'group') do not always have a clear-cut meaning in natural populations. Our understanding of the mechanisms that favour cooperative behaviour may benefit from studies that explicitly include the intricacies of particular real-world systems.

Here, we develop and analyse models for investigating cooperation between mussels in self-organized mussel beds. Mussels live in a harsh environment where they compete for food while risking dislodgement by wave stress and predation by birds and other animals (Bertness & Grosholz, 1985; Hunt & Scheibling, 2001, 2002; Van de Koppel *et al.* 2005). In order to survive, mussels

move into aggregations and affix themselves to neighbouring conspecifics using byssus threads (a glue-like substance; Maas Geesteranus, 1942). By doing so, neighbours become secured as well, making this interaction a cooperative act that is beneficial to both parties, while generating costs only for the contributing mussel.

For at least three reasons, existing theoretical models are not directly applicable to cooperative behaviour in mussel beds. In the first place, cooperation among mussels depends on two traits: the movement and attachment strategies of the mussels involved. Movement affects attachment: since byssus threads have a limited length, attachment requires the presence of conspecifics in the vicinity, and the clustering of individuals is to a large extent caused by their movement strategy (De Jager *et al.*, 2011; Liu *et al.*, 2013). Conversely, attachment directly affects movement, because mussels attached to many neighbours are strongly restricted in their movement. Accordingly, models of the evolution of mussel cooperation should consider the joint evolution of movement and attachment strategies.

A second reason is that the spatial structure in which mussels interact with their neighbours is not a given a priori pattern but an emergent property of the interplay of movement and attachment (Van de Koppel *et al.*, 2008). The characteristic labyrinth-like pattern frequently observed in mussel beds can only persist due to between-mussel attachments; without such byssal attachments (and, hence, cooperation), there would be no spatial structure. As a consequence, there is a reciprocal causality (Laland *et al.*, 2011) between movement and attachment strategies (which are shaped by selective forces and strongly depend on the spatial configuration) and spatial structure (which is an emergent property reflecting the underlying movement and attachment patterns).

A final reason is that mussel attachment leads to the formation of clumps, and the survival of a mussel in times of intense water movement is positively related to the size of its clump. This adds a new level of selection, where fitness is also determined by the size of the clump. However, hierarchical selection in mussel beds is more complicated than described in standard models of group structured populations (Van Boven & Weissing, 1999; Traulson & Nowak, 2006; Thompson

2000; Kohn, 2008; Burton *et al.*, 2012; Molleman *et al.*, 2013). The 'groups' (mussel clumps) are not defined by external features, but instead are emergent properties of mussel movement and attachment and accordingly are highly dynamic and variable in size.

To understand the evolution of cooperation in mussel beds, we therefore need to develop a model that considers the joint evolution of several traits, the emergence of spatial structure, and multilevel selection in a population with dynamic group structure. To this end, we extend the standard methods of evolutionary analysis to cope with the complexities that are inherent to systems with self-organized interaction structures. In a first step, we study the evolution of attachment and movement separately; for each (fixed) attachment strategy, we determine the evolutionarily stable pattern of movement, and for each given movement strategy, we determine the evolutionarily stable investment into byssus threads and, hence, attachment. In a second step, we consider the joint evolution of attachment and movement. From the separate analyses, we can in many situations identify the joint evolutionarily stable strategies for both traits. This information is, however, often not sufficient for making evolutionary predictions. To get a more detailed picture, we need to derive the two-dimensional selection gradient determining the joint evolution of movement and attachment. We show how these gradients can be obtained from individual-based simulations. Based on the selection gradient, we can then study how the evolutionary dynamics of attachment and movement are affected by environmental factors such as food availability and predation risk. Finally, we incorporate the effect of clump formation on survival and fitness by introducing a second level of selection in the analysis. We compare simulations runs of a model including only individual-level selection with results of a multilevel selection model to examine the effect and importance of the different levels of selection.

Methods

1. *A model for the joint evolution of movement and attachment in self-organized mussel beds*

Our model implicitly includes two time scales: a short time scale (within generations) at which behavioural and ecological processes take place; and a longer time scale (across generations) at which the heritable characteristics of a population change due to evolution by natural selection. Within a generation, individuals move and attach to each other, leading to pattern formation, which in turn affects dislodgement risk by predation and wave stress and food intake (which depends on competition). These short-term processes are explicitly represented in individual-based simulations. The long-term simulations subsequently allow us to estimate the fitness consequences for a spectrum of heritable strategies. These fitness estimates will subsequently be used to predict the outcome of adaptive evolution.

Movement and attachment

In natural mussel beds, young mussels move around until they have aggregated into a labyrinth-like pattern. Such a pattern may be viewed as an optimal compromise between minimizing predation pressure and wave stress (requiring dense local aggregation) on the one hand and avoidance to minimize competition (requiring low competitor density at a larger scale) on the other (Van de Koppel *et al.*, 2005; Van de Koppel *et al.*, 2008). As shown in Van de Koppel *et al.* (2008), a self-organized labyrinth-like pattern can emerge from the movements of individual mussels that follow the rule to leave their spot if (a) the mussel density in their local 'attachment range' (the range where mussels can affix themselves to conspecifics and thereby find protection from predation and wave stress) is too low, or if (b) the mussel density in the larger 'competition range' (the range where mussels experience competition for food from others) is too high. This rule is illustrated in Figure 6.1A.

Here, we adopt this model of aggregative movement. Three parameters of this model are kept fixed at values that were estimated from experimental data (Van de Koppel *et al.*, 2008, De Jager *et al.* 2011): the size of the attachment range, the size of the competition range, and the competition threshold density (determining whether a mussel will stay or leave in order to avoid competition). In contrast, the attachment threshold density τ (determining whether a mussel will stay or leave in order to find a denser cluster of conspecifics) is an evolving
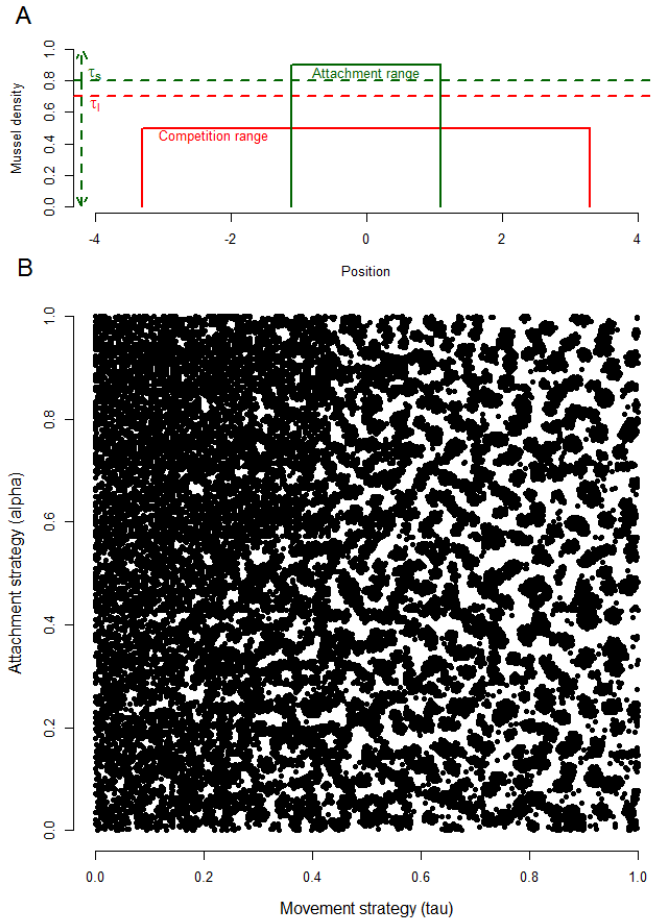
Figure 6.1: Illustration of the parameters determining the movement strategy of a mussel (**A**) and the joint effect of the evolvable parameters α (attachment) and τ (movement threshold) on spatial pattern formation (**B**). (**A**) In the model, the movement decisions of mussels depend on the density of conspecifics at two scales: the density of mussels in the attachment range (where mussels can attach to each other by byssus threads) and the density of competitors in the competition range. A mussel is inclined to move away if the density in the competition range is larger than 0.7 mussels cm^{-2} and/or if the density in the attachment range is smaller than the threshold τ. The threshold τ and the byssus attachment rate α are the evolvable parameters in our model. (**B**) Illustration of the patterns generated by mussel populations with different combinations of the movement threshold τ and the attachment rate α. Different spatial patterns emerge, ranging from random distributions (τ < 0.3), to labyrinths (0.3 < τ < 0.7) and dense clumps (τ > 0.7), for different combinations of α and τ. The picture was created by joining the final mussel distributions of 5x5 simulations.

parameter in our model. As illustrated in Figure 6.1B, the value of τ strongly affects the spatial distribution of mussels in the mussel bed.

More specifically, our individual-based model considers 1600 individuals with a cross section of 1 cm that are initially spread evenly on a 25 x 25 cm surface. Within a generation, there are 500 decision moments, where each individual has to make a movement or an attachment decision. At a decision moment, the 'local density' (i.e., the density of mussels within the attachment range of 1.1 cm ø) and the 'long-range density' (i.e., the density of mussels within the competition range of 3.3 cm ø) is calculated for each individual. These densities are compared with the competition threshold density (0.7 individuals/cm^2) and the attachment threshold density (the heritable parameter τ). If the local density is lower than the attachment threshold density, or if the long-range density is higher than the competition threshold density, the individual moves away in search for a better spot. Those individuals that move away make a step in a random direction, where the step length is drawn from a power law distribution, as the movement of solitary mussels can be approximated by a Lévy walk (De Jager *et al.*, 2011). Whenever a moving individual encounters a conspecific, the move ends prematurely (De Jager *et al.*, 2014).

Mussel beds are regularly threatened by wave stress, currents, and predation. Because dislodged mussels are less efficient filter feeders and are more prone to predation (Hunt & Scheibling, 2001), we assume that they have a lower survival chance than properly affixed individuals. In order to reduce the risk of dislodgement, mussels produce byssus threads to attach themselves to conspecifics. In the model, individuals can attach byssus threads to neighbours in their attachment range (1.1 cm ø). If an individual does not move during a simulation step and if suitable neighbours are present, it attaches itself to a random neighbour with probability α (0 ≤ $α$ ≤ 1). This parameter is a heritable strategy that can be interpreted as the cooperation tendency of a mussel.

A trade-off exists between movement and attachment: while moving, an individual cannot attach, and attached individuals cannot move away because of their binds. As real mussels are able to remove some of the byssus threads attached

to them, the individuals in our model can destroy the attachment in a decision moment and move away in a subsequent one if they are attached with a single byssus thread only. To put some boundaries to our model, each individual can attach a maximum of 50 byssus threads to its neighbours within the 500 time steps of each simulation run. No additional byssus threads are produced once this maximum is reached.

Evolutionarily stable movement and attachment strategies

All these actions have their costs and benefits in terms of Darwinian fitness. Moving into a patterned distribution takes energy, but also helps an individual in finding conspecifics to attach to. Consequently, attaching to a neighbour requires the production of a byssus thread, but can improve a mussel's survival. We assume that fitness corresponds to expected lifetime reproductive success of a semelparous organism, that is to the product of the probability to survive until reproduction (S) and expected fecundity (F) once reproductive age has been reached. We assume that fecundity is determined by food availability (which depends on the food influx and the density of conspecifics in the competition range), the total costs of movement, and the total costs of attachment (see Appendix A for details). We further assume that the survival probability of an individual is positively related to the number n of neighbours this individual is connected with via byssus threads. To be more specific, we assume that $S(n)$ is a logistic function of n, which is characterized by a single parameter n_{50} that corresponds to the number of attached neighbours required for a 50% survival probability (see Appendix A for details). This parameter can be viewed as a measure of predation risk: the higher the risk, the more attachments are necessary to achieve 50% survival.

The above considerations allow us to calculate in each within-generation simulation a fitness value for each genotype, where genotypes are characterized by the combination of a movement strategy τ and a cooperation strategy α. Subsequently, these fitness values can be used for making evolutionary predictions.
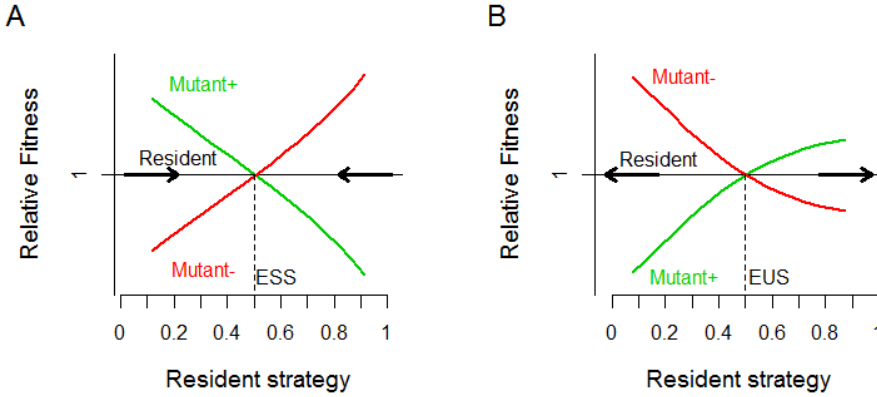
Figure 6.2: Relative fitness of 'plus mutants' (green) and 'minus mutants' (red) for a range of resident strategies. A mutant will invade the resident population if its relative fitness is larger than one. (**A**) In this scenario, 'plus' mutants (i.e. mutants with a higher trait value than the resident) can invade if the resident strategy is below 0.5, while 'minus' mutants can invade if the resident strategy is above 0.5. Accordingly, gene substitution events will shift the resident strategy to 0.5, which is an evolutionary attractor and an evolutionarily stable strategy (ESS). In (**B**), long-term selection is in the direction of smaller trait values if the resident strategy is below 0.5, while it shifts the population to higher trait values if the resident strategy is above 0.5. In this case, 0.5 is an evolutionary repellor and an evolutionarily unstable strategy (EUS). The population will converge to one of the extreme strategies; whether it converges to 0 or to 1 depends on the initial conditions.

Two-dimensional selection gradients

In a first step, we take a 'univariate' approach by separately considering the evolution of movement and the evolution of attachment, keeping the other strategic parameter at a fixed value. Suppose, for example, that the attachment strategy is a fixed value α. To determine which value of the movement strategy τ is evolutionarily stable (given this value of α), we performed for 21 equidistant values of τ ($0 \leq \tau \leq 1$) 100 replicate within-generation simulations as follows. We started the simulation with a population of 1600 mussels, 2 of which were mutants. The residents were characterized by a movement threshold density τ while the 2 mutant individuals were given a threshold density that was either higher or lower than that of the resident (plus mutant: $\tau^+ = \tau + \delta$, minus mutant: $\tau^- = \tau - \delta$; where $\delta = 0.1$). During the simulation, these movement threshold densities determined when the individuals stopped moving and, accordingly, when a final configuration of the

mussel bed was reached. After 500 simulation steps, the moved distance, number of byssal attachments, number of attached neighbours, and group size were recorded for each mutant and a random resident. From these data we first calculated the relative fitness of both types of mutant by averaging over the 100 simulations. Subsequently we fitted a linear regression line through these fitness estimates. This line corresponds to the local selection gradient. Plotting these values results in a graph as in Figure 6.2. Whenever we present fitness estimates in a figure, the linear-regression predictors are used, since they are less affected by stochasticity than the primary fitness estimates. When the fitness curves of plus and minus mutants intersect at a value τ^* of the movement strategy, this value can either be an evolutionary attractor (Fig. 6.2A) or an evolutionary repellor (Fig. 6.2B, Geritz *et al.*, 1998). τ^* is an attractor if any resident strategies different from τ^* can be invaded by mutants "in the direction of τ^*", that is, by plus mutants if the resident is smaller than τ^* and by minus mutants if the resident strategy is larger than τ^*. This happens in the scenario depicted in Figure 6.2A, since plus mutants have a higher fitness than the resident when the resident is to the left of $\tau^* = 0.5$, while minus mutants have a higher fitness than the resident when the resident is to the right of τ^*. The opposite pattern is depicted in Figure 6.2B. Here, each resident strategy differing from τ^* is invaded by mutants that drive the system even further away from τ^*. Accordingly, τ^* is in this case an evolutionary repellor.

For a given set of parameter values, the evolutionary attractors and repellors τ^* can be determined as a function of the given attachment strategy α. This is illustrated by the blue curve in Figure 6.3A. In the example shown, the blue curve is solid, indicating that in all cases the value $\tau^*(\alpha)$ is an evolutionary attractor. In later examples, evolutionary repellors can also occur: they would be symbolized by a dashed curve. Similarly, for any given value τ of the movement strategy, the evolutionary attractors and repellors α^* of the attachment strategy can be identified. The corresponding curve $\alpha^*(\tau)$ is represented by a red curve in Figure 6.3A. The intersection point of the blue and the red curves is special, since this is the only point where τ^* and α^* are both evolutionary attractors: for any other combination of strategies, upcoming mutants could either destabilize the movement strategy or the attachment strategy.

The situation is not always as clear-cut as in Figure 6.3A. The blue and red curves indicating the lines representing the univariate evolutionary attractors and repellors may intersect at various points, or they may not intersect at all. To get a better picture of the selective forces acting on the two strategies, we need to determine the vector field of selection gradients. To this end, we simulated mussel bed formation with a population consisting of 1592 residents and 8 mutants. The residents were characterized by a resident movement threshold density τ and resident attachment strategy α, whereas the mutants differed in their strategy from the residents with respect to the movement strategy (τ^+ or τ^-), the attachment strategy (α^+ or α^-), or both, resulting in 8 possible mutant strategies (i.e., $\tau^-\alpha^-$, $\tau^-\alpha$, $\tau^-\alpha^+$, $\tau\alpha^-$, $\tau\alpha^+$, $\tau^+\alpha^-$, $\tau^+\alpha$, $\tau^+\alpha^+$). As before, we first determined the relative fitness of the eight mutant strategies and subsequently obtained the selection gradient by a (multiple) linear regression of these fitness values on mutant strategy (see Appendix B). This method is illustrated in Figure 6.3B.

## 1. *Group-level selection in patterned mussel beds*

Up to now, we have only considered the possibility that the survival of a mussel is affected by the degree to which it is attached to its immediate neighbours. Close attachment to immediate neighbours can protect against predation, if predators have a preference for loosely attached food that can be picked up and eaten at a faster rate. Attachment to neighbours can, however, have an additional effect. The totality of individuals that are connected by byssus threads forms a network, which – depending on the spatial configuration of the mussels – can be quite large. All the mussels sticking together form a clump, and it is plausible that larger clumps can be less easily dislodged and washed away by the action of waves than smaller clumps. In other words, we consider it likely that there is a second level of selection, namely the size of the group to which a given mussel is attached.

To investigate this hypothesis, we performed a simple field experiment on an intertidal flat near the island of Schiermonnikoog, Netherlands (53˚47' N 6˚21' E). We collected mussels from an existing mussel bed and relocated them to create 80 groups of 1, 3, 10, and 30 mussels, respectively. Groups were placed parallel to the shoreline with a minimum distance of 10 cm between groups. Two days after the start of the experiment, we recorded the presence and absence of groups. As
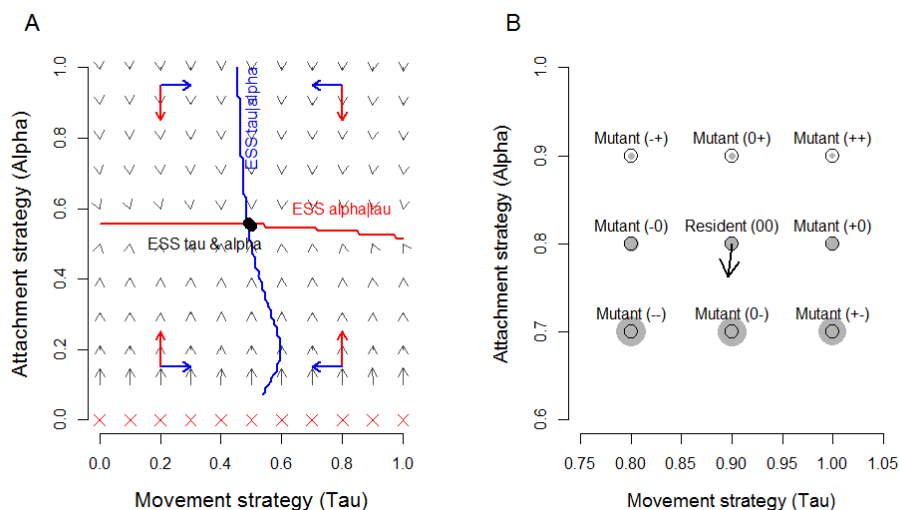
Figure 6.3: Illustration of the method for predicting the outcome of the joint evolution of mussel movement and attachment strategies. (**A**) The red curve indicates the evolutionarily and convergence stable attachment level $\alpha^*(\tau)$ for a given movement threshold τ. The blue curve indicates the evolutionarily and convergence stable movement threshold $\tau^*(\alpha)$ for a given attachment strategy α. The intersection point of the two curves (black dot) indicates the joint evolutionarily stable strategy combination (JESS). The arrowheads point into the direction of the long-term selection gradient. (**B**) Determination of the long-term selection gradient by means of individual-based simulations. The size of the grey dots represent the relative fitness of the 8 mutants and the resident (relative fitness of the resident equals one). Considering the distance in trait space between resident and mutants and the relative fitness of the mutants, we calculated the direction in which selective forces are strongest and indicated this direction with an arrow (see Appendix C). Here we used the following parameter values: $n_{50} = 2$, $\kappa_1 = 1$, $\kappa_2 = 0.005$, $\kappa_3 = 0.005$ (without group-level selection).

shown in Figure 6.4, there was a clear positive relationship between the size of a group and the probability of finding the group back after 48 hours (Chi Square test of independence: $\chi^2 = 14.4$, df = 3, p = 0.002). Due to wave stress and strong currents, small groups of mussels are apparently more easily dislodged from the sediment and removed from their original location than larger clumps.
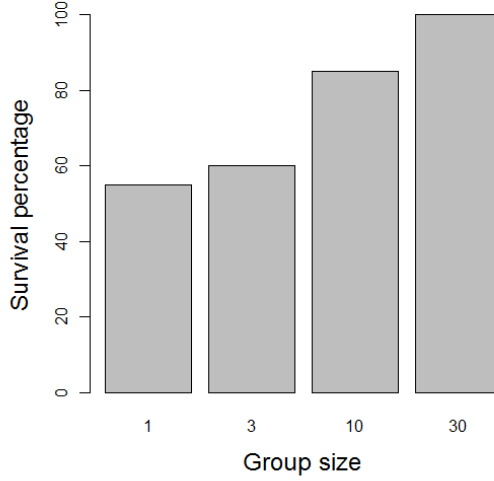
Figure 6.4: Effect of clump size on the dislodgement of mussel clumps in a field experiment. Small clumps were dislodged significantly more often than large clumps Chi Square test: $\chi^2 = 14.4$, df = 3, p = 0.002).

Incorporating group-level selection in the model

Dislodgement of mussel clusters is likely to decrease the survival chance of all mussels within the detached clump. We incorporated this effect by assuming that overall survival has two components: individual-level survival $S_{IL(n)}$ that depends on the number n of attached neighbours as described above; and group-level survival $S_{GL(g)}$ that is positively related to the size g of the group (clump) to which an individual is attached. A group is specified as the number of mussels that is directly and indirectly linked to the focal individual (including itself). We assume that $S_{GL(g)}$ is a logistic function of g. In our baseline scenario, survival is just given by individual-level processes: $S = S_{IL(n)}$. In the multi-level scenario of the model, we assume that survival is given by the geometric mean of individual-level survival $S_{IL(n)}$ and group-level survival $S_{GL(g)}$.
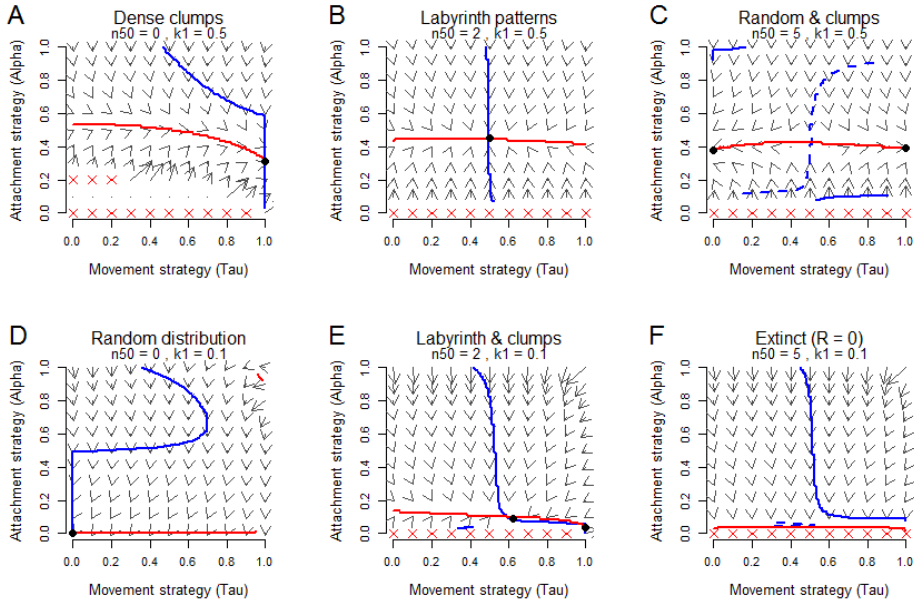
Figure 6.5: Effect of food availability and predation risk on the joint evolution of mussel movement and attachment strategies. The top row shows the results of our analysis for an intermediate level of food availability (κ1 = 0.5). In the bottom-row panels, food is sparse (κ1 = 0.1). From left to right, predation risk increases, from no predation (n50 = 0) to low predation (n50 = 2) to intermediate predation (n50 = 5). The red and blue lines illustrate the ESS of respectively the attachment and movement strategies given a constant, non-evolving level of the other trait. The intersection between the two lines correspond to the joint ESS (JESS), which is marked by a black dot. The arrows indicate the direction of evolution. Self-organized pattern formation depends on the evolved attachment and movement strategies. Because the evolutionary outcome is strongly affected by the environmental conditions, different spatial patterns emerge within the different situations. Only in (**B**), we find a single attractor leading to the emergence of labyrinth-like patterns. Depending on the initial values of α and τ, random distributions can be generated in the case of (**C**) and (**D**), labyrinth-like patterns can emerge when the fitness landscape resembles that of (**B**) or (**E**), and dense clumps can be produced in the case of (**A**), (**C**), and (**E**). Parameter values used for these figures are: $\kappa_2 = 0.005$ and $\kappa_3 = 0.005$; these figures were created with simulations that exclude higher-order levels of selection.

Results

1. Evolution in the absence of group-level selection

Analysis of the model that uses single-level selection revealed that a variety of qualitatively different evolutionary outcomes are possible at different levels of food

availability and predation risk, as represented in Figure 6.5. We ran a multitude of simulations of the joint evolution of movement and attachment in a model that only considers individual-level selection (S_{ILS}, see appendix A), for a range of different combinations of the four key parameters: predation risk (n_{50}), food availability (κ_1), costs of movement (κ_2) and costs of byssus thread production and attachment (κ_3). For conciseness, we here focus on the environmental parameters, n_{50} and κ_1. We found that with single-level selection, the evolution of attachment is mostly independent of the movement strategy. The red lines in Figure 6.5 correspond to those levels of attachment, which, for a given movement threshold, are predicted to be the outcome of long-term evolution. In all six panels, these lines are almost horizontal, indicating that, in a given environment, the outcome of evolution on attachment is only marginally affected by the movement strategy. The effect of food availability on the evolved level of cooperative attachment is straightforward; when food is scarce, low investment in attachment evolves, whereas intermediate cooperativeness results from simulations with higher food densities. Changes in predation risk do not seem to alter the evolution of attachment as much as food availability. Out of all possible combinations of predation risk and food availability, highest attachment levels evolve when predation risk is low and food availability is high.

The effect of joint evolution under different conditions is less straightforward for the resulting movement strategy (Figure 6.5, blue lines). Now, we not only found evolutionary attractors (solid blue lines) but also evolutionary repellors (dashed blue lines in Fig. 6.5C). Moreover, the evolved movement strategy can strongly depend on the attachment strategy of the population. Depending on the environment (the combination of food availability and predation risk), quite different evolutionary outcomes were observed. In Fig. 6.5B, for example, the same intermediate movement strategy will evolve, irrespective of the attachment strategy. In Fig. 6.5A, an intermediate movement strategy will only evolve in case of a high attachment tendency; in case of low investment in attachment, the movement threshold evolves to the highest possible value. In Fig. 6.5C, the movement threshold will either evolve to lowest possible value or to the highest possible value, depending on the initial conditions.

Overall, joint evolution results in a variety of qualitatively different combinations of movement and cooperation strategies. We investigate the effect of food availability and predation risk on the joint evolution of the movement threshold density τ and the attachment level α. When both traits can evolve, the evolution of one trait can lead to further evolution of the other. Imagine that, for a given attachment level, the movement strategy evolves to a certain value. Given the evolved movement strategy, attachment is likely to evolve to its own evolutionary attractor. At this new attachment level, the movement strategy might not be at its adaptive value and hence evolves to another level. This process continues until both movement and attachment are at the joint evolutionarily stable strategy (Joint-ESS). Using a univariate analysis, we can locate this point as the intersection of the two lines in Fig. 6.5 that indicate the two unilateral types of attractor. A more refined picture emerges by looking at the selection gradients. In Figure 6.5, the gradient vector fields are indicated by arrows pointing in the expected direction of evolution from every strategy combination. The joint ESS are illustrated by a black circle. In each of the six scenarios, the joint ESS is located at a different position in 2D-trait space.

The evolutionary outcomes in Figure 6.5 correspond to the formation of different spatial patterns in the mussel bed. As we discussed earlier, the pattern that is generated in a self-organized mussel bed strongly depends on the movement threshold density and the level of attachment (Figure 6.1B). For low values of the movement threshold density, the population is homogeneously distributed, even more so at high levels of attachment (as attachment prevents movement). At intermediate levels of aggregative movement, labyrinth-like patterns are produced, and high movement threshold densities give rise to dense mussel clumps. Hence, homogeneous mussel beds are generated in Figure 6.5C and D, labyrinth-like patterns in Figure 6.5B and E, and dense clumps in Figure 6.5A and C.

## 2. *Introducing multilevel selection*

We found that including multi-level selection, triggered by higher survival in large clusters, reduced the range of possible outcomes, and favoured the emergence of ESS strategies that generate labyrinth-like patterns. The combination of movement and attachment strategy strongly affects the size distribution of the clumps of
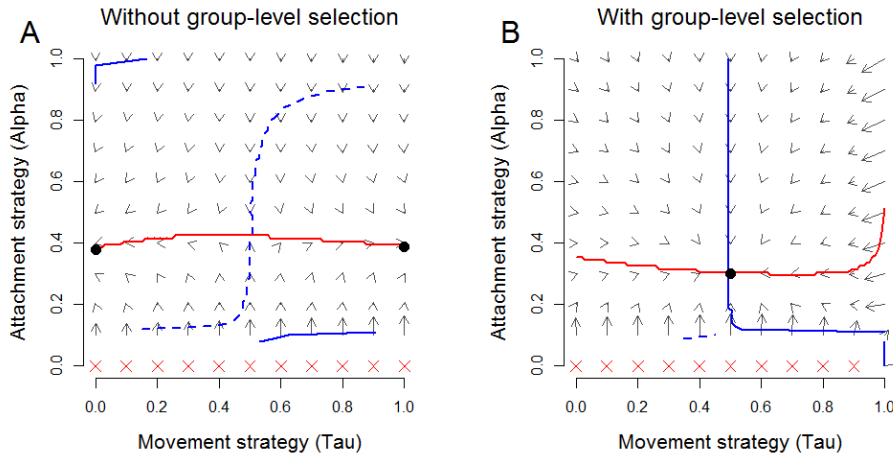
Figure 6.6: The addition of group-level selection can have a large effect on the joint evolution of movement and attachment and, as a result, on spatial pattern formation. For example, without group-level selection, either a randomly distributed mussel bed or dense mussel clumps are generated for the situation in Figure 6.5C, depending on initial conditions (**A**). Adding group-level selection to the situation depicted in Figure 6.5C results in evolution towards intermediate levels of the movement threshold density and attachment strategy, which give rise to labyrinth-like patterns (**B**).

mussels that result from between-mussel attachment. It is likely (Fig. 6.4) that being part of a larger clump reduces the risk of becoming dislodged by wave action and strong currents. We therefore repeated our simulation, but now also included the effects of clump-size related survival (a group-level process) in our fitness measure. As an illustration, we compare the outcome of simulations with and without group-level selection in the scenario of Figure 6.5c in Figure 6.6. While the evolutionarily stable attachment level (red lines) are not affected very much, the direction of selection on the movement strategy (blue lines) gets reversed by the addition of group-level selection. As a consequence, the two evolutionary attractors in Figure 6.6A (corresponding to either a random distribution in case of $\tau^* = 0$ or to a highly clumped distribution in case of $\tau^* = 1$) are replaced by a single joint evolutionarily stable strategy with an intermediate value of τ^*, corresponding to a labyrinth-like distribution of mussels. Figure 6.7 provides a more comprehensive analysis of the effect of multi-level selection on spatial pattern formation. For a broad range of environmental conditions (food availability and predation risk), the
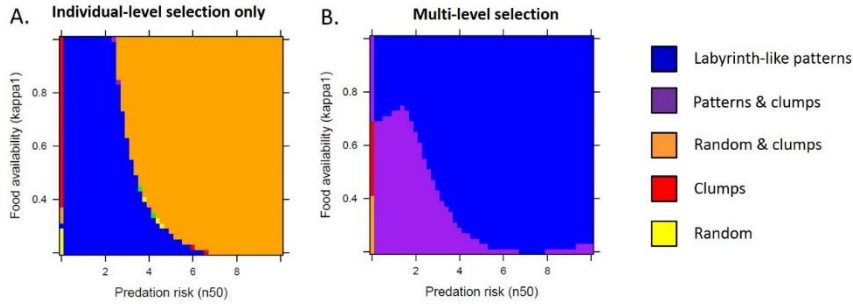
Figure 6.7: Evolved spatial patterns in case of individual-level selection (**A**) and multi-level selection (**B**) in relation to predation risk and food availability. The blue areas indicate environmental conditions leading to a combination of movement and attachment strategies that result in labyrinth-like patterns (see Figure 6.1B), which are characteristic for mussel beds. The purple areas correspond to conditions that can alternatively result in labyrinth-like patterns or dense clumps, depending on the initial conditions. The orange areas indicate conditions leading either to dense clumps or to a random distribution of mussels, again depending on initial conditions. Conditions indicated by red give rise to densely clumped populations, while those indicated by yellow lead to random distributions.

evolutionary outcomes are classified according to the resulting spatial distribution of mussels in the absence (Fig. 6.7A) and in the presence (Fig. 6.7B) of group-level selection. A comparison of both outcomes clearly reveals that the inclusion of group-level selection is favourable for the emergence of labyrinth-like patterns, which occur under a much broader range of conditions than in the absence of group-level selection. The same conclusion was drawn for other environmental scenarios (results not shown). As labyrinth-like patterns are a predominant feature of mussel beds, we conclude that group-level selection is potentially an important driver of spatial self-organization in mussel beds.

Discussion

We developed an eco-evolutionary model for the joint evolution of movement and attachment in mussel beds, to understand how cooperation can emerge in a spatially structured system. Here, the interplay of ecological (spatial pattern formation determining selection gradients) and evolutionary processes (adaptive changes in the parameters determining the process of pattern formation) proved critical in explaining both the adaptations of the mussels and the spatial structure

of the mussel bed. To study this interplay, we used a three-step approach: (i) individual-based simulations of within-generation dynamics of pattern formation, (ii) distilling the selection gradient vector field from these simulations, and (iii) inferring the direction and long-term outcome of evolution by means of adaptive dynamics techniques. We demonstrate that the interplay between ecological and evolutionary processes, characterized by the simultaneous evolution of multiple traits and the generation of large-scale spatial structures, significantly alters evolutionary processes.

Our model makes use of many previous studies that provided a rather detailed picture of mussel movement and the spatial self-organization of mussel beds (e.g., Van de Koppel *et al.*, 2008; De Jager *et al.*, 2011). This allowed us to take over parameters of the movement model that are well supported by experimental and field data. Other aspects of our model are less well supported. In particular, our assumptions on the costs and benefits of movement and attachment are more based on plausibility arguments than on empirical evidence. For this reason, our model cannot yield specific, quantitative predictions. Yet, we hope that it provides interesting qualitative insights into how eco-evolutionary feedbacks shape the spatial structure of mussel beds.

It is widely acknowledged that spatial structure plays a crucial role for the evolution of cooperation (Nowak & May, 1992; Ohtsuki *et al.*, 2006; Allen *et al.*, 2013). Most model studies consider spatial structure as externally given and fixed (e.g. Nowak & May, 1992; Vainstein & Arenzon, 2001; Zhang *et al.*, 2005; Ohtsuki *et al.*, 2006; Hui & McGeoch, 2007; Allen *et al.*, 2013). In contrast, our model takes account of the fact that in many organisms spatial population structure is actively modified by the activities of the organisms themselves and therefore emerges through spatial self-organization (e.g. Bonabeau *et al.*, 1997; Gautrais *et al.*, 2004; Jeanson *et al.*, 2005; Moussaid *et al.*, 2009; De Jager *et al.* 2011). Our study highlights that this can be of crucial importance for evolutionary processes, changing evolutionary outcomes.

In most evolutionary models, cooperativeness is considered a univariate trait. However, cooperation is an intricate process that manifests itself in multiple

aspects. In order to get a good impression of cooperation in real-world systems, a multivariate approach is often a necessity. Our study highlights that investigating the evolution of just a single trait without considering mutually dependent companion traits can be misleading. Even though the joint evolution of multiple traits is likely the rule rather than the exception, the eco-evolutionary analysis of multivariate evolution is still in its infancy (Leimar, 2009; Metz & De Kovel, 2013). Yet, studying the interplay of multiple traits that – through the interactions of their ecological functions - define the fitness of individual organisms may prove crucial for a thorough understanding of eco-evolutionary dynamics.

An important insight from our model is the emergence of multi-level selection from the aggregative movement of the mussels. By aggregating into tight clumps, mussels improve their own survival, but also that of the others in the group, as the persistence of clumps of mussels is determined by group-level properties such as clump size. As persistence on a mussel bed strongly affects survival, there is a considerable effect of the properties of the clump on individual fitness. Strikingly, this clump effect emerges from the evolution of traits that determine aggregative movement and attachment, through the processes of ecological self-organization (De Jager *et al.*, 2011). Earlier empirical and theoretical studies on group-level selection make use of clearly defined groups, which are rarely intermixed between generations (e.g. Wade, 1967; Wade, 1977; Craig, 1982; Goodnight, 1985). By keeping groups intact, multigenerational population differentiation can occur, which augments selection between groups (Wade, 1978; Harrison & Hastings, 1996; Goodnight & Stevens, 1997). The individuals in natural mussel beds are derived from a highly mixed common pool of offspring, and different groups are therefore not genetically isolated. In contrast to statements in the literature (e.g. Harrison & Hastings, 1996), our model demonstrates that homogenization of groups does not prevent group selection to be effective.

Our study highlights the importance of ecological self-organization on the effect of selection pressures in real-world populations. Interestingly, selection at the group level in the context of self-organized mussel beds is an emerging feature of individual-level interactions. In contrast with other studies on group-level selection (Maynard Smith, 1964; Williams, 1966; Okasha, 2004; West *et al.*, 2007 & 2008;

Leigh, 2010; Burton *et al.*, 2012), selective forces at the group level are not always opposing selection processes occurring at the individual level. As such, our model provides a more realistic view of multilevel selection in nature, where group-level selection does not only express itself as a force counteracting individual-level selection, but also as one enhancing selection. To understand evolutionary processes in the context of real-world ecosystems, it is crucial to realize that the interplay of ecological and evolutionary processes can be an important determinant of the adaptations of individual species.

Appendix A: Model assumptions on fitness

We consider a population with discrete, non-overlapping generations. The reproductive contribution of individuals to the next generation is given by the product of survival until reproduction (S) and fecundity (F):

$$W = F \cdot S. \tag{6.1}$$

We assume that fecundity is proportional to the energy available upon reproduction, and that this energy is given by some baseline level minus the energy spent on movement and the energy spent on the production of byssal attachments:

$$F = \kappa_1 - \kappa_2 \cdot D - \kappa_3 \cdot A. \tag{6.2}$$

Here, κ_1 is the total amount of energy available for movement, byssus production, and reproduction, κ_2 is the energy it takes to move one unit centimetre, and κ_3 is the energy used for creating and attaching a single byssus thread. D represents the total distance moved per individual during the simulation and A is the number of byssus threads produced by this individual.

In our model, survival can act on the individual level and on the level of mussel clumps. We assume that individual-level survival (S_{IL}) is positively related by the number of neighbours N to which a mussel is directly attached by byssus threads. To be specific, individual-level survival is given by a logistic function:

$$S_{IL}(N) = (1 + e^{\lambda_n \cdot (n_{50} - N)})^{-1}. \tag{6.3}$$

The parameter n_{50} denotes that density of attached neighbours for which this survival probability is equal to 50%. To reduce the number of model parameters, we assumed that in all scenarios considered the survival probability in the absence of attached neighbours was constant and given by $S_{IL}(0) = 0.01$. As a consequence, we can get rid of the parameter λ_n and re-write (6.3) as follows:

$$S_{IL}(N) = (1 + 99 * e^{-\ln(99)N/n_{50}})^{-1}.$$
(6.4)

Similarly, we assume that group-level survival is positively related to group (= clump) size G and given by the logistic function:

$$S_{GL} = (1 + 99 * e^{-\ln(99)G/g_{50}})^{-1}. \qquad (6.5)$$

G is the total number of individuals that is directly and indirectly linked to the focal individual by byssal attachments to either this individual, its neighbours, the neighbours of its neighbours, etcetera; g_{50} denotes the clump size for which the group-level survival probability is equal to 50%.

In the first part of our analysis, we only considered individual-level selection. This was done by equating overall survival with individual-level survival: $S = S_{IL}(N)$. In the second part, we assumed that overall survival is given by the geometric mean of individual-level and group-level survival:

$$S = S_{IL}^{0.5} \cdot S_{GL}^{0.5}. \qquad (6.6)$$

Appendix B: Determination of selection gradients by linear regression

Each simulation with the IBM gives us a distance moved (D), byssus threads attached (A), number of attached neighbours (N), and group size (G) for one individual of every mutant type (see Figure 6,3B) and one resident. Given a set of parameter values (κ_1, κ_2, κ_3, n_{50}, and g_{50}), we calculated the fitness of each of these individuals (see Appendix A). Because the IBM is highly stochastic, we repeated each simulation 100 times, for 21 x 21 different resident strategy combinations of attachment and movement. These simulations thereby provided 100 x 21 x 21 x 9 = 396900 data points, which we used in a multiple linear regression to smoothen the IBM results. We estimated the fitness of an individual with movement strategy τ and attachment strategy α in a resident population that uses strategies τ_{res}, α_{res} using linear regression in R (lm, R Core Team; 2014):

$$
\begin{aligned}
W(\tau, \alpha | \tau_{res}, \alpha_{res}) = {} & \beta_{0000} + \beta_{1000}\tau_{res} + \beta_{0100}\alpha_{res} + \beta_{0010}\tau + \beta_{0001}\alpha + \\
& \beta_{1100}\tau_{res}\alpha_{res} + \beta_{1010}\tau_{res}\tau + \beta_{1001}\tau_{res}\alpha + \beta_{0110}\alpha_{res}\tau + \beta_{0101}\alpha_{res}\alpha + \\
& \beta_{0011}\tau\alpha + \beta_{1110}\tau_{res}\alpha_{res}\tau + \beta_{1101}\tau_{res}\alpha_{res}\alpha + \beta_{1011}\tau_{res}\tau\alpha + \beta_{0111}\alpha_{res}\tau\alpha + \\
& \beta_{1111}\tau_{res}\alpha_{res}\tau\alpha,
\end{aligned}
\tag{6.7}
$$

where $\beta_{0000} - \beta_{1111}$ are the regression coefficients. The relative fitness of each mutant can now be estimated as $W(\tau,\alpha \mid \tau_{res},\alpha_{res}) / W(\tau_{res},\alpha_{res} \mid \tau_{res},\alpha_{res})$. Considering the relative fitness of the 8 mutants for each resident strategy combination, we determined the vector fields of the selection gradients.

7

General discussion:

Patterning in mussel beds explained by the interplay of multilevel selection and spatial self-organization

Monique de Jager

General Discussion

Nature often is amazingly complex. A wide variety of complex spatial patterns can be found throughout nature, ranging from the organization of molecules (Hogeweg & Takeuchi, 2002) to the formation of regular, self-organized patterns at the scale of entire ecosystems (i.e. Klausmeier, 1999; Rietkerk *et al.*, 2004a&b; Van de Koppel *et al.*, 2005 & 2008; Eppinga *et al.*, 2009). Self-organized patterns in ecosystems develop from the actions of and interactions between organisms. The behaviour of these individuals is an important driving force behind spatial self-organization. Yet, this behaviour has evolved to its present form partly as a consequence of this self-made environment. Hence, feedback between self-organization of ecosystems and the evolution of individual behaviour is quite apparent. Nevertheless, scientists generally research self-organization and evolution separately and thereby disregard this feedback (but see Kéfi et al., 2008; Xavier et al., 2009). Neglecting eco-evolutionary feedbacks in self-organized ecosystems might have considerable consequences, especially when incorrect conclusions are drawn from ecological models.

Throughout the chapters of this thesis, I have demonstrated that close feedback between the evolution of individual behaviour and the spatial complexity of their community is essential to explain the cooperative behaviour and movement strategies of organisms. To examine eco-evolutionary feedbacks in self-organized systems, I used intertidal mussels as my main experimental system and model template. By moving into clumps and attaching to close neighbours, mussels build extensive spatial networks that minimize losses due to predation and wave dislodgment (Hunt & Scheibling, 2001, 2002; Van de Koppel *et al.*, 2005, 2008). Mussels were found to apply a specific movement strategy – a Lévy walk – that maximizes the speed of pattern formation (**Chapter 2**). The active aggregation of mussels into labyrinth-like patterns promotes the evolution of between-mussel cooperation, where mussels affix themselves with byssus threads to neighbouring conspecifics to decrease dislodgment risk by wave stress and predation (**Chapter 5**). In turn, the labyrinth-like pattern is the consequence of multilevel selection processes acting on the joint evolution of aggregative movement and between-mussel cooperation (**Chapter 6**). The results shown in this thesis leave me to conclude that feedback between ecological and evolutionary processes are

fundamental to self-organization of mussel beds and, most likely, to many other complex ecosystems.

In this chapter, I discuss the most important results presented in my dissertation. A detailed account of the work described here can be found in the previous chapters. In my thesis, I have focused mainly on the effect of eco-evolutionary feedback on two behaviours: movement and cooperation. In the following sections, I first discuss how mussel movement strategies are affected by self-made environmental complexity. Second, I deliberate on the effect of the self-generated spatial population structure on the evolution of cooperation and, in turn, on the influence of evolution on spatial self-organization. In the final section, I review the main conclusions that can be drawn from my findings. In general, my results suggest that eco-evolutionary feedbacks have important consequences for both the behaviour of individuals and the complexity of ecosystems.

Ecological interactions drive animal movement patterns

How feedback leads to Lévy walks

Over the past years, ecologists have found a growing body of empirical evidence on Lévy walks in animal movement patterns. A Lévy walk is a random search strategy which alternates many small steps with occasional long moves and is therefore superdiffusive by nature (Viswanathan *et al.*, 2000; Codling *et al.*, 2008). With modern technology advancing GPS tracking systems and high-resolution imaging, superdiffusive Lévy-like movements have been observed in a wide variety of species, such as soil amoebas, bees, seabirds, seals, spider monkeys, predatory fish, and even humans (Heinrich, 1979; Viswanathan *et al.*, 1996; Sims *et al.*, 2000; Austin *et al.*, 2004; Ramos-Fernandez *et al.*, 2004; Bertrand *et al.*, 2007; Reynolds *et al.*, 2007). One of the main concerns about these empirical findings is that the notion of Lévy movement being a widespread phenomenon clashes with classical optimal foraging theory. In theory, an organism adopts a certain movement strategy if it optimizes the individual's search efficiency. Computer simulations have shown that Lévy walks are only optimal under highly specific conditions, which are quite rare in nature (Viswanathan *et al.*, 1999; Bartumeus *et al.*, 2005; Sims *et al.*, 2008; Bartumeus, 2009; Reynolds & Bartumeus, 2009). Therefore, Lévy-

like movement should not be as omnipresent as is suggested by the broad range of empirical studies. How and why Lévy walks have evolved in these systems is an important question that, until now, has remained unanswered (Reynold & Rhodes, 2009).

The theoretical models predicting the rare occurrence of Lévy walks in nature generally disregard some key aspects of standard animal life. For one, most animals are not alone; they often share their habitat and resources with other individuals. Studies on the search efficiency of different movement strategies all base their conclusions on models of single individuals, without any interference of other organisms. Another essential aspect that is frequently overlooked concerns movement of the resource. By taking these ecological interactions in account, other conclusions might be drawn than those found in previous papers (Viswanathan *et al.*, 1999; Bartumeus *et al.*, 2005; Sims *et al.*, 2008; Bartumeus, 2009; Reynolds & Bartumeus, 2009). Furthermore, an examination of eco-evolutionary dynamics might aid in understanding why many animal species are moving in a Lévy-like fashion. In contrast to earlier models of search efficiency, I incorporate natural encounters with other moving individuals in my individual-based model and thereby examine search efficiency within a more realistic setting.

In **Chapter 2** of this thesis, I demonstrate how Lévy walks in mussel movements may have evolved through feedback between mussel movement and spatial patterning. Using mesocosm experiments, I observed mussels moving in a Lévy-like fashion when solitarily searching for conspecifics. Whereas previous studies on seach efficiency have disregarded most ecological encounters (Viswanathan et al., 1999; Bartumeus et al., 2005; Sims et al., 2008; Bartumeus, 2009; Reynolds & Bartumeus, 2009), I show that interactions with the biotic environment are of key importance to explain the occurrence of Lévy walks in mussel beds. Lévy movement can result from feedback between mussel movement behaviour and self-organized environmental complexity. Mussels that efficiently move into an aggregation save valuable time and energy: speeding up pattern formation decreases the time spend being vulnerable to predation and wave disturbance, and limited displacement reduces the energy spend on movement. In self-organized mussel beds, a Lévy walk is a very efficient random search strategy

(see Fig. 2.2). Individuals that use an efficient search strategy, such as a Lévy walk, are likely to gain higher fitness over less efficient conspecifics, thereby increasing the frequency of efficiently moving individuals in the next generation. Simultaneously, pattern formation is accelerated with each increase in Lévy walkers within the population, which again enhances fitness advantages of efficient individuals. Overall, an eco-evolutionary feedback can explain how individual search strategy and large-scale, self-organized pattern formation leads to the evolution of Lévy-like movement in intertidal mussel beds.

Although I address a specific study system, the assumption that movement strategies can evolve through eco-evolutionary feedback may be broadly applicable. By replacing the externally determined environment – which has been the default template in studies on search efficiency – with an environment that is to a large extent shaped by the organisms themselves, Lévy walks may be found within a much broader range of conditions than was previously believed. This feedback between animal movement and environmental heterogeneity provides a potential explanation for the numerous empirical observations of Lévy walks throughout nature (Ramos-Fernandez *et al.*, 2004; Reynolds *et al.*, 2007; Sims *et al.*, 2008; Humphries *et al.*, 2010). Because animal movement patterns are for a substantial part reflected in the spatial distributions of their resources (Adler *et al.*, 2001; Boyer & Lopez-Corona, 2009), eco-evolutionary interactions between animal movement and environmental complexity are not limited to aggregation with conspecifics, but also occur in the search for resources shared with conspecifics. My study reveals that eco-evolutionary feedback between animal movement and habitat complexity is of key importance in understanding both the evolution and the ecology of animal movement strategies.

A close encounter with Brownian motion

Having a sufficiently accurate representation of animal movement in ecological models is of crucial importance for the truthfulness of model results. Although previous studies have shown the occurrence of superdiffusive movement in many animal species (Ramos-Fernandez *et al.*, 2004; Klafter & Sokolov 2005; Reynolds *et al.*, 2007; Sims *et al.*, 2008; Humphries *et al.*, 2010), normal diffusion – which is based on Brownian movement patterns – remains the default template for animal

movement in most ecological models (Skellam 1951; Kareiva & Shigesada 1983; Benhamou 2007; Sims *et al.* 2008; Edwards *et al.* 2012). The most curious thing about the use of diffusion as a description of animal movement is that it (i) is based on the generality of the physical process of diffusion rather than on empirical observations of animal movement and (ii) that it is used as being density-independent, which contradicts the original mechanism as put forward by Einstein, where interactions between particles generate Brownian motion (Einstein, 1905; Langevin, 1908).

Similar to Brown's observations of pollen grains moving in a Brownian fashion (Brown, 1828), we observed mussels moving in Brownian patterns, especially when found in high density mussel clumps. Albert Einstein explained the Brownian movements of dissolved particles like pollen grains as the consequence of collisions with water molecules (Einstein, 1905; Langevin, 1908). In **Chapter 3** of this thesis, I demonstrate that animal movements are similarly affected by their environment, as intended steps are prematurely ended whenever an obstacle, such as a resource or predator, is encountered.

Our findings have some major implications for current ecological modelling. First, Brownian motion should no longer be used as the default animal movement pattern, because it is not necessarily the intrinsic movement strategy for many animals (Klafter & Sokolov 2005). Second, animal movement should be described as a density-dependent process. Using a simple model, I have shown how *any* intrinsic movement pattern can become Brownian-like in resource-rich environments. My own empirical observations as well as those of others of animals displaying Lévy-like movement in areas with low resource density and Brownian movement patterns in dense environments further confirm that animal movement is a density-dependent process (Bartumeus *et al.*, 2003; De Knegt *et al.*, 2007; Humphries *et al.*, 2010; Humphries *et al.*, 2012). As Brownian motion is currently used as a default template of animal movement, ecological models of resource-poor habitats might strongly deviate from reality. A better understanding of the interaction between ecological encounters and animal movement is needed to improve theoretical models and to explain how animal movement patterns may influence natural processes.

Using ecological interactions to identify real Lévy walks

Whether the superdiffusive movement patterns observed in nature are actual Lévy walks or consist of multiple different movement modes is currently highly debated (Benhamou 2007; Petrovskii *et al.*, 2011; Jansen *et al.*, 2012; De Jager *et al.*, 2011). Researchers argue that the power law distributions that indicate a Lévy walk may actually be composed of a collection of multiple movement strategies (Benhamou 2007; Petrovskii *et al.*, 2011). For instance, the Lévy-like shape of a step length distribution could be an artefact of pooling the movement trajectories of different individuals (Petrovskii *et al.*, 2011). Analysis of single movement paths, as I did in **Chapters 3** and **4**, can prevent this confusion. Furthermore, a movement trajectory that seems Lévy-like might be generated by a composite movement strategy, where an organism shifts from one movement mode to another with changing environmental conditions, such as ecological encounters (Jansen *et al.*, 2012; De Jager *et al.*, 2012b). Using the traditional approach of fitting movement strategies to step length distributions, one cannot distinguish between true Lévy walks and composite multi-scale walks. In **Chapter 4** of this thesis, I am able to differentiate Lévy-like movement patterns from composite Brownian walks by examining the overlap between ecological encounters and clusters of small steps. A characteristic of Lévy walks is that clusters of small steps arise at random locations, irrespective of the underlying resource distribution. In contrast, a composite walk will result in small-step clusters only at resource patches. By recording the frequency of small step clusters coinciding with food patches, I demonstrated that mud snails are using a Lévy-like search strategy instead of a composite Brownian walk. We observed clear clusters of local search on bare substrate, and in bare areas in between food patches, despite the absence of food that was presumed to trigger local search. In all cases where both the movement path and resource availability can be recorded, this novel technique can help gaining insight in the composition of the used movement strategy. The additional information obtained from recording ecological encounters can be of key importance when disentangling different movement strategies. Using this novel method, I can validate that Lévy walks are intrinsic strategies rather than a mixture of reactions to a complex environment. This result changes our understanding of Lévy movement

substantially, especially for those who did not believe that these scale-free strategies could exist.

Eco-evolutionary feedback drives spatial self-organization

How cooperation is affected by spatial population structure

The evolution of cooperation is one of the most frequently investigated enigmas in evolutionary ecology (Doebeli & Hauert, 2005; Lehman & Keller, 2006; West, Griffin & Gardner, 2007, 2008). It is common knowledge that spatial population structure can affect the evolution of cooperation through the clustering of cooperative relatives (Nowak & May, 1992; Vainstein & Arenzon, 2001; Ishibuch & Namikawa, 2005; Zhang *et al.*, 2005; Kun *et al.*, 2006; Ohtsuki *et al.*, 2006; Hui & McGeoch, 2007; Kéfi *et al.*, 2008; Szamado *et al.*, 2008); however, it is not straightforward how spatial structure can affect cooperation when offspring is dispersed over a wide range rather than locally. In game theory, where cooperative strategies are played out against each other, theorists generally assume local interactions and local dispersal of cooperative strategies. Yet, many species that indeed interact locally, still disperse over a wide range (Godfrey & Kerr, 2009). Hence, current models are insufficient in explaining the influence of active aggregation on the evolution of cooperation in populations with wide-ranging dispersal.

In **Chapter 5** of this thesis, I demonstrate that local dispersal is not a prerequisite to find an effect of spatial population structure on the evolution of dispersal. As mussels aggregate into patterned mussel beds, they actively promote cooperation between unrelated conspecifics. Taking cooperation in mussel beds as an example, I suggest that active movement into spatial patterns can be a fundamental solution to the question of how cooperation can evolve in species with wide ranging dispersal. Indeed, many natural populations seem to be spatially aggregated (Bel'kovich, 1991; Heppner, 1997; Camazine *et al.*, 2001; Parrish *et al.*, 2002; Bonner, 2009); finding out how spatial heterogeneity can alter an individual's cooperative investment for any of these species would be of great interest to those who seek the holy grail of the evolution of cooperation.

Spatial self-organization causes and results from the interplay of multilevel selection and joint evolution

Models explaining ecological or evolutionary processes should be sufficiently simple to deliver understandable results and limit computational time. Yet, they should not be too simple, in which case incorrect conclusions might be drawn. For instance, overly simplistic models of search efficiency could not explain the widespread prevalence of Lévy walks in nature, as I argue in **Chapter 2** (Viswanathan *et al.*, 1999; Bartumeus *et al.*, 2005; Sims *et al.*, 2008; Bartumeus, 2009; Reynolds & Bartumeus, 2009). Similarly, models of the evolution of cooperation are also generally based on basic assumptions that are rarely met in real world systems, and may therefore give incorrect results. For example, the occurrence of lattice-structured populations in nature is definitely not as omnipresent as the prevalence of theoretical cooperation studies that use lattice-structured models might suggest (i.e. Nowak & May, 1992; Lindgren & Nordahl, 1994; Brauchli, Killingback, & Doebeli, 1999).

In models of cooperation, we often neglect the fact that most organisms are mobile and can decide on where and when to aggregate or cooperate. Moreover, the decision to aggregate is a behavioural strategy which can, or even has to evolve simultaneous with cooperative behaviour. In this thesis, I show that this joint evolution of movement and cooperation leads to the emergence of different large-scale patterns than when only a single trait is involved. Yet, my work revealed that multilevel selection provided a superior explanation of the patterns that we observe in real mussel beds. The spatial structure that emerges within the population can be of great importance for the survival of the organisms, and adds another – generally neglected – level of selection. To enhance our understanding of cooperation in nature, case-specific, realistic models are needed that are more specifically tailored to a particular real-world system.

In **Chapter 6** of my thesis, I demonstrate how the interplay between movement and cooperative behaviour generates an additional level of selection

emerging from self-organization, which provides a superior explanation for labyrinth-like patterns observed in mussel beds. Using a novel technique, I show that joint evolution of two traits can result in different evolutionary stable strategies than when only a single trait is allowed to evolve. This feedback between the evolution of one trait and the evolution of another trait can give rise to strategies that considerably deviate from the conclusions drawn with a single-trait model. I illustrate this by comparing the resulting aggregative movement behaviour of mussels – which for a large part drives self-organized patterning of mussel beds – between a model that involves a constant level of cooperation and one that includes the evolution of both cooperation and movement. Although I use two jointly evolving traits as an example, it is highly probable that more traits evolve simultaneously; it would be a great challenge to model joint evolution of more than two traits.

The joint evolution of aggregative movement and cooperative behaviour in mussels underlies the emergence of spatially patterned mussel beds. Due to the structure of these spatial patterns, self-organization in mussels gives rise to a second level of selection: selection at the clump level. With a simple field experiment, I demonstrated that small clumps of mussels are more easily dislodged than large clusters, which indicates that clump size affects mussel survival. By including clump-level selection in my model of joint evolution, labyrinth-like patterns emerge more frequently from the joint evolution of movement and cooperation than when only considering individual-level selection. This result indicates that selection at higher levels than the individual can be of great importance for the fate of the entire population; also, it shows that overlooking mechanisms of selection can have vast consequences for the accuracy of model outcomes.

In the end…

Spatial patterning is ubiquitous in nature and is known to emerge from self-organization in many ecosystems (Klausmeier, 1999; Mistr & Bercovici, 2003; Rietkerk *et al.*, 2004a; Rietkerk *et al.*, 2004b; Van de Koppel *et al.*, 2005; Van de Koppel & Crain, 2006; Van de Koppel *et al.*, 2008; Eppinga *et al.*, 2009). Patterns as diverse as gaps, spots, labyrinths and stripes can be generated by simple

interactions between organisms and may enhance the system's resilience. Ecological models have been created to increase our understanding of self-organization in patterned ecosystems and to predict how these systems will react to changes in environmental conditions (Rietkerk *et al.*, 2004). Yet, by disregarding evolution of self-organizing traits, incorrect conclusions may be drawn from these models. By taking evolutionary processes into account, I demonstrate that eco-evolutionary feedback is of key importance for spatial patterning in self-organized ecosystems and their response to environmental changes. Because evolutionary adaptation can change interactions between organisms, it may also affect the spatial complexity of ecosystems. In turn, spatial patterns are in part responsible for the fitness differences between individuals, leading to the next adaptation. Within this feedback, complex dynamics can arise, such as the joint evolution of multiple traits or the emergence of a higher-order level of selection through self-organization into large-scale patterns. Understanding eco-evolutionary dynamics is of crucial importance if we want to predict how ecosystems respond to man-made changes to the environment, such as accelerated global warming or habitat fragmentation. The research presented in this thesis will provide us more insight into eco-evolutionary feedbacks in self-organized ecosystems and will hopefully be an inspiration for future research within this exciting field of science.

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Summary

Spatial patterns in natural systems may appear amazingly complex. Yet, they can often be explained by a few simple rules. In self-organized ecosystems, complex spatial patterns at the ecosystem scale arise as the consequence of actions of and interactions between organisms at a local scale. Aggregation into large-scale patterns may, however, also affect the survival and fitness of individuals within the ecosystem. As a consequence, pattern-producing behaviour in turn may have evolved as an adaptation to this self-generated environment in what is called an eco-evolutionary feedback process. Strikingly, both empirical and theoretical studies on eco-evolutionary feedbacks in self-organized ecosystems are rare. In this dissertation, I investigated the interplay between the ecological process of pattern formation and the evolution of two patterning-related traits: movement and attachment.

I investigated the interplay between the evolution of self-organizing behaviour and the emergent large-scale patterns by performing both ecological experiments and eco-evolutionary computer simulations. For this purpose, I used mussel beds as my main model system. On intertidal sandbanks, young mussels move into labyrinth-like patterns after settlement. Mussels need sufficient neighbours in close proximity to decrease the risk of being dislodged by wave stress or predation. To accomplish this, mussels attach a glue-like substance called byssus threads to other individuals, and form dense clumps. However, gaps in between dense mussel clumps are needed to reduce competition for suspended algae. Because competition occurs over a larger range than attachment, self-organized patterns emerge in the mussel bed in the form of regularly spaced, labyrinth-like strings. The formation of labyrinth-shaped patterns increases the within-clump density of mussels while keeping the long-range mussel density low enough to prevent food competition. Two behavioural traits are mainly responsible for self-organization in mussel beds: movement and attachment. Without movement, mussels cannot search for conspecifics to aggregate with; without attachment (in the form of byssal threads), self-generated spatial patterns will not last very long, as unattached individuals are easily dislodged by waves. Investigating the eco-evolutionary feedback between mussel bed formation and the evolution of

movement and attachment can provide us with interesting insights into eco-evolutionary feedbacks in self-organized ecosystems in general.

Using movement trajectories recorded during mesocosm experiments, I observed that mussels use a particular movement strategy. Movement patterns of solitary mussels are similar to a Lévy walk, where many short steps are alternated with very long moves. Lévy walks are frequently observed in nature, yet theoretical models suggest that habitats in which Lévy walks are optimal are rare, as Lévy walks are only optimal when resources are scarce and heterogeneously distributed. In **Chapter 2**, I argue that the occurrence of Lévy-like movements in mussel beds is due to the eco-evolutionary feedback between self-organized pattern formation and mussel movement. To prove this hypothesis, I simulated mussel bed formation with an individual-based model, where I varied the movement strategy used by the virtual mussels between model runs. The results of these simulations show that a spatially patterned mussel bed is generated most efficiently when mussels make use of a Lévy walk. Further evolutionary analyses, where I test for the invasion success of mutant movement strategies in a mussel population in which all other individuals adopt a resident movement strategy, demonstrate that Lévy walks evolve in my simulated self-organized mussel beds. Because Lévy walks accelerate pattern formation and the spatial pattern in turn increases the survival of these Lévy walkers, my results suggest that, in mussel beds, Lévy walks evolve through an eco-evolutionary feedback between mussel movement and self-organized patterning. Although my model is specifically designed to simulate mussel movement in self-organized mussel beds, the conclusions drawn from this study may explain why Lévy walks are found under much broader conditions than is currently explained in mathematical models.

Despite the increasing prevalence of observations of Lévy walks in nature, empiricists more and more notice that organisms might do a Lévy walk in one environment, but a Brownian walk in another. Lévy walks are frequently observed in the movement patterns of organisms that are searching for resources in resource-poor habitats, whereas their movements appear more Brownian-like, with more intermediate-sized steps and fewer large moves, in resource-rich areas. This phenomenon is often explained as an active switch in movement strategy to

optimize search efficiency in both environments. Opposing this view, I hypothesized in **Chapter 3** that the intrinsic movement strategy does not change but rather that the observed movement pattern is the consequence of interactions with the environment. Following Einstein's perspective on Brownian motion in atoms and molecules, I argued that collisions with other objects such as resources or conspecifics causes a move to be prematurely ended. In areas with few objects to encounter, an organism's movement pattern would not be unrecognizably altered. In dense environments, however, the frequent occurrence of encounters transforms any movement strategy into a Brownian-like pattern. By analysing mussel movement in five different density treatments, I show that observed movement patterns become more Brownian-like with increasing mussel density. In **Chapter 4**, I found similar results for the movements of mud snails. I verified that this shift to Brownian motion is caused by collisions with conspecifics by disentangling truncated steps and moves into free space, demonstrating that the movement strategy does not change when only considering non-truncated steps. With individual-based model simulations, I showed that an active shift from Lévy to Brownian motion with increasing mussel density is unnecessary, as Lévy walks are equally efficient as Brownian movement in creating spatially patterned mussel beds at high mussel densities. Furthermore, I analytically confirmed the hypothesis that any movement strategy becomes more Brownian-like with increasing encounter rates using a simple argument. My results suggest that observed Brownian patterns in the movement trajectories of animals in their natural habitat can be the consequence of superdiffusive intrinsic movement that is altered by target density.

Whether Lévy walks observed in nature are actual Lévy walks or the product of a mixture of different strategies (a 'composite Brownian walk') is currently under debate. Using traditional methods, one cannot distinguish between the two movement types. In **Chapter 4**, a novel technique is demonstrated that helps distinguishing between true Lévy walks and composite movement strategies, by examining whether clusters of small steps coincide with resource patches (which would be indicative of a composite Brownian walk). Using a mud snail experiment as an example, it was shown that local search clusters are not only produced in food patches but also on bare soil, demonstrating that true Lévy walks

may indeed exist in nature. The ability to extract intrinsic movement strategies from observed movement patterns (**Chapter 3**) and to distinguish between different movement strategies (**Chapter 4**) can have great implications for the representation of animal movement in ecological modelling: the use of Brownian motion as a default template for animal movement is not always justifiable and should be replaced by a more realistic, density-dependent type of movement template.

Mussels, as well as many other organisms, actively aggregate into groups, where they cooperate with neighbouring conspecifics. Because cooperation can be exploited by individuals that do not contribute, the widespread occurrence of cooperation in nature remains puzzling. Theoretical studies have shown that the spatial structure of a population can promote the evolution of cooperation. However, these studies consider local dispersal to be the driving factor behind both the spatial patterning and the occurrence of cooperation, thereby disregarding the fact that many species disperse over a wide range and yet cooperate locally. In **Chapter 5**, I demonstrated how spatial population structure affects the evolution of investment into byssal thread attachments in spatially patterned mussel beds. Using a simple model, I showed that active aggregation into dense mussel clumps gives rise to the highest levels of cooperativeness over a wide range of environmental stress. These results suggest that active clustering can promote the evolution of cooperation even when offspring are widely dispersed.

Cooperation and aggregative movement are two fundamental behaviours that form the foundation of self-organization in mussel beds. Without movement into clusters, mussels are unable to attach their byssus threads to neighbouring conspecifics, and without cooperation, movement into clusters would be a useless endeavour. Because movement and cooperative behaviour are quite dependent on one another, evolution of one of these traits is likely to affect evolution of the other and, subsequently, the spatial pattern that will be generated in the mussel bed. In **Chapter 6** of this thesis, I showed that the joint evolution of cooperation and aggregative movement can result in differently patterned mussel beds than when only one of the two behaviours is allowed to evolve in isolation. In most evolutionary models, evolution of other than the one focal trait is habitually

disregarded; my results demonstrate that this may lead to drawing the wrong conclusions.

The self-organized pattern that emerges from the individuals' movement and cooperation in turn also affects the persistence of mussel clumps. With a simple field experiment, I showed that not only inadequately attached mussels can become dislodged by wave stress or predation, but that similarly, small mussel clumps are also more vulnerable to dislodgement than large clumps. Dislodgement often implies removal from the mussel beds into suboptimal habitats with high risk of predation and low food availability. Hence, mussel mortality is linked to the persistence of clumps formed by the self-organization process, and clump persistence thereby influences the selection of particular traits. Hence, a loop develops, where the ecological process of pattern formation adjusts selection processes acting upon the mussels, which than in turn alter the ecological process of pattern formation. Adding this group-level mechanism of selection to our model in **Chapter 6** leads to a substantially higher occurrence of the emergence of labyrinth-like patterns than simulations with individual-level selection only. As these patterns are frequently observed in natural mussel beds, these results suggest that multi-level selection is of key importance in the eco-evolutionary feedback that leads to the formation of spatially patterned mussel beds.

My findings demonstrate that eco-evolutionary feedbacks are of great importance for the evolution of traits that trigger spatial self-organization in ecological systems. At the individual level, self-organizing traits such as movement or attachment can evolve through the interplay between evolution of individual behaviour and the spatial complexity of the community. As large-scale, self-organized patterns are generated by the actions of and interactions between individuals, pattern formation is similarly affected by this eco-evolutionary feedback that often involves traits that modify the environment. In more general terms, an organism's behaviour can affect its environment, which in turn influences the fitness of this individual and of others. The eco-evolutionary feedback that arises from the interplay between individual behaviour and spatial patterning can fundamentally alter the mechanisms that drive evolutionary

change by generating a group effect on survival, leading to an additional selection process affecting individual fitness. To truly understand ecological and evolutionary processes in nature, it is of key importance to study eco-evolutionary interactions as they develop in the complex settings of the natural world.

Samenvatting

Ruimtelijke patronen in natuurlijke systemen lijken soms ongelooflijk complex. Toch kunnen ze vaak verklaard worden met een paar eenvoudige regels. Grootschalige, complexe ruimtelijke patronen in zelfgeorganiseerde ecosystemen zijn bijvoorbeeld het gevolg van de lokale interacties tussen organismen. Met andere woorden, de complexiteit van het ecosysteem wordt veroorzaakt door de eigenschappen en het gedrag van organismen. Aggregeren in grootschalige patronen kan echter ook de overleving en fitness van de individuen beïnvloeden. Hierdoor kan het patroonproducerende gedrag weer zijn geëvolueerd als een aanpassing aan de door de organismen zelf gegenereerde omgeving door middel van een zogenaamd eco-evolutionair terugkoppelingsproces. Opvallend is dat zowel empirische als theoretische studies over eco-evolutionaire terugkoppelingen in zelfgeorganiseerde ecosystemen ontbreken. In dit proefschrift heb ik onderzoek gedaan naar de interactie tussen ecologische patroonvorming en de evolutie van patroongerelateerde kenmerken zoals beweging en aanhechting.

Ik onderzocht de interactie tussen de evolutie van zelforganiserend gedrag en de resulterende grootschalige patronen door middel van zowel experimenten als computersimulaties. Hiervoor gebruikte ik mosselbanken als belangrijkste modelsysteem. Jonge mossels in mosselbedden op intertidale zandbanken aggregeren in labyrintachtige patronen. Mosselen hebben voldoende buren in hun nabijheid nodig om het risico op predatie en losslaan door golven te verminderen. Om dit te bereiken hechten mosselen zich met hun zogenaamde byssusdraden aan andere individuen en vormen daarbij dichte kluwens. Om de competitie voor voedsel – algen – te verminderen, moet er echter genoeg open ruimte tussen de kluwens aanwezig zijn. Doordat voedselconcurrentie een effect heeft over een grotere afstand dan het lokale hechten aan buren, ontstaan zelfgeorganiseerde patronen in het mosselbed in de vorm van regelmatige labyrintachtige structuren. De vorming van de patronen verhoogt de dichtheid van mosselen binnenin de mosselklomp terwijl de dichtheid op grotere schaal laag genoeg blijft om voedselconcurrentie te voorkomen. Twee gedragskenmerken zijn de belangrijkste factoren in de vorming van de patronen: beweging en aanhechting. Zonder beweging kunnen mosselen niet aggregeren en zonder hechting van byssusdraden aan nabij liggende buren zal de gegenereerde ruimtelijke structuur niet lang

bestaan, aangezien losse individuen gemakkelijk door de golven kunnen worden weggespoeld. Het onderzoeken van de terugkoppeling tussen mosselbedvorming en de evolutie van beweging en aanhechting kan ons interessante inzichten opleveren in de implicaties van eco-evolutionaire interacties in zelf-georganiseerde ecosystemen.

Gedurende de experimenten werd duidelijk dat mosselen gebruikmaken van een speciale bewegingsstrategie. De bewegingspatronen van solitaire mosselen zijn vergelijkbaar met een Lévy walk, waarin veel korte "stapjes" afgewisseld worden met lange, nagenoeg rechtlijnige, bewegingen. Lévy bewegingen worden frequent waargenomen in de natuur, bijvoorbeeld in mariene roofdieren en mieren. Theoretische modellen suggereren echter dat de omstandigheden waarin deze Lévy bewegingen optimaal zijn juist zeer zeldzaam zijn. In **Hoofdstuk 2** beargumenteer ik dat het voorkomen van Lévy-achtige bewegingen in mosselbedden het gevolg is van eco-evolutionaire terugkoppeling tussen patroonvorming en de ontwikkeling van de bewegingsstrategie van de mossel. Om deze hypothese te onderbouwen simuleerde ik de vorming van mosselbedden met een model dat gebaseerd is op individueel gedrag (een 'individual-based model'), waarin ik de bewegingsstrategie van de virtuele mossels varieerde tussen de verschillende simulaties. Uit de resultaten van deze simulaties blijkt dat patronen het snelst gevormd worden wanneer de mosselen gebruikmaken van een Lévy walk. Een evolutionaire analyse, waarin ik getest heb welke mutant strategieën kunnen binnendringen in een bestaande populatie, wijst uit dat de Lévy walk van nature evolueert in mosselbedden met patronen. De reden hiervoor is dat de Lévy walk de patroonvorming versnelt en het ruimtelijk patroon op zijn beurt de overlevingskansen van de Lévy-mossels verhoogt. Dit resultaat suggereert dat, in mosselbedden, Lévy bewegingen evolueren als gevolg van een sterke interactie tussen ecologische en evolutionaire processen. Hoewel mijn model specifiek van toepassing is op mossels in zelfgeorganiseerde mosselbanken, kunnen de conclusies uit deze studie wellicht ook toepasbaar zijn voor andere organismen en ecosystemen.

Ondanks het toenemende aantal observaties van Lévy bewegingen in de natuur vinden empirici ook regelmatig dat organismen een Lévy walk in de ene

omgeving doen maar een Brownse beweging in een andere. Lévy bewegingspatronen worden vaak waargenomen bij organismen die op zoek zijn naar voedsel in arme habitats, terwijl Brownse bewegingspatronen, die bestaan uit stappen van steeds ongeveer dezelfde grootte, voornamelijk in voedselrijke gebieden voorkomen. Dit fenomeen wordt vaak uitgelegd als een actieve verandering in bewegingsstrategie waarmee de zoekefficiëntie in beide omgevingen geoptimaliseerd wordt. In **Hoofdstuk 3** laat ik zien dat, in tegenstelling tot de bovengenoemde visie, de intrinsieke bewegingsstrategie van mossels niet verandert bij verschillende omgevingsomstandigheden, maar dat het waargenomen bewegingspatroon het gevolg is van interacties met omgevingsobjecten zoals andere mossels. Hierbij moet opgemerkt worden dat mossels niet zoeken naar voedsel, maar naar soortgenoten om zich aan vast te hechten. Door middel van analyses van de bewegingen van mossels in experimenten met verschillende mosseldichtheden, vond ik dat botsingen met andere mosselen de beweging van mossels beïnvloeden, waarbij voornamelijk lange bewegingen afgebroken worden. Door middel van het analyseren van mosselbewegingen in vijf verschillende dichtheden, laat ik zien dat de waargenomen bewegingspatronen daardoor meer op de Brownse patronen gaan lijken met toenemende mosseldichtheid. Ik heb geverifieerd dat deze verschuiving naar Brownse bewegingspatronen wordt veroorzaakt door botsingen met soortgenoten met een simpele analyse, waarbij ik de onafgebroken en afgebroken stappen uiteenhaal. Hieruit blijkt dat het bewegingspatroon niet verandert wanneer alleen de onafgebroken stappen bekeken worden. Met simulaties liet ik zien dat een actieve verschuiving van Lévy naar Brownse beweging met toenemende dichtheid onnodig is, aangezien de Lévy strategie even efficiënt is als de Brownse bewegingsstrategie bij hoge dichtheden. Verder heb ik mijn hypothese, dat elke strategie meer Brown-achtig wordt met toenemende botsingen, analytisch onderbouwd met behulp van een eenvoudig wiskundig argument. Deze conclusies kunnen grote gevolgen hebben voor de manier waarop de beweging van dieren geïncorporeerd wordt in ecologische modellen: het gebruik van een simpele Brownse beweging als een standaard template voor de beweging van dieren is niet altijd gerechtvaardigd en zou vervangen moeten worden door een realistisch, dichtheid-afhankelijk bewegingstype.

Er is momenteel veel discussie gaande over de vraag of Lévy walks die waargenomen zijn in de natuur, daadwerkelijk Lévy walks zijn of dat ze ontstaan zijn uit een mix van meerdere bewegingsstrategieën. Traditionele methoden die gebruikt worden om Lévy walks te ontdekken kunnen geen onderscheid maken tussen echte Lévy walks en de zogenaamde 'composite Brownian walks', In **Hoofdstuk 4** wordt een nieuwe methode gedemonstreerd die helpt om vast te stellen om welke van de twee bewegingsstrategieën het gaat. Deze methode houdt in dat de positie van clusters van kleine bewegingen vergeleken wordt met de aanwezigheid van voedsel op deze plekken (wat indicatief is voor een composite Brownian walk). Met een experiment met slakjes die op algen grazen hebben we aangetoond dat kleine-bewegings-clusters niet alleen voorkomen in voedselrijke gebieden maar ook op de kale grond, wat demonstreert dat Lévy walks daadwerkelijk kunnen bestaan in de natuur.

Mosselen, net als vele andere organismen, aggregeren actief in groepen, alwaar zij samenwerken met soortgenoten. Omdat deze samenwerking, ook wel coöperatie genoemd, misbruikt kan worden door individuen die geen bijdrage leveren, blijft het wijdverspreide gebruik van coöperatie in de natuur een puzzel. Theoretische studies hebben aangetoond dat de ruimtelijke structuur van een populatie de evolutie van coöperatie kan promoten. Maar deze studies beschouwen lokale verspreiding als een belangrijke voorwaarde voor de evolutie van coöperatie, daarbij uit het oog verliezend dat vele soorten zich verspreiden over grote afstanden en toch lokaal coöpereren. In **Hoofdstuk 5** toon ik aan hoe ruimtelijke structuren invloed hebben op de evolutie van investering in byssusdraden in ruimtelijk gestructureerde mosselbedden. Met behulp van een simpel model toon ik aan dat patroonvorming in mosselpopulaties het toch mogelijk maakt dat coöperatief gedrag evolueert en resulteert in een hoge mate van coöperatie in een breed scala van omgevingsstress. Deze resultaten suggereren dat actieve clustering de evolutie van samenwerking kan bevorderen, zelfs wanneer nageslacht wijd verspreid wordt.

Samenwerking en aggregatieve beweging zijn twee fundamentele gedragingen die de basis van zelforganisatie in mosselbanken vormen. Zonder actieve bewegingen die leiden tot het vormen van clusters zijn mosselen niet in

staat hun byssusdraden te hechten aan naburige soortgenoten, en zonder samenwerking zou het aggregeren in clusters een nutteloze inspanning zijn. Omdat beweging en coöperatief gedrag zeer afhankelijk zijn van elkaar, zal de evolutie van een van deze eigenschappen waarschijnlijk door het beïnvloeden van het ruimtelijk patroon ook de evolutie van de andere eigenschap beïnvloeden. In **Hoofdstuk 6** van dit proefschrift heb ik laten zien dat de gezamenlijke evolutie van het aanhechtings- en bewegingsgedrag kan resulteren in een ander patroon op mosselbank-niveau dan wanneer slechts een van de eigenschappen op zichzelf staand evolueert. In de meeste evolutionaire modellen wordt co-evolutie van meerdere eigenschappen binnen hetzelfde organismen gewoonlijk buiten beschouwing gelaten; mijn resultaten tonen aan dat dit kan leiden tot het trekken van de verkeerde conclusies.

Het zelfgeorganiseerde patroon dat naar voren komt uit de beweging en de aanhechting van de individuen heeft een belangrijk effect op de overlevingskansen van mossels binnen de mosselklompen. Met een eenvoudig veldexperiment liet ik zien dat niet alleen individuele mosselen losgeslagen kunnen worden door golfslag of predatie, maar dat de overleving voor een belangrijk deel wordt bepaald door het al of niet losslaan van de klomp waarin individuele mossels zich bevinden. Mijn experimenten lieten daarbij zien dat kleine mosselklompen meer kwetsbaar zijn voor het losraken dan grote klompen. Het losraken impliceert vaak verwijdering uit mosselbanken en verhoogt de kans dat de mosselen in een suboptimale omgeving met een hoog risico op predatie en lage beschikbaarheid van voedsel terecht komen. Hierdoor is mosselsterfte verbonden met de standvastigheid van klompen die gevormd zijn door zelforganisatie; deze klompen beïnvloeden daardoor selectie van specifieke eigenschappen. Hierbij ontstaat een terugkoppeling waarin het ecologische proces van patroonvorming de evolutionaire selectieprocessen beïnvloedt, die dan op hun beurt het ecologische proces van patroonvorming aanpassen. Het toevoegen van dit selectiemechanisme op groepsniveau aan ons model in **Hoofdstuk 6** geeft een heel interessant resultaat. Zonder dit selectiemechanisme op groepsniveau kunnen slechts voor een heel beperkt aantal parameterwaardes de vorming van de labyrintachtige patronen verklaard worden. Meestal vormen er zich dan losse klompjes, of blijven de mossels willekeurig verspreid. Met selectie op groepsniveau vormen zich voor nagenoeg

alle parameterwaardes de geobserveerde labyrintachtige patronen. Deze labyrintachtige patronen worden vaak waargenomen in natuurlijke mosselbanken, wat suggereert dat multi-level selectie van groot belang is in de eco-evolutionaire interactie die leidt tot de vorming van ruimtelijke patronen in mosselbanken.

Mijn bevindingen tonen aan dat eco-evolutionaire terugkoppelingen van groot belang zijn voor het ontstaan van ruimtelijke patronen in zelfgeorganiseerde ecosystemen. Op individueel niveau kunnen zelforganiserende eigenschappen, zoals beweging of aanhechting, evolueren door de wisselwerking tussen de evolutie van het individuele gedrag en de ruimtelijke complexiteit van de gemeenschap. Deze grootschalige, zelfgeorganiseerde patronen worden op hun beurt gegenereerd door de acties van en interacties tussen individuen; er is daarom duidelijk sprake van een eco-evolutionaire feedback. Deze interactie vindt hoogstwaarschijnlijk niet alleen plaats in ecosystemen met zelforganiserende, regelmatige patronen, zoals mosselbedden, maar zal waarschijnlijk plaatsvinden in elk ecosysteem waar organismen zelf hun ruimtelijke verdeling beïnvloeden. In meer algemene termen kunnen we zeggen dat wanneer het gedrag van een organisme invloed heeft op zijn omgeving, deze omgeving op zijn beurt de fitness van zowel dit individu als dat van anderen zal beïnvloeden. De eco-evolutionaire terugkoppeling die voortvloeit uit het samenspel tussen individueel gedrag en ruimtelijke patroonsvorming kan de evolutionaire mechanismen fundamenteel veranderen, bijvoorbeeld door verschillen tussen groepen te genereren welke kunnen leiden tot selectie op een hoger niveau dan het individu. Om de eigenschappen van organismen in de complexe natuur goed te doorgronden is het van cruciaal belang inzicht te krijgen in de interactie tussen ecologische en evolutionaire processen, ook in systemen waar de relatie tussen organismen en de ruimtelijke structuur van het ecosysteem minder rechtlijnig is.

Acknowledgements

Dear reader,

To be honest, I have been procrastinating immensely when writing my acknowledgements. I think this has something to do with the facts that (i) the acknowledgements will probably be the most frequently read part of my thesis, while (ii) it is also the part that is most error-prone. Though I do not take your help and kindness for granted, my memory is flawed sometimes (here I can already say thanks, because I'm quite sure I owe this to my children), and making a list of all people who I would like to acknowledge for their help of any sorts over the last years is quite a challenge. Here, at last, is my attempt to thank you all; please do not be disappointed if your name is nowhere to be found.

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About the author

My name is Monique de Jager-Out and I'm the author of this dissertation. I was born in the early hours of a beautiful winter's day in 1984 in a small suburban town south of Rotterdam, the Netherlands, as the beloved second daughter of Henk de Jager and Gré de Jager-Jonas. Pretty much my entire youth I spend in this town, Spijkenisse; my preschool, primary school, and high school were all within biking distance of my home. Even my husband Mark was born here; we met at a high school graduation party and never really parted again. Like many small suburban towns, Spijkenisse is devoid of universities; therefore, I commuted to Leiden instead, where I studied biology from 2003 to 2008. For my bachelor thesis I investigated the spatial dynamics of a prisoner's dilemma (a cooperation game where cheating can be advantageous), my first master project involved developing a website for photo-identification of humpback whales, and for my second master project I spend three months in Cameroon to investigate the spatial distribution of large carnivores. During my time in Leiden, I developed an interest in eco-evolutionary dynamics, spatial processes, and individual-based modelling. One of the researchers there gave me the advice to stop investigating cute and fluffy big animals (meaning whales and lions) and start focusing on the less attractive organisms, if I ever would like to be taken seriously. Hence, when the vacancy of PhD-student at the NIOO-CEME popped up, I immediately replied. From 2008 to 2012, I worked full-time at the NIOO-CEME (now NIOZ Yerseke). After my son Logan was born in July 2012, I was on maternity leave until October and started working again part-time on a scholarship of the RUG. Although my thesis wasn't finished, we moved to Zürich, Switzerland, in 2013, where I worked as a postdoctoral researcher at the plant ecology group of the ETH. Raising two kids in a foreign country is exponentially more difficult than raising one, so soon after the birth of our daughter Caitlin in August 2014, we moved back to the Netherlands, where I am now working as a postdoctoral researcher at the ecology and biodiversity group of Utrecht University.

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