A MICROCOSM STUDY ON FACTORS AFFECTING MOVEMENTS OF TERRESTRIAL ISOPODS (*ARMADILLIDIUM* AND *PORCELLIO*) AWAY FROM FAMILIAR HABITAT.

BY

Panditha Vidana Sasindu Lakmini Gunawardana

B.Sc., Wayamba University of Sri Lanka, 2006

A THESIS SUBMITTED IN PARTIAL FULFILMENT OF THE REQUIREMENTS FOR THE DEGREE OF

MASTER OF SCIENCE

IN

ENVIRONMENTAL SCIENCES

This thesis has been accepted as conforming to the required standard by:

Karl W. Larsen (PhD), Thesis Supervisor,
Department of Natural Resource Sciences, Thompson Rivers University

Louis Gosselin (PhD)
Department of Biological Sciences, Thompson Rivers University

Matthew Reudink (PhD)
Department of Biological Sciences, Thompson Rivers University

Shane Rollans (PhD)
Department of Mathematics & Statistics, Thompson Rivers University

James F. Hare (PhD), External Examiner
Department of Biological Sciences, University of Manitoba

November 2017

Thompson Rivers University

ABSTRACT

Connectivity among habitat patches promotes landscape-wide movements that are important for population viability. In studies on animal movement, the relative effects of conditions within familiar ("home") habitat and those encountered while en route to other habitat patches have been rarely quantified. To address this issue, I conducted a microcosm study that allowed me to experimentally manipulate factors while providing large sample sizes.

For this work I used two closely-related but morphologically-dissimilar species of terrestrial isopods (O. Isopoda: *Armadillidium vulgare* and *Porcellio scaber*). As typical for the taxa, these species are reliant on pseudotracheae for respiration and thus generally are associated with moist environments. A significant difference between the two species, however, is that the highly mineralized carapace of *Armadillidium* allows it to tolerate and resist desiccation moreso than *Porcellio*; however, in contrast *Armadillidium* shows slower and more lumbering movements than *Porcellio*.

My experimental microcosms consisted of one familiar habitat (‘home’) connected by a 3 m movement corridor to a ‘destination’ habitat. Movements of individual isopods within these corridors were quantified using web camera checkpoints and unique markings applied on each animal. Using this system, I conducted two experiments, one focusing on the effects of conditions within the home habitat, the other focusing on conditions within the travel corridor itself. In both experiments I manipulated two factors in a cross-factorial design, and examined the effects on departure rates from the home habitat along with other movement metrics. I also tested how these responses differed between the two species.

In the first study, I manipulated humidity (3 levels) and food (3 levels) within the home habitat. Thirty-six trials were run in total for each species, each trial involving 16 (8 ♂, 8 ♀) animals. Humidity of the home habitat had an increasing impact on the number of individuals completing at least one trip from home to destination habitat and on the total time individuals spent away from home. Similarly, food levels at home affected the amount of time individuals spent at home, number of times individuals left home, number of trips individuals completed from home to destination and the amount of time spent outside the home. Both species showed statistically significant differences in movement patterns for all the metrics I tested; for example *Porcellio* showed a greater tendency to depart from the home especially when humidity was low.

In the second study, I held conditions within the home environment constant but manipulated humidity within (3 levels) and permeability (3 levels) within the corridor. The latter was achieved by manipulating the density of pebbles in the corridor, thus increasing the degree of difficulty associated with travel by the isopods. Here I conducted 45 trials per species utilizing 16 (8 ♂, 8 ♀) animals each trial. This study revealed the movement tendencies of less-mobile *Armadillidium* were mostly affected by the reduced permeability of the corridor, whereas *Porcellio*'s travels were mainly affected by humidity. This is likely attributable to *Armadillidium* being less mobile than *Porcellio*, and *Porcellio* being relatively less tolerant of lower humidity.

Overall, the results of these experiments indicate that animal movement out of home habitats is not only affected by conditions therein, but also conditions encountered en route to other habitats. Further, even closely-related species may show markedly different responses, presumably due to their individual suite of adaptions. Additional work is needed to fully understand the factors influencing animal movement across landscapes, but this study demonstrates how such movements may occur in response to factors within and between habitats, as well as phylogenetic constraints.

Key words: connectivity, home habitat, movement corridor, microcosm experiments, *Armadillidium vulgare*, *Porcellio scaber*, humidity, corridor permeability.

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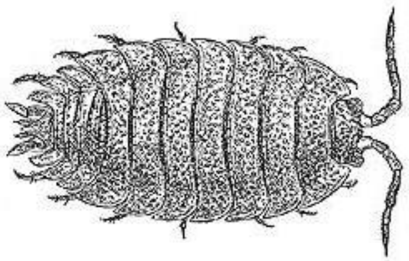
ACKNOWLEDGEMENTS

This thesis is the result of a long and challenging journey to reach my life goals. First and foremost, I thank Dr. Karl W. Larsen for persistently encouraging, enabling and fighting for me to pursue this M.Sc. I'm very grateful for the time and energy you have invested in my education and my personal development. I also owe gratitude to Dr. Shane Rollans and Susan Kinniburgh for helping me with all the statistical challenges I had throughout the study. A special thanks to Kimberly Perreault, my predecessor in isopod study, for meticulous record keeping and making me realize "roly poly work is cool". Further thanks are extended to my committee members, Drs. Louis Gosselin and Matthew Reudink for their valuable input and words of encouragement, and to Dr. James Hare for agreeing to act as my external examiner.

This work was supported by an NSERC Discovery Grant to my supervisor. Further, I thank TRU World for the financial award for my first year that contributed to tuition fees. Again, a huge thanks to M.Sc. (Environmental Science) Program and the Thompson Rivers University Student Union for support to present my work at an international conference.

In the course of my studies I benefited greatly from support by other faculty and staff at Thompson Rivers University, including Dr. Wendy Gardner, Dr. Nancy Flood, Dave Pouw and Debbie Gill. Thanks to Eric Spilker for getting me through the roly poly tedium. My fellow "Larsen labmates" - Emily Lomas, Amy Duncan, Jo Anne Hales, Cheryl Blair, and Malcolm McAdie - provided laughs, support, and kept me up to date with "Canadian way of life".

And finally, innumerable thanks to my daughter for making me realize I can create great miracles and my husband for constantly pushing me to reach for the stars.



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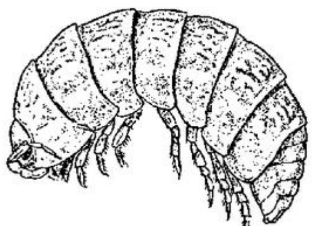

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CHAPTER 1. MOVEMENT OF ANIMALS AND LANDSCAPE CONNECTIVITY

INTRODUCTION

Movements of animals from one location to another play vital roles in many ecological processes, such as the evolution of new species (Bowler & Benton, 2005), the prevention of inbreeding depression (Keller & Waller, 2002; Szulkin & Sheldon, 2008), the dispersal of adaptive alleles (Garant *et al*., 2000) and / or the establishment of new populations (Bushar *et al*., 2015). For any given species, movements vary both spatially and temporally; for instance, over short temporal and fine spatial scales, movements may be influenced by the patchwork of food and/or habitat features used in foraging or sheltering, whereas at larger scales, animals may relocate in response to social factors or habitat changes across landscape boundaries (Wiens, 1992). Therefore, studying animal movement patterns across a broad array of ecological systems will aid in unravelling the interactions between time, season, space, resources, and social interactions - all processes that are otherwise difficult to understand comprehensively (Cushman *et al*., 2005). Further, movement rates of animals from a particular habitat(s) are useful and a relatively easy-to-measure metric that can contribute to parameterizing connectivity models (Dickson *et al*., 2005; Chetkiewicz & Boyce 2009 and Nogeire *et al*., 2015).

Movements of animals occur across different spatial and temporal scales for a number of reasons, and hence a large number of terms have arisen in an attempt to provide more specific definitions. For example, the term ‘dispersal’ has been applied to movement over many different spatial scales (often arbitrary - Johnson & Gaines, 1990), and with many possible proximate causes and potential functions (Bowler & Benton, 2005; Ronce, 2007). One of the more prominent uses of the term applies to movement from natal to breeding habitat, or movement between breeding patches (Clobert *et al*., 2001). However, there is evidence to support that other forms of movements act in concert with natal and breeding dispersal (Wiens, 2001) and thus may be very important. For example, exploratory movements may be critical for allowing animals to discover areas with greater resources without making immediate and permanent relocations. In a dynamic environment, understanding exploration behaviour of animals helps in turn to explain diverse space use patterns across multiple scales, from momentary movement decisions to travel paths (Spencer, 2012), home range utilization distributions, shifting home ranges, and patterns of home range overlap among individuals. It is this type of movement that I examine in this thesis, and hereafter I use the word "movement" to refer to exploratory travel out of and between patches of habitats.

What cue(s) trigger an animal's decision to move? As suggested, animals move for many reasons: to acquire resources, to avoid predators and other agents of mortality, to avoid competition (e.g. natal dispersal), and to be near conspecifics for mating and other social interactions (conspecific attraction). A belief that the prime driver behind animal movement is the acquisition of resources has led to an increasing number of studies examining the value of movement strategies, with variously-distributed food sources (Viswanathan *et al*., 2008; Schlesinger, 2009). Clearly, movement behaviours are related to survival and reproduction, and hence subject to natural selection (Fahrig, 2001). Classical habitat selection models predict that individuals should disperse and be distributed in the environment so as to maximize their fitness (Hutto, 1985; Fretwell & Lucas, 1970). These models assume that individuals have 'free movements' between patches and perfect knowledge on the quality of patches when they make a settlement decision (Rosenzweig, 1991). A better understanding of these factors will be needed to accurately predict how populations will respond to habitat fragmentation, climate change, and the invasion and spread of alien species (Bowler & Benton, 2005). In turn, effective conservation measures will require knowledge of not only how different factors affect population persistence, but also how the magnitudes of these factors can cause different movement behaviours of animal species.

The movements of animals from one habitat to another can be intuitively considered a product of the decision to leave the home habitat, and the decision to extend the movement to a new habitat. Accordingly, an individual relocates to a new habitat patch goes through a series of stages: departure from the home habitat/population, travel through a movement corridor (transit) and arrival at the new habitat (Weisser, 2001). Depending on the physiological state of the organism and the complexity of the landscape movement stages, movement behaviour may be plastic (Crist, *et al*., 1992). During the "travel" phase, animals may proceed on a course, become stationary, or retrace a previous route - depending on the conditions of the environment. This scale-dependent movement behaviour and the fact that animals vary in size, vagility, physiology and life history characteristics has made it difficult to compare movement processes among species and environments. Numerous empirical studies have focused on the movement of animals within and outside their preferred habitats, and shown that some species change their behaviour when traversing through different types of habitat (Kindvall, 1999; Haddad *et al*., 2003; Hein *et al*., 2003). Additionally, edge permeability, (i.e. the probability of leaving a patch) has been investigated particularly in studies examining corridors (transit) as a means to promote habitat connectivity (Schultz & Crone, 2001; Hein *et al*., 2003). Assessing how landscapes influence movement therefore requires a consideration of how the scale of landscape patterns interacts with the scale on which organisms respond.

The quality of a habitat and the local availability of resources are important factors triggering emigration, as animals should be more likely to leave habitats of lower quality or with limited resources (Bonte *et al*., 2008; Mathieu *et al*., 2010). Different locations in a landscape are associated with different costs and benefits, and movements of individuals should be determined by the combination of costs and benefits it encounters (Larsen, 1994; Weins, 2001). Risks and benefits of moving to a new habitat will vary among species, such that movement strategies likely will be highly species-specific. Broad differences in movement patterns of organisms can be seen in animals belonging to narrow taxonomic groups, causing movement to be considered as a species-specific fixed trait (Stevens, 2010). Dispersing individuals will encounter different environmental conditions and challenges compared with non-dispersers. Thus it is not surprising that movement propensity tends to be associated with whole suites of characteristics promoting movement success and settlement success (Wolf & Weissing, 2012).

Understanding how habitat structures influences permeability to animal movement is key to managing complex landscapes for conservation (Turchin, 1998; Ricketts, 2001; Vandermeer & Carvajal, 2001). Individual habitat types within this matrix may be differentially permeable to a different species (Ricketts, 2001; Ries & Debinski, 2001; Rodrıguezet *et al*., 2001). A reduction, reconfiguration and /or loss of connectivity between native habitats (‘fragmentation’) due to anthropogenic or natural factors is one such reason for a reduction in matrix permeability.

Metapopulations characterised by low levels of movement between populations inhabiting small, isolated patches will be at greater risk of extinction than those occupying more connected patches (Hanski & Gilpin, 1997). Additionally, the ability of populations to move across habitats appears increasingly important given expected range shifts with climate change (McLaughlin *et al.*, 2002). Some studies, however, have ignored the fact that animals may move through the non-habitat matrix (Beier & Noss, 1998; Ricketts, 2001; Hudgens & Haddad, 2003).

In many studies, (particularly earlier ones) direct observations of individual movement patterns were difficult (Ims & Yoccoz, 1997), hence the rise in popularity of indirect methods for studying dispersal, such as mark–recapture and genetic assessments. Radio-telemetry is another tool now used widely by field biologists, but data sets containing only intermittent and relatively small numbers of locations per animal provide only a snapshot of the space-use patterns by those individuals carrying the transmitters. With the advancement of technology, miniaturized GPS (global positioning system) and satellite tags now can generate copious amounts of location data with exceptional accuracy for many species (Kays *et al.*, 2015). Further, there has been an exponential improvement in tracking technology, leading to smaller devices that return millions of movement steps for ever-smaller animals. However, field experiments that use these novel tracking devices are expensive and still difficult to implement on particular species over certain scales.

Micro- and mesocosm studies can be used to overcome the challenges and expense of collecting precise movements of large numbers of animals (particular smaller species) (Weins, 2001). Such studies provide a powerful means to obtain significant sample sizes while isolating specific causes and effects through controlled experimentation and adequate replication. Many experimental systems have been useful in the development of ecological theory, but their application to real-world situations may be limited by assumptions that all patches are equivalent in quantity and quality, and that all individuals are equally capable of moving one place to another (Fahrig & Merriam, 1994). Careful design of experimental models therefore is required to extrapolate results to actual problems in conservation biology.

For this thesis, I used experimental microcosms to study the movements of animals under different environmental conditions in the home (familiar) habitat and in a movement corridor. I decided to incorporate two closely-related species in these studies garner insight into how shifts in environmental conditions create different responses due to species-specific morphological and physiological constraints. I chose to work with terrestrial isopods, allowing their morphological and physiological adaptations to guide my selection of species. Terrestrial isopods are the most successful colonizers of terrestrial habitats among the crustaceans (Hornung, 2011). Most crustacean exoskeletons are composed of four layers (epicuticle, exocuticle, endocuticle, and the membranous layer - see Travis, 1955) of which the epicuticular layer is most important in inhibiting water loss (Cloudsley-Thompson, 1977). Despite the fact that the cuticle of isopods is relatively permeable to water (Quinlan & Hadley, 1983), members of this taxa are able to survive under a wide variety of terrestrial conditions. Members of the genus *Armadillidium* (‘pill bugs’) tolerate relatively dry conditions because they are more capable of absorbing water vapour directly from an unsaturated atmosphere (Edney, 1960) than members of genus *Porcellio* (Smigel & Gibbs, 2008). However, the latter are more mobile, due to adaptations in   skeletal construction. These adaptations reflect the ecological strategy and behavioural patterns of each species (Schmalfus &Yair, 1984). *Porcellio scaber* (‘woodlice’) for example, avoids predation by running away or clinging to substrates, thereby protecting the soft ventral surface of the body. To do this requires a relatively thin and somewhat flexible cuticle that contains only moderate amounts of mineral (Figure 1A). Conversely, *A. vulgare* and its congeners possess a thick, strongly minearlized cuticle, but they are capable of rolling into a near-perfect sphere in response to desiccation and predators (Hild *et al*., 2008) (Figure 1B and IC).

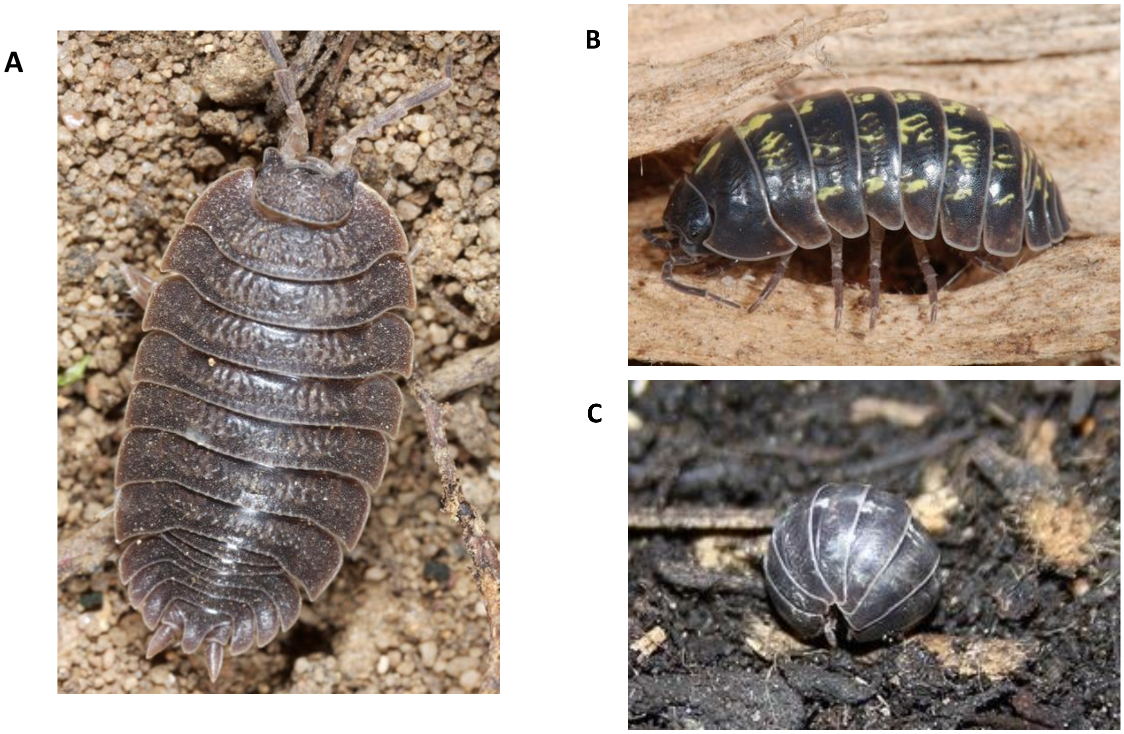

Figure 1. A. *Porcellio scaber* (‘woodlouse’) possesses a soft ventral surface of the body, with a flexible cuticle. B *Armadillidium vulgare* (‘pill bugs’) is equipped with an inflexible cuticle that is strongly mineralized under normal conditions. B – *A. vulgare* rolls into a perfect sphere under threatening conditions.

The most primitive terrestrial isopods uptake oxygen through pleopod-endopods that function as gills (Hoese, 1982). More advanced taxa, adapted to drier conditions, conduct respiration through more specialized structures termed pseudotracheae. The two species of isopods used in my studies (*A. vulgare* and *P. scaber*) both possess these pseudotracheae (Leistikow & Araujo 2001). The presence of these structures enables oxygen intake in drier environments, but water loss through evaporation still occurs across the pleopods, being significantly higher in *Porcellio* than *Armadillidium* (Edney, 1960; Schmidt & Wägele, 2001). The diets of *Armadillidium* and *Porcellio* are quite similar, consisting mostly of decaying organic material such as leaf litter, wood, fungi, and bacterial mats (Paoletti & Hassall, 1999). Thus, under natural conditions, humidity rather than food levels is believed to be more critical to survival, as under drier conditions the animals are forced to spend less time foraging and more time sheltering (Dias *et al*., 2012). The close relatedness of these two species, coupled with their divergent morphology, physiology and behaviour, prompted me to compare how these two species responded to different triggers that affect their decisions to leave the home habitat and to continue movement into new habitat.

In my first experiment (Chapter 2), I manipulated two parameters (food and humidity) in the home habitat of isopod colonies to understand the effect on the movements of these animals out of familiar environment. In this experiment, the environment within the corridor connecting the home habitat to a ‘destination’ was held constant and relatively favourable to both species. In the second experiment (Chapter 3), I reversed these conditions, holding conditions in the home habitat consistent while manipulating two environmental conditions (permeability and humidity) within the movement corridors. In both experiments, I collected various forms and metrics of movement data from the animals, allowing me to test the effect of these environmental factors and their interactions. In Chapter 4, I discuss the applicability of thesis within the context of natural scenarios.

This study collectively examines how main factors and their interactions, in home habitats and connecting travel corridors, contribute to movement ‘decisions’ made by animals. Information of this nature eventually will allow us to understand how movements and colonization between habitat patches are influenced by habitat and corridor conditions. Furthermore, results of this study may be extrapolated to fragmented natural ecosystems that contain different species and environmental conditions. All told, furthering our knowledge in these directions is critical for effective and efficient conservation of species.

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CHAPTER 2

MOVEMENT OUT OF FAMILIAR HABITAT I:
THE EFFECT OF THE HOME ENVIRONMENT

INTRODUCTION

Relocation or movement from one habitat to another profoundly influences a number of important parameters in animal ecology (Ovaskainen & Hanski 2004; Bowler & Benton, 2005; Garant *et al*., 2007 and Szulkin & Sheldon, 2008). How and when animals relocate from a familiar or ‘home’ habitat have a bearing on most demographic parameters, along with dispersal, gene flow, population dynamics, animal behaviour, conservation biology and fitness (Clobert *et al*., 2001 and Zollner & Lima, 2005). More recently, an understanding of the factors governing animal movement has been recognized as essential to predicting and possibly mitigating the impacts of global climate change (McClintock *et al*., 2013). However, we have a poor understanding of how environmental conditions in home habitats trigger departures to other habitat locations or patches. This knowledge gap stems in part from the fact that, historically, tracking the precise movements of individual animals has been hindered by logistics and technology. Although this hurdle has now been partially rectified through advances such as extrinsic markers (Roper *et al.*, 2003), stable isotopes (Wunder, 2012) and population genetic techniques (Ramos *et al.*, 2016), the factors driving “decisions” to relocate out of a particular home habitat by different species remain poorly addressed.

Intuitively, conditions within the home range of an animal (i.e. "home habitat") should play an important role in affecting movements out of that area, even those of an exploratory nature. Most animals, particularly mammals, store information about their home range in cognitive maps and learn to associate objects or events with locations on this map (Spencer, 2012). Thus movements reflect the way an animal perceives and reacts to its environment (Benhamou, 2014). Presumably, when the benefits of remaining in familiar habitat (such as access to food and mates) are outweighed by the costs of monitoring, defending, maintaining, and accessing critical resources, animals should attempt relocation (Charnov 1976 and Krebs *et al*., 1978). The benefits from relocation notwithstanding, such movement also may entail costs. Animals that travel into unfamiliar habitat may be subject to additional risk relating to predation and / or foraging efficiency (Baker & Rao, 2004 and Noyce & Garshelis, 2011).

Because the risks and benefits of moving to new habitat will vary among species, movement strategies likely will be species-specific, influenced by different rates of development, movement, breeding, life spans, and mortality. When resource quality is variable in space and time, different species are expected to evolve responsive movement patterns, such that travel distances or speed increases with decreasing availability of time period (Fahrig, 2007). Additionally, in most mobile animals, locomotory and navigation constraints cause broad differences in movement patterns of organisms belonging to contrasted taxa. Such huge inter-specific differences in the ability to move among local habitat patches are the main reason why movement is considered a species-specific fixed trait (Stevens *et al*., 2010). However, few studies have demonstrated that animals may show movement / dispersal behaviour even if there is no evidence of immediate benefits from their movement (Mathieu *et al.*, 2010), perhaps following a riskier path, purposely or mistakenly, depending on their level of information about the environment and their motivational state (Russell *et al.*, 2003).

Until recently, most movement models have assumed that animals are either omniscient or ignorant about resource distributions in time and space (Spencer, 2012). Despite numerous attempts to understand animal space use and movement patterns with respect to resource distribution, it remains challenging to isolate the specific effects of any one factor (much less more than one) on animal movement in the field. Furthermore, the distances animals move and the time and expense of studying movements often renders field studies even more daunting. Experimental model systems can be used to overcome the logistical difficulties of field experiments (Weins, 2001) and they provide a better means of achieving significant sample sizes while demonstrating specific causes and effects.

In this study, I used experimental microcosms to test the effects of conditions in the home habitat on the outward movements of two closely-related invertebrate species in the Order Isopoda (Sub

Phylum Crustacea). Due to their tractable nature, isopods have been used frequently as model organisms in laboratory studies investigating ecology and physiology (Escher *et al*., 2000; Baker and Rao, 2004 and Dias *et al*., 2012) This taxon includes the most successful colonizers of terrestrial habitats among the crustaceans (Hornung, 2011), yet they remain tied to humid environments due to a reliance on pseudotrachea for oxygen uptake (Dias *et al*., 2012). Thus, most species are cryptic, being associated with cool and humid areas, sheltering beneath stones and bark, and/or demonstrating nocturnal activity patterns (Ayari *et al*., 2016). Terrestrial isopods can be grouped by their skeletal construction into categories correlated to ecological strategies and behavioural patterns (Schmalfuss, 1984). Members of the genus *Porcellio* ('woodlouse') avoid predation by running away or clinging to a substrate, thus protecting the soft ventral surface of the body. Their cuticle is relatively thin and flexible, containing moderate amounts of mineral. Conversely, *Armadillidium* ('pillbugs') possesses a thick, inflexible and heavily-mineralized cuticle that affords protection after the animal has rolled into a perfect sphere (Hild *et al.,* 2008). These differences in morphology result in different locomotory performance: preliminary speed trials (Gunawardana unpubl.) showed *A. vulgare* travelled considerably slower over 3 meters ($\bar{x}$= 0. 95 cm/sec ± 0.49 SD, n = 40) than *P. scaber* ($\bar{x}$ = 2.1 cm/sec ± 0.18 SD, n = 40) (t = 3.77, df = 44.9, P < 0.001). At the same time, difference in cuticles and other adaptations result in *Armadillidium* being able to tolerate drier environments than *Porcellio* (Schmidt & Wägele, 2001; Smigel & Gibbs 2008). In one study, water loss by *Porcellio scaber* was measured as 40% higher than *Armadillidium vulgare* (Edney, 2012). Other aspects of the two animals are similar: their diets consist mostly of organic materials such as leaf litter, decayed wood, fungi, and bacterial mats (Paoletti & Hassall, 1999). Images of the two study animals and further details on their comparative natural history appear in Chapter 1 of this thesis.

Creating microcosm colonies of both *A. vulgare* and *P. scaber* allowed me to manipulate resources in the home environment, record the effect of varying resources on movements away from home, and more importantly, reveal how an interaction of factors influenced movement. Through this work, I improve our understanding of how different environmental conditions in concert affect exploratory movements away from the home habitat, for different species with different adaptations. The specific objectives of my study were to (i) quantify how individual environmental changes (humidity, food availability, and their interaction) affect the timing and magnitude of movements out of the home habitat (i.e. initial departure), (ii) quantify how these same parameters (humidity, food availability, and their interaction) influence movement patterns after the initial departure out of the home habitat has been made, and (iii) examine how movements in response to the home habitat conditions (initially, and after leaving the home habitat) differ between the two species. To this end, I altered humidity (thus affecting respiration and overall physiological condition) and food levels at the home environment (habitat) of the isopods and monitored movements out of the habitat within a corridor. Conditions in the corridor were held constant in this experiment across all treatments, being manipulated in a separate study reported in Chapter 3.

I predicted that both species would respond to lower humidity and food levels in the home habitat through increased departures, and that *Porcellio* would show a more marked response to humidity than *Armadillidium*, given the species' reduced tolerance to lower humidity. I predicted the changes in food levels would produce a more muted difference in departure frequencies because under unfavorable humidity conditions both species reportedly spend more time sheltering than foraging (Acton 2012). Furthermore, the greater inherent mobility of *Porcellio* (Dailey *et al.*, 2009) led me to predict that once individuals of this species initiated departures from the home environment, they would travel further than *Armadillidium* in search of new habitat. Finally, I expected that interactions between the two main treatments with each species ability to withstand such conditions would result in more pronounced effects on movement behaviour of two isopod species.

METHODS

General maintenance of animals

This study occurred from May 2013 to August 2013. Animals purchased from a commercial biological supply (Ward's science, New York, USA) house were used to establish source colonies for several months prior to the experiment. These colonies were housed in plastic containers covered with mesh lids. A layer of potting soil (≈ 3 cm deep) and assorted wooden debris provided habitat structure. The isopods were fed a commercial mix of young leafy greens *ad libitum*, and water was sprayed onto the soil twice a week. The colony room was on a synchronized 12 L: 12 D schedule using wide-spectrum artificial daylight lighting. Artificial dawn (07:00) and dusk (19:00) allowed the isopods to establish circadian rhythms (Refinetti, 2000) conducive to nocturnal foraging (Tuck & Hassall, 2005). Temperature ($\bar{x}$ = 19°C ± 2 SE) and humidity (65% ± 5% SE) were kept relatively constant via the climate control system of the building and a Hunter® model 33250 humidifier. Seven days prior to the experiment, animals transplanted into smaller containers (see below) were moved into a large, windowed laboratory to allow adjustment to the ambient, experimental lighting, and also allow a re-adjustment of circadian rhythms (Refinetii, 2000) and nocturnal foraging patterns (Tuck & Hassall, 2005). The temperature of this room was near-identical to that in the colony room. Also at this time, the crude daily food consumption rate (g/animal) were determined using 16 individual animals of each species (with four replicates) over two weeks. This rate was used later as a standard for food provision in the experiment.

Microcosm Design

My basic experimental microcosm system consisted of one familiar habitat ('home') connected by a movement corridor to a 'destination' habitat (Figure 2-1). Plastic containers 21×21×10.5 cm were used to create these two types of habitats. Each pair of habitats were connected via 3 m movement corridor 'troughs', constructed out of 5.5×7.5 cm aluminium rain gutters cut length-wise and attached to the habitat containers using PVC gutter adapters. The length of the troughs was based partly on previous work (Perreault, 2009) and my own pilot study that suggested 3 m resulted in marked variance in the distance travelled by the two species by a sample of isopods over a 12 hr period.

A 2.5 cm deep Plaster of Paris layer was used to create a substrate foundation in the habitat containers and the corridors. This porous layer aided in the maintenance of relative humidity levels and prevented the isopods from burrowing. On top of this layer, 1 cm of dried, sterile potting soil (Miracle Grow™) was spread and then dampened accordingly to achieve specific

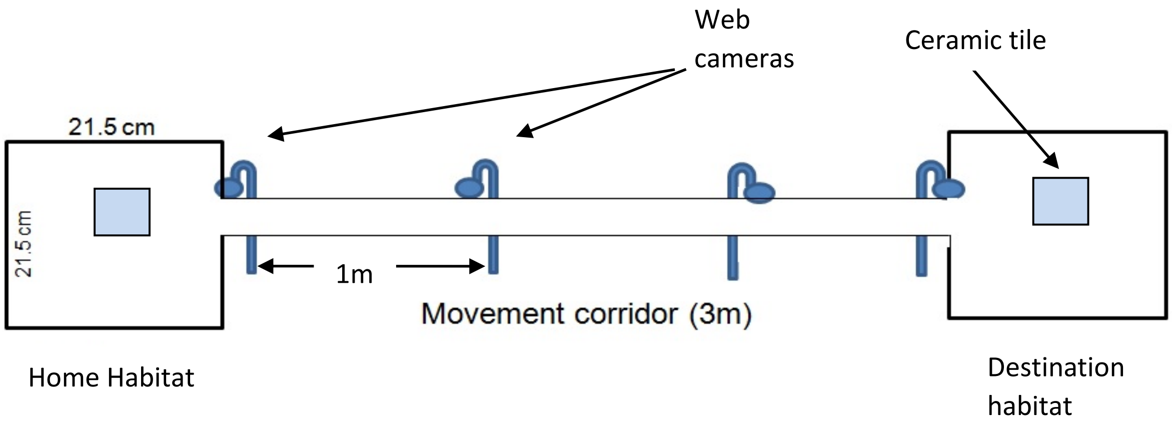

Figure 2-1. Diagrammatic representation of experimental microcosm.

humidity levels (see below). To establish shelter, a ceramic tile measuring 11cm ×11cm, was placed supported at the corners by four glass marbles into each habitat container. Whenever a new trial was conducted, all soil was replaced and the walls and the Plaster of Paris substrate were rinsed with distilled water.

Preparation and selection of animals for experiments

All animals used in the experiment were haphazardly selected from the colony and then measured and weighed. Using 50% maturity length as a cut-off, I selected 576 adult individuals of each of *Armadillidium* (1.25 cm ± 0.11cm; 0.091 g ± 0.07) and *Porcellio* (1.59 cm ± 0.12 cm; 0.15 g ± 0.03). Each trial consisted of a group of 16 animals (8 ♂: 8♀) placed into a home habitat container. To allow recognition through images captured by web cameras, each animal received a carapace mark unique within its trial group, applied using white nail polish (Figure 2-2D). Length (± 0.1 cm), weight (± 0.001 g) and gender also were recorded. The isopods were released into the home habitat containers 48 hours prior to each trial; during this time the passageways into the movement corridors were sealed off using a plastic sheet.

Manipulation of the home habitat (food and humidity)

Different combinations of food (3 levels) and humidity (3 levels) were applied to the home habitats. Humidity levels were set using the tolerance measurements established by Warburg (1987): low 30-40%, medium (≈sufficient) 60-70%, and high over 90%. These levels were established in the home habitat through the application of distilled water through a fine-mist spray bottle. To verify consistent conditions during pilot tests and actual experimental trials, I situated a calibrated hygro-data logger (Maxim Onewire Viewer™) in each home habitat that monitored relative humidity and temperature on an hourly basis. To achieve the lowest humidity levels, water was sprayed into the home habitats just prior to the initial introduction of isopods (for the 48 hour acclimation period). The other two humidity levels (medium and high) were established during the acclimation period by different regimes of water spraying in the home containers in combination with a plastic food wrap applied over top (small holes in the film ensured air passage). Using the same techniques, the conditions of all the destination habitats

Figure 2-2. Construction of habitat containers and connection corridors: a pair of plastic sandwich containers were connected to one another via a PVC gutter pipe; the floor of each container and the corridors were layered with 2.5 cm Plaster of Paris to serve as substrate (2A). The habitat containers also were provisioned with ≈ 1cm of sterile potting soil and a raised ceramic tile that provided cover (2B). Each and every individual's size was measured (2C) and individuals were provided with a distinct mark (2D) to be identified during the experiment.

and movement corridors (regardless of the home container treatment) were maintained at medium relative humidity (60 % - 70 %).

Similar to humidity, food levels in the home containers were set at low, medium (~ sufficient), and high, based on average food per capita consumption rates determined in pilot trials. This pilot work revealed only slight, non - significant differences in food consumption rates between individuals of the two species, hence identical amounts of food were provided to the two species within each food level category. The lowest level represented ~ 50% of the normal food consumption of both species (~ 0.35g/day); the medium level matched the average consumption rate (0.7g/day) and the highest level represented twice this amount (~ 1.5g). The medium food level also was applied to all containers during the acclimation period. During the experimental trials (72 hr, see below), unconsumed food was removed every 24 hours and replaced with new material in amounts consistent with the specific treatment level. All told, I ran a total of 72 trials i.e. ((3 levels humidity × 3 levels food) × 2 species) × 4 replicates (Figure 2.3), involving a total of 1152 animals (16 animals/trial). All trials were performed in the same room, at a mean temperature of 19 ± 1.84 (mean ± SE) ^{o}C. Windows provided all of the ambient lighting during the trials. The experiment was conducted in May, June and July of 2013. As limitations of lab space and hardware prevented me from running all trials simultaneously, I ran the experiment in trial batches, with all 9 combinations of treatments for each species being represented in each batch. To negate the possible impact of different light levels throughout the room, the locations of the different treatments were systematically rotated across batches. Trials were initiated at 10:00 hr by removing the plastic food wrap barrier between the home container and the movement corridor, and activating the four webcams. Trial duration was 72 h.

Collection of movement data

The movements of isopods along the corridors were monitored using web cameras (Nice Eshop™ and Creative Live!™) positioned at checkpoints. To monitor departures of animals from the home habitat, one web camera was positioned immediately above the exit of the home container. Three other web cameras were situated at 1 m intervals away, including the entrance

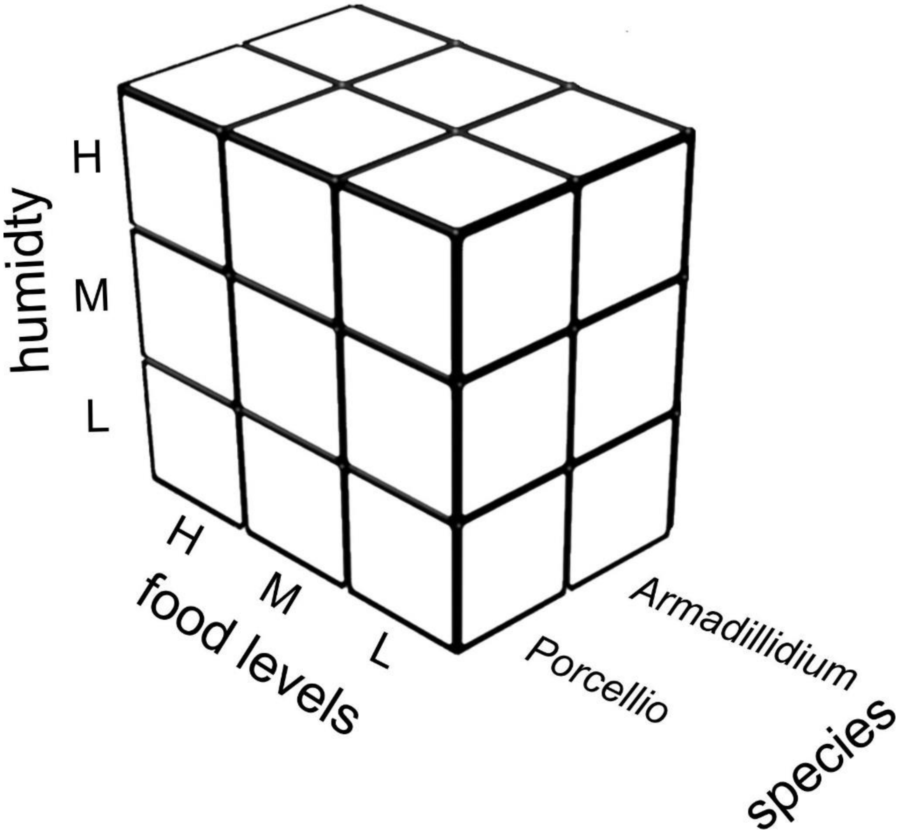

Figure 2-3. Factorial design of treatments used at home habitat level: 3 levels of Humidity × 3 levels food × 2 species (*Porcellio scaber* and *Armadillidium vulgare*) I conducted four replicates of each combination.

to the destination habitat (Figure 2-1). To allow nocturnal tracking of the animals, infrared LED lights were attached to each webcam, and all webcams were either converted to infrared capability by removing the infrared (IR) filter from the lenses and adding an IR LED externally or were originally constructed by the manufacturers (Model no- MYB997 and SKU039166) for IR sensitivity. The four webcams on each corridor were connected to a single laptop computer running Security Monitor Pro® version 3.12 security camera software. The motion-sensitive software detected the passage of isopods at each checkpoint and recorded them as digital images. Review of the digital images collected during the trials allowed me to identify departures from the home containers by individuals (and the timing of such), as well as distances moved within the corridors. These forays by the animals included multiple and/or partial trips from the home container to the destination container. From this information, I was able to calculate the following response variables:

NUMLEFT - the total number of animals that departed from the home container at least once during each trial.
NUMTRIP – the number of individuals in each trial that completed at least one trip between their home habitat and the destination habitat (i.e. these animals were recorded at the camera positioned immediate outside the destination habitat at least once).
NUMDEPART - the total number of times each individual departed from its home habitat during the trial.
TIMEHOME - the time (in seconds) elapsing before each individual animal departed from the home container and initiated its first foray into the corridor. For animals that never left the home container this equated to 259,200 s (= 72 hr).
TIMEAWAY - for each trial period, I calculated the total time (min) each individual spent away from its home habitat; this was the sum of all foray times (i.e. time spent in the corridor) and the time spent in the destination habitat. For animals that never left their home habitat, this value was set to 0 min.
To confirm the efficacy of the web camera checkpoint stations, at the end of each trial, I visually identified and crosschecked the identity of the individual animals in the two habitat containers using the webcam photo history of each animal’s travels.

Data Analysis

I used R (vers 3.0.2) statistical software for data analysis with $\alpha = 0.05$. As noted above, there were three response variables that constituted count data (NUMLEFT, NUMTRIP and NUMDEPART); of those, two variables (NUMLEFT, NUMTRIP) were calculated for each trial. The NUMDEPART variable instead was calculated for each individual. I used general linear models (GLM) to analyse the effects of the treatment levels (species, humidity, food) on these response variables. However, both NUMLEFT and NUMTRIP had set upper limits imposed on their values due to the fixed number of animals per trial (n=16), so I tested these using a GLM binomial test. NUMDEPART had no such imposed limit as each animal was able to conduct multiple departures from the home containers, so for this response metric I tested the effect using GLM Poisson analysis. My data for GLM Poisson and GLM Binomial showed over dispersion most of the time, hence I used GLM Quasi Poisson and GLM Quasi binomial tests instead. The other two response variables (TIMELEFT and TIMEAWAY) were calculated for each individual within each trial (total number of individuals = 1152). I used ANOVA (F- tests) for analyses involving these two variables, with a trial identification number entered into the model to account for variation within each group. Square-root and log-transformations also were performed on the TIMELEFT and TIMEAWAY variables (respectively) to achieve normal distributions. When interaction effects were significant, I omitted reporting the main factor effects and presented only interaction effects. Finally, post-hoc separation tests were done using Tukey's test.

RESULTS

Number of animals departing from home habitat (NUMLEFT)

Large proportions of individuals (97% of *Porcellio* and 89 % of *Armadillidium*) departed from their home habitat at least once during the trial. Humidity in the home container had a near-significant effect on the number of animals leaving home (t = 3.6, df = 71, $P = 0.06$). A higher number of individuals (98 %) of both species left home under low humidity, compared to the medium (91%) and high (89 %) levels (Figure 2-4). The interaction effect of food with species had a significant impact on NUMLEFT (i.e. species × food; t = 2.54, df = 71, $P = 0.014$; Figure 2-5). Fewer *Armadillidium* left home habitat under medium level of food than that of other food

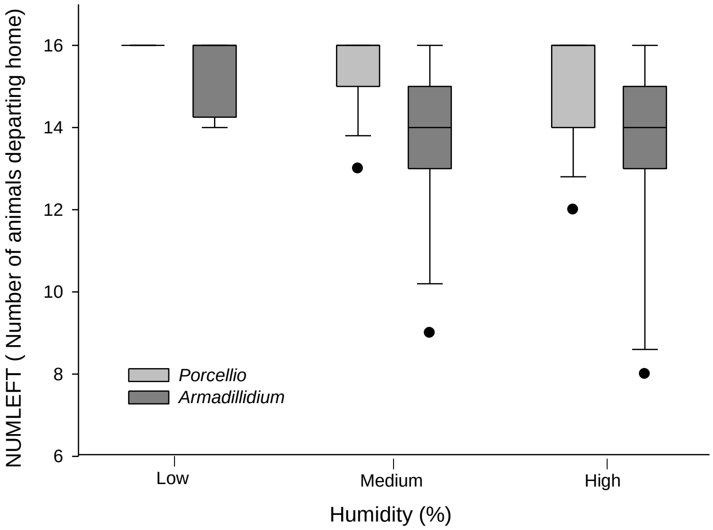

Figure 2-4. Box plots displaying NUMLEFT (Number of individuals departing from home habitats) under different humidity regimes. Each box represents the values from treatment combinations of three humidity levels with each species (n = 192). The center represents the middle 50%, the data set and is derived using the lower and upper quartile values. The median value is displayed inside the box and individual dots are the outliers of each box plot.

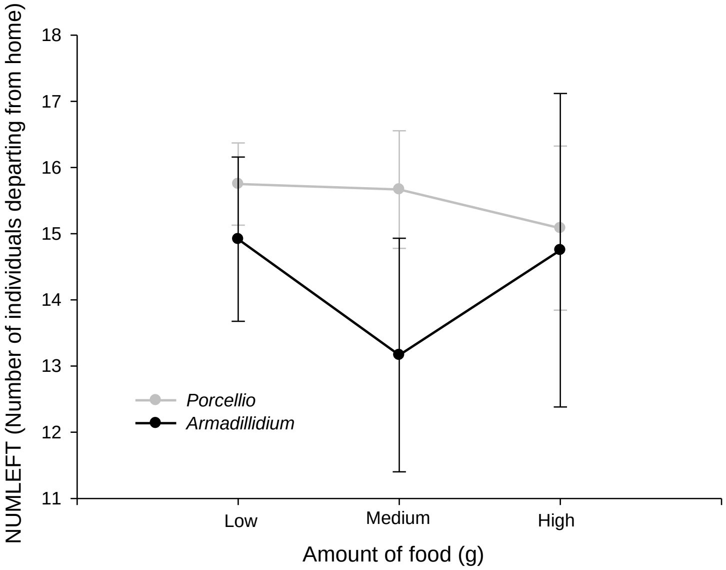

Figure 2-5. Effect of food levels and species on the number departing from home containers. Data points represent mean values of treatment combinations (+/- 1 SD) from each of three food levels, for each species.

levels, whereas *Porcellio* did not show a significant change in NUMLEFT under different food levels.

Time elapsing before individuals left the home environment (TIMEHOME)

After the exits to the home habitats were opened, *Porcellio* departed from their respective home habitats earlier than *Armadillidium* ($\bar{x}$ = 21.1 min ± 16.13 SD, n = 576 vs $\bar{x}$ = 27.2 min ± 30.20 SD, n = 576). Strong interaction effects were seen between species × humidity (F = 3.76, df = 2, 1131, *P* = 0.024; Figure 2-6), species × food (F = 4.37, df = 2, 1131, *P* = 0.013; Figure 2-7) and food × humidity (F = 2.44, df = 4, 1131, *P* = 0.045; Figure 2-8). Under the medium humidity conditions at home, both *Porcellio* (25.1 min ± 14.43SD) and *Armadillidium* (29.3 min ± 12.42SD) spent significantly higher amount of time at home. On the other hand, under medium levels of food at home *Porcellio* showed significantly higher TIMEHOME (27.6 min ± 15.6 SD) where as *Armadillidium* TIMEHOME was not affected by the amount of food levels at home. The low humidity and low food combination resulted in individuals spending significantly less time in their home habitat ($\bar{x}$ =16.7min, SD = 12.03, n = 64).

The number of times each individual departed from its home habitat during the trial. (NUMDEPART)

A large proportion of individual animals made multiple trips in and out of the home habitat (96 % *Porcellio* vs. 89% *Armadillidium*), and the NUMDEPART were affected by all the treatments. There were strong interaction effects between all factors, including a three-way interaction of humidity × food × species (t = -3.12, df = 1151, *P* = 0.001) that influenced NUMDEPART. Under low humidity, *Porcellio* made multiple trips back and forth from the corridor, for a mean number of 5.1 (SD = 3.2) departures out of the home habitat. Conversely, *Armadillidium* only made an average of 1.9 (SD = 1.1) departures from the home habitat container. Under low food levels, the average number of departures from the home habitat was higher for *Porcellio* ($\bar{x}$ = 8.1, SD = 3.0) than *Armadillidium* ($\bar{x}$ = 2.2, SD = 1.1). The combined effect of low humidity + low level of food at home resulted in the highest number of NUMDEPARTS by both species (*Porcellio* $\bar{x}$ = 8.12 ± 3.3 SD and *Armadillidium* $\bar{x}$ = 2.32 ± 1.4 SD), whereas the opposite effect was created by the high humidity + high food combination (*Porcellio* $\bar{x}$ = 2.25 ± 1.11 SD and *Armadillidium* $\bar{x}$ = 1.84 ± 0.84 SD).

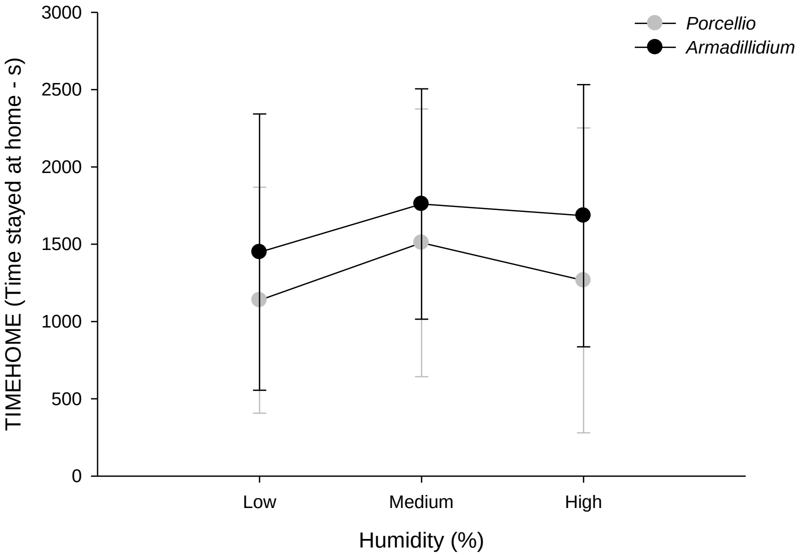

Figure 2-6. Interaction plot of humidity and species for mean time (seconds) individuals remained in home (familiar) habitat (n = 192) after the entranceway to a connecting corridor was opened.

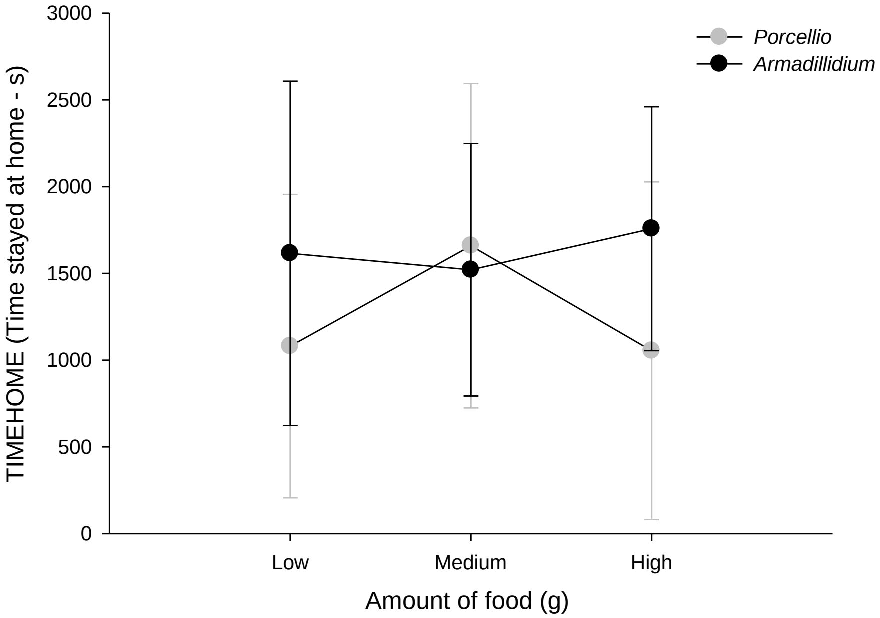

Figure 2-7. Interaction plot of food and species for the mean time (seconds) individuals remained in home habitat (n = 192) after the entranceway to a connecting corridor was opened.

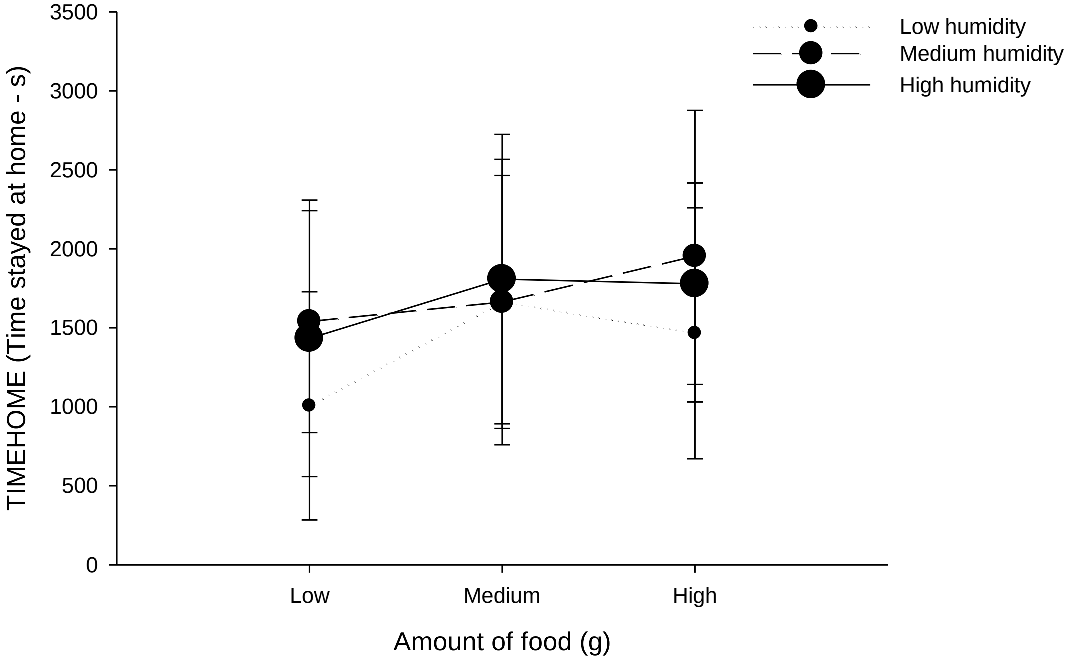

Figure 2-8. Interaction plot humidity and food for mean time (seconds) individuals remained in home habitat (n = 192) after the entranceway to a connecting corridor was opened.

Number of individuals completing the journey (NUMTRIP)

A relatively higher number of *Porcellio* reached the destination habitat, showing a distinct difference between two species (t = -3.89, DF = 71, $P < 0.001$) in this measurement. Out of those individuals that departed from the home habitat at least once, only approximately two thirds (≈72 % of *Porcellio* and ≈61% of *Armadillidium*) completed the journey to the destination habitat, instead returning to the home habitat after travelling only part-way through the corridor. The number of individuals reaching the destination habitat increased when humidity conditions were low at home (t = 15.45, df = 71, $P < 0.001$) followed by the medium humidity. A similar effect was seen for low food levels (t = 4.37, df = 71, $P < 0.001$) followed by the medium amount of food in the home habitat. The biggest response was shown under the low level of humidity where ~ 90% *Porcellio* and ~ 79% *Armadillidium* completed the journey through the movement corridor. The percentages declined to ~ 71% and ~ 59% under medium humidity and ~ 55% to ~ 47% under high humidity for *Porcellio* and *Armadillidium* respectively (Figure 2-9). Similarly, the low amount of food provided in the home habitat also caused a direct increment in the number of individuals completing the distance to the destination habitat i.e., low levels of food at home resulted in ~ 75% *Porcellio* and ~ 71% *Armadillidium* completing the distance, under medium food level, ~ 74 % *Porcellio* and ~ 59 % *Armadillidium;* under high levels of food, ~ 67 % of *Porcellio* and ~ 54 % *Armadillidium*).

At the end of each trial, ~ 99% of *Porcellio* that had departed from the home container had returned and remained there, regardless of the distance they travelled in the corridor. Only seven of *Porcellio* were present in the destination habitat at the end of the study. In comparison, ~ 37% of all *Armadillidium* (211 individuals) in the study remained in the destination habitat at the end of the trials. Most of these *Armadillidium* individuals originated from home habitats subjected to low humidity (180 individuals), low food (139 individuals), or both (117 individuals).

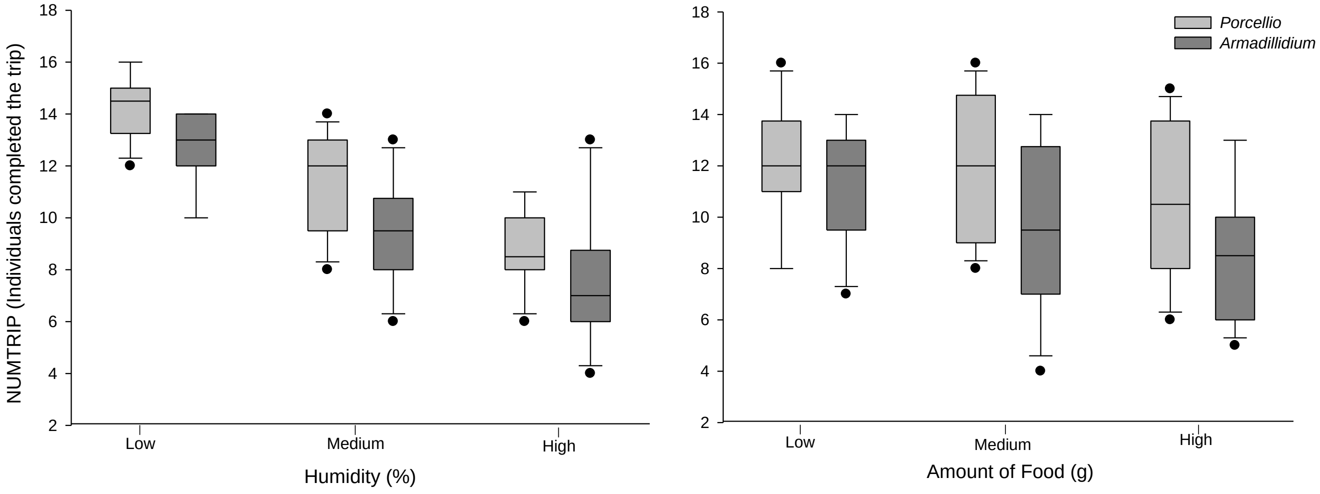

Figure 2-9. Number of individuals travelling the corridor at least once to reach the destination habitat container, grouped according to different conditions within the home habitat container. The center represents the middle 50%, the data set and is derived using the lower and upper quartile values. The median value is displayed inside the box and individual dots are the outliers of each box plot.

Total time spent away from home (TIMEAWAY)

In general, individuals of both species spent more than half of each trial in the home habitat, under all of the experimental conditions. However, when individuals did depart, the differences in time away from the home habitat (i.e. in the corridor and/or in the destination habitat) was strongly affected by all the factors tested and a three-way interaction of species × humidity × food (F = 4.6, df = 4, 1122, *P* = 0.001). The highest impact for TIMEAWAY was shown by low food and low humidity combination where *Porcellio* spent 7.5 hrs (SD = 3.46) and *Armadillidium* spent 17.4 (SD = 6.53) hrs away. On the other hand *Porcellio* spent the lowest TIMEAWAY under the medium humidity and high food availability ($\bar{x}$ = 2.4 hrs, SD = 1.41) whereas it was medium humidity and medium food availability for *Armadillidium.*

All results for this experiment are summarized in Table 2-1.

Measurement	Sig	Direction of effect
NUMLEFT		
Humidity	.	Low humidity level led to highest number of departures for both species.
species × food	*	*Armadillidium* showed fewer departures under medium food level than other two food levels.
TIMEHOME		
species × humidity	*	Under medium humidity both *Porcellio* and *Armadillidium* spent more time at home than other humidity levels.
species × food	*	*Porcellio* spent more time at home under medium food levels.
humidity × food	*	low food + low humidity led to earlier departures by both species where as high humid + high food levels created an opposite effect.
NUMDEPART		
species×food×humidity	**	Low humidity + low food led more trips by *Porcellio* than *Armadillidium.*
NUMTRIP		
Humidity	***	Highest number of trips were made under low humidity conditions at home
Food	***	Low food levels led to more travels by the individuals.
Species	***	*Porcellio* did more travels than *Armadillidium*.
TIMEAWAY		
species×food×humidity	***	Low humidity + low food led the longest TIMEAWAY by *Armadillidium* followed by *Porcellio*.

Table 2-1: Summary of species and treatment effects on movement metrics of two isopod species within an experimental microcosm. ns = non-significant, '***' 0.001, '**' 0.01, '*' 0.05, '**.**' 0.1. All interactions not shown on this table were insignificant (all P > 0.05) and main effects are not reported when interaction effects were significant. See Methods for response variable definitions.

DISCUSSION

In this experiment, I analyzed the movements of two different but closely-related isopods species out of their home habitat, in response to varying conditions of food abundance and humidity. Animal relocation presumably is a response to social or habitat changes, yet short temporal and fine spatial movements should be influenced by the patch configuration of food or vegetation used in foraging and/or other requirements for homeostasis (Crist *et al.,* 1992). Thus, I make the assumption that changes in the movement response variables were a result of conditions manipulated in the home habitat. The results of the study revealed the propensity of animals to leave their familiar home habitat (initial departure) was greatest when conditions therein were relatively inhospitable. However, differences in the tolerance levels of the two species to these conditions led to different intensities of movements out of familiar home habitat.

Respiration by terrestrial isopods in general is hampered by drier environments, and *Porcellio,* being less adapted than *Armadillidium* to desiccation (Smigel & Gibbs, 2008), showed greater departure rates (NUMLEFT), more return trips in and out of the movement corridor (NUMDEPART) and a higher number of individuals completing the trip from home to destination (NUMPRIPS). In addition, after leaving drier home habitats, both species displayed ‘exploratory’ periods, suggesting the relatively harsher conditions prompted the animals to allocate more time in search of favourable habitat. The slower movement speeds of *Armadillidium* may have simply resulted in that species being away from home longer (in the movement corridor or in the destination habitat), especially when the animal can deal with the threat of desiccation by rolling up. In addition, greater numbers of *Armadillidium* remained in the destination habitat at the conclusion of each trial, adding to their total time away from the home habitat.

In this study both species responded predictably to changes in food levels, but one of the species (*Porcellio*) showed a relatively amplified response. These results dovetail with work on birds by Robinson & Holmes (1982), that showed rapidly-foraging species (i.e. *Porcellio* in this study) make significantly more prey attacks per unit time whereas slow searchers (i.e. *Armadillidium*) scrutinize substrates more thoroughly and appear to make more cryptic choices. Boitani & Fuller (2000) suggest that cost and benefits of movement must ultimately be assessed by the impact on fitness, and when food becomes a critical resource, these costs and benefits should be calculated in terms of energy. Locomotion in general is an energetically costly activity (Alerstam *et al*., 2003). The daily food requirement for the animals used in this experiment was measured prior to the experiment while both species were resting in their home habitats with limited movement activities. Therefore, for the greater response demonstrated by *Porcellio* under lower food availability can be due to the set food levels were insufficient to meet their energy demand of *Porcellio* given that they showed greater movements out of their home habitat.

Factors such as those isolated in this study are interconnected with a host of other factors under natural conditions. Therefore, animal responses towards environmental changes ideally should be measured in terms of interaction effects. Unfortunately, these sorts of interactions are difficult to detect in field studies because of numerous undefined factors likely exerting influence on the response metric(s). Therefore, the interaction effects of the main treatment factors (species, humidity, food) that I observed in my study perhaps are the most interesting outcome of the study. This study exemplifies how combinations of factors may influence the propensity of animals to move, something extremely difficult to document in natural systems. The putative suboptimal conditions (i.e. low food and humidity) appeared to alter little the movement behaviour of the animals in isolation, yet the combined effects generated significant response(s). Most importantly, results of this study reveal that interaction effect of individual environmental parameters (such as relative humidity) with the ability of individual species to endure such conditions produces different movement responses, even among closely related species. Such response would not have been so clearly visible had I only used one species of isopods in this study.

The vast majority of my study animals made at least one departure foray from the home environment, even under optimal environmental conditions (high humidity, plentiful food). This suggests a strong inclination for these two species to at least temporarily explore unfamiliar habitat. In this study, 16 adult isopods were restricted to a relatively small home habitat ‘patch’ during the acclimation period. Thus is perhaps not surprising that individuals of both species displayed a strong tendency to explore out of their home habitat, irrespective of the conditions within the home habitat. Certainly, individuals of both species can be found travelling away from cover objects at night or during moist weather (Larsen pers. observ.). However, as this strong departure effect was consistent between all the experimental trials, I do not think this initial restriction of movement refute the results of my study. On the other hand, the majority of the animals returned to the home habitat containers, and/or still spent a large proportion of their time there. Familiarity with the home habitat (if only for 48 hours) may have played a pivotal role here. However, collectively over one-third of *Armadillidium* individuals remained in the destination habitats at the end of the trials, suggesting that familiar habitat had been at least temporarily abandoned by some individuals. Terrestrial isopods gain physiological benefits from residing with conspecifics (Hassall *et al*., 2005) during periods of low humidity, but the morphology of *Armadillidium* makes it more resistant to such conditions. Thus, compared to *Armadillidium, Porcellio* showed less of an inclination to 'settle' in the destination habitat, even if conditions of the home habitat was relatively unfavorable. Previous research suggests that some animals respond to multiple changes in their surrounding in a hierarchical fashion, whereby they initially consider one factor but, if information is unavailable, they then resort to another type of criteria (Kingsford *et al*., 2002; Diaz *et al*., 2003 and Robinson *et al*., 2011). Thus, a possible reason for the relatively higher number of *Porcellio* returning and staying in the home habitat could be greater vagility, allowing them to return to familiar habitat but having a greater capability to relocate in the future, should conditions worsen.

Microcosm studies allow greater opportunity for variable manipulation, yet they admittedly provide an artificial environment that may limit behavioral responses. Although the length of my corridor (3 m) was based upon pilot work, it nonetheless placed an upper limit on the distance animals could move. Individuals of both of these species will relocate and at least temporarily settle under neighbouring cover objects (Hassall, 1996 ; Dias *et al*., 2012; Larsen, unpubl.), but whether the repeated movements between the two habitats as documented in this study were 'natural' or not is unclear. Still, the initial cascade of movements out of the home habitats does not negate the significance of my work given the controlled experimental conditions; these data still reveal how the intensity and frequency of movements reflect incremental benefits of moving away from familiar, home habitat. Creating an experimental arena that allows animals to move from patch to patch, over varying distances, would be desirable but also exceedingly more difficult to monitor remotely, especially if replication also was sought.

The overarching result from this study is that environmental conditions (humidity and food) in home (familiar) habitat will exert a direct effect on the movement tendencies of animals, particularly through interaction effects. Although the patterns of these responses were consistent between two closely-related species, the magnitude of the responses were different, likely due to differences in morphology, physiology and mobility. Interaction effects between the habitat variables suggest combinations of stressors may produce synergistic effects. This study demonstrates how various degrees of environmental change result in animals making forays (short-term and perhaps longer in duration) from familiar habitat. Animal space-use models suggest that individuals separate themselves and move through their environment in a way that increases fitness and avoids risks (Spencer, 2012). My study supports this claim by showing the tendency to travel away from unhospitable home habitat may be inflated or deflated by species-specific adaptations. Although my study does not address how long-term, gradual deterioration in habitat will influence abandonment, it does reveal that variation in habitat condition will prompt relocation according to a gradient of disturbance.

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CHAPTER 3

MOVEMENT OUT OF FAMILIAR HABITAT II: THE EFFECT OF CONDITIONS IN CONNECTING HABITAT.

INTRODUCTION

Corridors provide connectivity between fragmented patches of habitats for wildlife (Haddad *et al.*, 2003). Corridors can exert positive effects on many different species and populations (Tischendorf & Fahring, 2000 and Eriksson, 2013) by influencing movement behaviour. Animals forced to relocate, due to innate tendencies and/or habitat saturation, often use corridors to facilitate movements. Such phenomena involving corridor usage (natural and anthropogenic) have been well-studied (Tewksbury *et al.*, 2002; Haddad *et al.*, 2003; Gregory & Beier, 2014 and Anderson *et al.*, 2015). Additionally, several studies have suggested that corridors can support residents rather than acting as only unsuitable matrix habitat, resulting in higher densities of animals within the corridors themselves than unsuitable matrix habitat (Machtans *et al.*, 1996; Perault & Lomolino, 2000 and Monkkonen & Mutanen, 2003). Conversely, research has also revealed that lower-quality corridors may actually promote movement through a compensatory mechanism (Andreassen *et al.*, 1996; Rosenberg *et al.*, 1998 and Gilliam & Fraser, 2001). What is less clear is, how different degrees of permeability within movement corridors affect the response of animals, particularly if they are originating from a favourable habitat.

The life history and locomotory ability of species likely influence the use of corridors (Haddad *et al.*, 2003). Despite the potential benefits of moving from one habitat to another, exploratory movements come with a cost (e.g., energetic demands, higher predation risk, and chances of missing breeding opportunities). Thus, animals face a trade-off between their need to familiarize themselves with their surrounding environment (including opportunities to colonize superior habitat) and their need to exploit already-familiar resources (Larsen & Boutin, 1994; Weins, 2001; Eliassen *et al*., 2007 and Berger-Tal *et al*., 2014). The cost of movements away from this familiar habitat through corridors, or otherwise will increase with time spent in the transient phase (Baker & Rao, 2004). However, few studies have shown that animals associated with patchy habitat and risky environments are capable of detecting suitable habitat from a distance (e.g. Conradt *et al*., 2001 and Hein *et al*., 2005), suggesting ‘uninformed’ exploration may be necessary (Smith & Sweatman 1974). To assess how corridor conditions influence movement probabilities requires an understanding of the scale of landscape patterns and the scale that organisms respond. Additionally, animals dispersing and or searching for resources must make decisions about whether or not to move, and/or cross boundaries, without prior knowledge of the associated risks that lie ahead (Fahrig, 2007). Hence, valuable insight both theoretical and applied will stem from a better understanding of if and how thresholds exist by which individuals initiate, discontinue and/or extend exploratory movements, and how such effects may differ among species based on their locomotory abilities and other characteristics.

Although a large body of literature exists concerning the effects of corridors natural and manmade on animal movement, many of these studies, particularly those conducted relatively early in the development of the field lack an experimental framework (Rosenberg *et al*., 1998). This introduces confounding factors and reduced statistical power (Gilbert-Norton *et al*., 2010). Complementing these *in situ* studies is experimental work involving micro - or mesocosms. Such studies, although fewer in number, have demonstrated that corridors promote movement across a diverse array of species, and that potential negative effects of corridors may be rare (Haddad *et al*., 2003; Gilbert-Norton *et al*., 2010 and Gregory & Beier, 2014). However, these studies also have their limitations, often operating on a case-by-case basis (Gilbert – Norton *et al*., 2010) and focusing on a single factor, a single species, or possessing limited replication. Multi-factorial experiments thus remain relatively rare, yet they afford the opportunity to begin understanding how interplaying factors i.e. resource levels, corridor porosity, affect animal movements, and how different species even those closely related may react to similar corridor properties.

Herein I report a microcosm study involving a two-factor experimental design and two different species. I conducted this work on two closely-related species of terrestrial isopods *Porcellio scaber* and *Armadillidium vulgare*, (P. Crustacea, O. Isopoda), with contrasting morphology and locomotory characteristics. In a previous study (Chapter 2), I used a similar microcosm paradigm to test how environmental conditions within the home habitat influenced departure movements by the animals out of the habitat and in a connecting corridor. To that end, I manipulated factors within the home habitat (food levels and humidity) while holding conditions within the corridors humidity and permeability constant and favourable for travel. In the present study, I reverse the situation by holding conditions within the home habitats constant while altering factors (permeability and humidity) within the corridors themselves.

My specific objectives in this study were to (i) test how conditions within the corridor encourage or discourage two isopod species to conduct exploratory movements in the movement corridors, (ii) quantify how changes in the same parameters in the movement corridor (humidity, permeability and their interaction) influence the progression of movement towards destination habitat, and (iii) examine how movements in response to the movement corridor conditions (initially, and after leaving the home habitat) differ between the two species. I manipulated two factors predicted to affect corridor movement in terrestrial isopods, namely humidity (affecting respiration and overall physiological condition – Hoese, 1982; Leistikow & Araujo, 2001; Schmidt & Wägele; 2001 and Edney, 2012) and permeability (pathway obstacles) given the fact that two species display different movement speeds and defensive strategies under threatening conditions. The use of the two different species provided insight into how shifts in the environmental are interpreted differently according to morphological constraints.

I predicted that humidity levels in the movement corridor would primarily affect *Porcellio*'s initiation and progression of the journey in the movement corridor than *Armadillidium*'s, given that the former shows a lower tolerance to drier conditions (see *Study species* under Methods below, and Chapter 2). At the same time, decreasing permeability (i.e., increasing obstacles in the corridor) was expected to affect the movements of both species after initiation of their journey, but the greater mobility of the *Porcellio* genus led me to predict lesser permeabilities would affect progression of *Armadillidium*'s journey more so than *Porcellio*'s. Interaction effects from humidity and permeability were also expected, given the combined effect of the aforementioned characteristics of two species, could lead to different effects from that of isolated treatment effects. Given the lack of experimental work conducted in this area, this study provides one of the initial solid illustrations of how different conditions intertwine to influence the movement 'decisions' of animals through a travel corridor leading away from familiar habitat.

METHODS

Study species

Terrestrial isopods are the most successful colonizers of terrestrial habitats among the crustaceans (Hornung, 2011). Although the taxa is generally restricted to moist habitats because, survivorship of terrestrial isopods is dependent on high humidity conditions, differences in the morphology of species within the group impart different capacities and behaviours to deal with drier conditions, and these in turn affect other aspects of their life histories. For example, *Armadillidium* (the ‘pill bug’) is relatively tolerant of drier conditions as they are capable of absorbing water vapor from unsaturated atmosphere directly (Edney, 2012). A thicker, flexible, and more heavily-minearlized cuticle also prevents water loss while allowing the genus to roll into a perfect sphere to reduce desiccation and avoid predation (Hild *et al.*, 2008). In contrast, *P. scaber* (the ‘woodlouse’) has a thinner and less flexible cuticle that contains only moderate amounts of mineral; this lighter exoskeleton enables the animal to avoid predation by running away or clinging to a substrate, protecting the soft ventral surface of the body. Preliminary studies by myself showed *Porcellio* averaged 2.1 cm/sec (SD ± 0.18, n = 40) over a 3 m route, compared to *Armadillidium* that travelled an average speed of 0. 95 cm/sec (SD ± 0.49, n = 40 (t = 3.77, df = 44.93, *P*= <0.001). In summary, *Armadillidium* is a relatively slower isopod, but one able to use drier habitat; *Porcellio* is lighter, faster, but more prone to desiccation. Further details on the ecology of these animals and their use as subjects in microcosm study are provided in Chapter 1.

General maintenance of animals

This work was conducted from May 2013 to August 2013. Source animals were purchased from a commercial biological supply house (Ward’s science, New York, USA) and used to establish larger colonies approximately two months prior to the experiment. These colonies were housed in plastic containers covered with a mesh lid. A layer of damp potting soil (≈ 2.5 cm deep) and assorted wooden debris provided habitat structure. Isopods in these colonies were fed commercial lettuce mix *ad libitum.* The colony room was on a synchronized 12 L:12 D schedule using wide-spectrum artificial daylight lighting, with artificial dawn (07:00) and dusk (19:00) schedules allowing the isopods to establish circadian rhythms (Refinetti, 2000) and normal nocturnal behaviour (Tuck & Hassall, 2005). Temperature (average) 19°C ± SE 2) and relative humidity (65% ± 4 SE) in the colony room was kept constant via the climate control system of the building and a Hunter® model 33250 humidifier. Also at this time, the baseline daily food consumption rate (i.e. 0.7 g of mixed green/ 16 animals/ day) was determined using containers housing 16 individual animals of each species (with four replicates) over two weeks. This rate was used later as a standard for food provision in the experiment.

Fourteen days prior to the experiment, the animals were transplanted into smaller containers (see below) and moved into a large, windowed laboratory in order to allow adjustment to natural lighting (Refinetii, 2000; Tuck & Hassall, 2005; Warburg, 1987). The temperature in this room was only marginally warmer (20 ºC) than that in the original colony room.

Microcosm Design

My basic experimental microcosm system consisted of one familiar habitat (‘home’) connected by a movement corridor to a destination habitat (see Figure 2-1 in Chapter 2). Plastic containers (21×21×10.5 cm) were used to create two habitat patches connected by a 3 m corridors. The corridors were constructed out of 5.5 cm × 7.5 cm aluminum rain gutters cut length-wise and attached to the habitat containers using PVC gutter adapters. The length of these corridors was determined partly from previous studies (Perreault, 2009) and on my own pilot study that suggested a 3 m length was sufficient to provide marked variance in the distance travelled by isopods over a 12 hr period by two species.

A 2.5 cm deep Plaster of Paris layer created a substrate in the habitat containers and corridors. This porous layer aided in the maintenance of relative humidity levels (see below) and prevented the isopods from burrowing. On top of this layer, 1 cm of sterile potting soil Miracle Grow® was spread and then dampened accordingly to achieve specific humidity levels (see below). Shelter in each container was provided by a ceramic tile (11 cm × 11 cm) raised slightly about 1 cm above the soil by four glass marbles (see the Figure 2-2 in Chapter 2). Whenever a new trial was conducted, all soil was replaced, cover objects were washed, and the corridor walls and Plaster of Paris substrate were rinsed and scrubbed thoroughly with distilled water.

Preparation and selection of animals for experiments

All animals used in the experiment were haphazardly selected from the source colonies. Using 50% maturity length as a cut-off, I selected 720 each of *Armadillidium* (1.32 cm ± 0.0021 SE; 0.108 g ± 0.0042 SE) and *Porcellio* (1.54 ± 0.0034 cm; 0.148 g ± 0.0056). In addition to length and weight, I also determined the gender of each animal to ensure equal numbers of males and females used in each trial. To permit individual identification, each animal received a unique carapace mark within its trial group, applied using white nail polish. The marked animals were introduced into the experimental home habitats (16 animals per container) but with the passageway into the movement corridor sealed off with a plastic sheet prior to the start of the trials 48 hrs later.

Manipulation of movement corridor environment

Three levels of corridor permeabilities and humidities were applied to the movement corridors (see Figure 2-3 for analogous design used in Chapter 2). Permeability was altered by adding different amounts of aquarium gravel to the pathway. Densities of 0, 15 and 35 gravel pebbles/meter were considered high, medium and low permeability conditions, respectively. Relative humidity levels were set using tolerance measurements established by Warburg (1987) that broadly covered both species: low 30-40%, medium (sufficient) 60-70%, and high 90%. These levels were maintained in the movement corridor through the application of distilled water through a fine-mist spray bottle. To verify consistent conditions during pilot tests and actual experimental trials, I situated a calibrated hygro-data logger (Maxim Onewire Viewer®) in each movement corridor to monitor relative humidity conditions. To achieve the low humidity level, water was sprayed into the movement corridor 48 hr prior to the start of the experiment, with no replenishment during the actual experiment. The other two humidity levels medium and high, were established during the acclimation period by different regimes of water sprayed in the home containers, in combination with a plastic food wrap applied over the corridor trough punctured to allow air passage. The conditions of all home habitats and destination habitats (regardless of the corridor treatment) were maintained at medium relative humidity (60 % - 70 %) and the baseline food levels (0.7g) All told, I ran 90 trials in total, i.e. ((3 levels humidity × 3 levels food) × 2 species) × 5 replicates, involving a total of 1440 animals (16 animals/trial). Limitations of table space and hardware prevented me from running all trials simultaneously, so I conducted the experiment in trial batches, with all 9 combinations of treatments for one species in each batch. To negate the possible impact of different light levels from the windows, the different treatments were rotated through the room over each trial. Trials were initiated at 10:00 hrs by removing the polyethylene film barrier separating the home container and the movement corridor, and activating webcams (see below). Trial duration was 72 h.

Collection of data

Movements of isopods within the travel corridors were monitored using web camera checkpoints and movement-detection software (Nice Eshop™ and Creative Live!™). One camera was positioned at the exit of the home habitat (checkpoint 1), and another at the entry to the destination habitat (Checkpoint 4). Two other web cameras were placed 1/3 (Checkpoint 2) and 2/3 (Checkpoint 3) of the distance along the corridor, respectively. To allow nocturnal tracking, infrared LED lights were attached to each webcam, and all webcams either had infrared capability or were converted by removing the IR filter from the lens and adding an external IR LED. The four webcams on each corridor were connected to a dedicated laptop computer running Security Monitor Pro® version 3.12 security camera software. This motion-sensitive software efficiently detected the passage of isopods at each checkpoint and recorded them as digital image files.

Review of the digital photographs collected during the trials enabled me to identify the departure (and timing of) by individuals from the home container, as well as minimum distances moved within the corridors. This included multiple departures and return movements to the home container. Multiple forays from the home container to the destination container, or partial trips, were recorded for some animals. Thus, when calculating distances travelled, I determined the minimum distance each animal travelled in the corridor, based on the distance from the home container (center of the ceramic tile cover object) to the furthest camera checkpoint where the animal was recorded on each foray. To further verify the efficacy of the web camera checkpoints, at the end of each trial, I cross-checked the identity of the isopods present in both the destination and home habitat corridors against my interpretation of the data supplied by the web cameras. At the end, the following metrics were calculated and compared across the treatments:

Numbers at check points - the number of animals passing each check point along the corridor was recorded for checkpoint 1 (No. Check point 1), checkpoint 2 (No. Checkpoint 2), checkpoint 3 (No. Check point 3) and checkpoint 4 (No. Check point 4) in to the destination habitat.

Foray distances (4 metrics) - I used the detections of individual animals at the four checkpoints to calculate minimum total distance travelled (TOTDIS), minimum distance of the first foray undertaken by each animal into the corridor (FIRSTDIS), the minimum distance of the longest foray shown by each animal (LONGESTDIS), and the mean minimum foray distance demonstrated by each animal (MEANDIS*).*

Total and mean time spent in the corridor – Using the time stamped photographs, I calculated how much time each individual spent between sequential pairs of web cameras, and from that I calculated the time spent by each animal on each foray out of the home habitat. As most of the individuals conducted several forays in the movement corridor, I calculated the TOTTIME (total time) they spent in the corridor and the MEANTIME spent on each foray by a given individual.

Speed of the movement – Total foray length of a given individual was divided by the total time spent in the corridor (TOTSPEED).

Data Analysis

Statistical analysis was conducted using R (vers 3.0.2). There were discrete data and continuous data with nominal predictors. All the parameters I tested were calculated from each individual in the given treatments (Total number of individuals =1152) except “individuals that passed each check point”, which were calculated per each home habitat (total number of home habitats or trials = 72). As I was dealing with categorical and nominal predictor variables with “nonlinear” response variables in the number of individuals at each check points metric, effects of treatments were tested using General Linear Models (GLM). Because the number of individuals passed each check point, had an upper limit of total number of animals per a home (16), a binomial GLM model was used for the analysis, and analysis was done separately for each check point. Additionally, these data for GLM Binomial showed over dispersion, and thus I used GLM Quasi binomial tests instead. Square Root and log transformations were done for the continuous data if the residuals of those parameters were not normal then followed by an ANOVA. In the ANOVA model trial number (replicate number) was included to account for variation within each group. To select the model that correctly represents each aspect, χ^2 tests were used. When interaction effects were significant, I did not report main factor effects and instead focus only on interactions. Finally, post-hoc separation tests were done using Tukey's test.

RESULTS

Number of animals passing each checkpoint

No. Checkpoint 1

During the experiment, most of the animals (≈ 71%) left their home habitat container at least once and traveled partially or completely through the corridor. A higher proportion of *Armadillidium (*84%) exited the home habitat (i.e. passing check point 1) than that seen for *Porcellio* (≈58% of total) (Figure 3.1). The interaction of species × humidity treatment affected the number of individuals passing the first checkpoint (t = 2.54, df = 89, $P < 0.05$; Figure 3-2) where significantly fewer *Porcellio* (24% of total) passed the first check point under low humidity than that of other humidities. At this point permeability of the corridors did not exert a significant impact (t = -1.13, df = 89, $P = 0.26$).

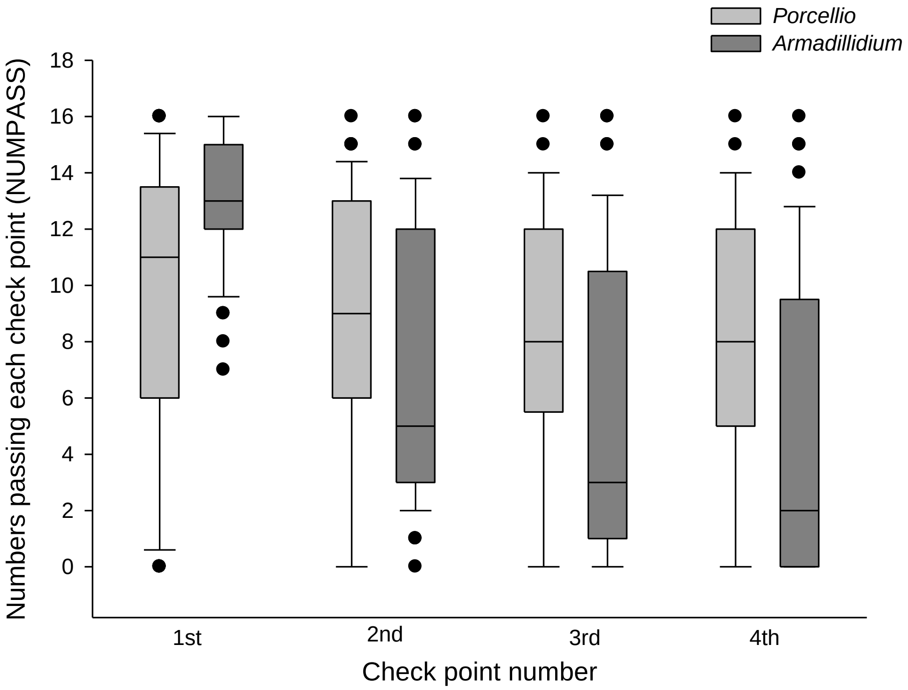


Figure 3-1. Number of animals of both species that passed each checkpoint (n = 720). Individual dots are the outliers of each box plot.

No. Checkpoint 2

The number of individuals passing Check point 2 differed significantly between the two species (t = 2.71, df = 89, $P < 0.01$). However, at this checkpoint higher numbers were recorded for *Porcellio* (≈53% of total individuals at home; Figure 3-1) than *Armadillidium* (≈42% of total). Interaction effects of permeability with humidity (t = -2.59, df = 89, $P = 0.01$; Figure 3-3) had a strong impact whereas interactions of permeability with species had a marginal effect (t = -1.18, df = 89, $P = 0.07$). Significantly low counts were recorded under low humid + low permeability corridors (≈ 7%) followed by medium humid + low permeability (≈ 16%) corridors than that of other conditions. Under high permeability, significantly higher numbers of *Armadillidium* passed the 2nd check point of the corridor (≈ 76% *Armadillidium* and ≈69% of *Porcellio*) and under the low permeability a significantly higher number of *Porcellio* were able to pass the 2nd check point (≈34% of *Porcellio* and ≈19% of *Armadillidium*).

No. Checkpoint 3

The effect of the humidity in the corridors continued to appear unimportant (t = -1.01, df = 89, $P = 0.31$) to animals reaching this check point. However the interaction effect of species × permeability had a significant impact on the No. Check point 3 count (t = -2.52, df = 89, $P < 0.05$; Figure 3-4). Approximately 72% of *Armadillidium* individuals passed Check Point 3 under high permeability whereas only 7% of *Armadillidium* travelled this distance under low permeability. Although the response seemed to be less pronounced, the same trend was shown by *Porcellio* under high and low permeabilities (≈67% and ≈29% respectively). In addition, only a marginal interaction effect was shown by permeability × humidity (t = -1.84, df = 89, $P = 0.07$). The highest number of individual *Porcellio* passed the 3rd check point under high permeability + high humidity corridors (≈ 91%) followed by high permeability + medium humidity corridors (≈64%). In comparison, the lowest No. Check point 3 counts were observed in low permeable + low humidity corridors (≈2%).

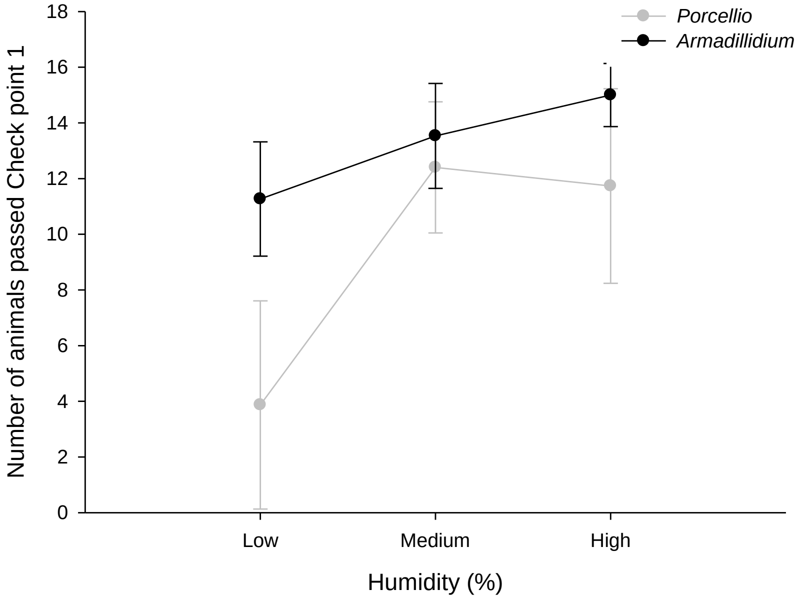


Figure 3-2: Interaction plot of humidity and species on the Number of animal appeared at checkpoint 1 (n = 240).

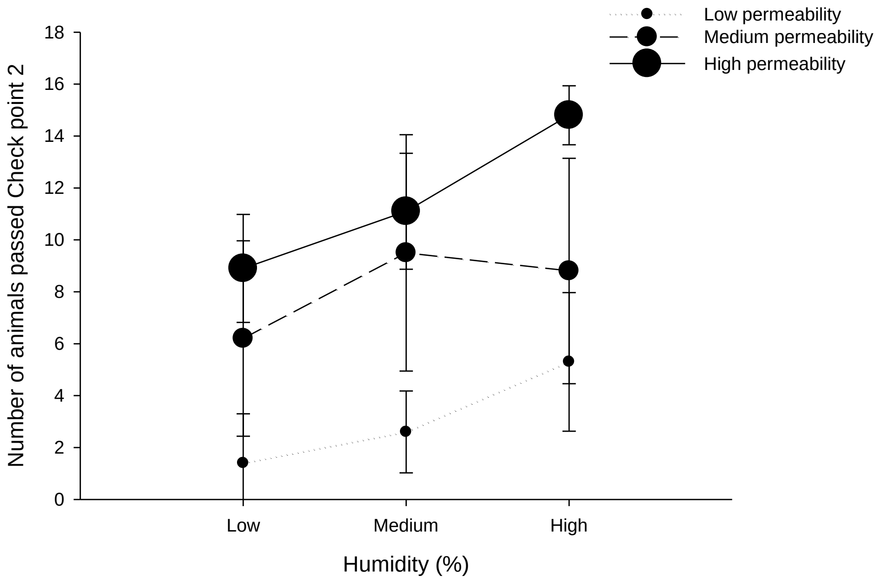


Figure 3-3. Interaction effect of Humidity and permeability on the number of animals that appeared at checkpoint 2.

No. Check point 4

Though higher numbers of *Armadillidium (*84%) exited the home habitat (i.e. passing the first checkpoint – see above), less than half of these individuals (≈32%) travelled the total length of the corridor to reach the destination habitat. In comparison, a fewer number of *Porcellio* (≈58% of all individuals) left the home habitat, yet a larger proportion (≈48%) of those individuals completed the journey through the corridor than *Armadillidium* (Figure 3-6). The number of individuals travelling the entire length of the corridor, and thus reaching the destination habitat (i.e. passing 4th check point) showed a significant influence from the interaction effects between species × permeability (t = -2.48, df = 89, *P* = 0.02; Figure 3.5). Under low corridor permeability, a higher proportion of *Armadillidium* entered the corridor (≈81%) compared to ≈41% *Porcellio.* However, this pattern was reversed at the end of the corridor (the 4th check point at the end of the destination habitat), where higher proportion of *Porcellio* (≈29%) than *Armadillidium* (≈5%) arrived at the destination habitat. Again a marginal interaction effect between permeability × humidity (t = -1.69, df = 89, *P* = 0.09) was shown for this metric. In both species, the highest number of individuals started and completed their forays under high permeability + high humidity corridors (*Porcellio*: ≈ 96% at the 1st check point and 89% at the 4th check point; *Armadillidium:* ≈93% at 1st check point and 90% at 4th check point) with the reverse occurring under low humidity + low permeability corridors (*Porcellio*: 70% at 1st check point and 2.5% at the 4th check point; *Armadillidium* ≈14% at 1st check point and zero at 4th check point).

Foray distances (TOTDIS and MEANDIS)

The total distance travelled by individuals of both species was influenced by the interaction of humidity with permeability (F = 2.503, df = 2,1420, *P* = 0.047; see figure 3.7). The longest distance travelled by both species was recorded under high permeability and medium humidity corridors ($\bar{x}$ = 16.61 ± 9.11m) followed by high permeability and high humidity corridors ($\bar{x}$ = 16.13 ± 10.51m). On the other, hand the shortest total distance travelled by two species was

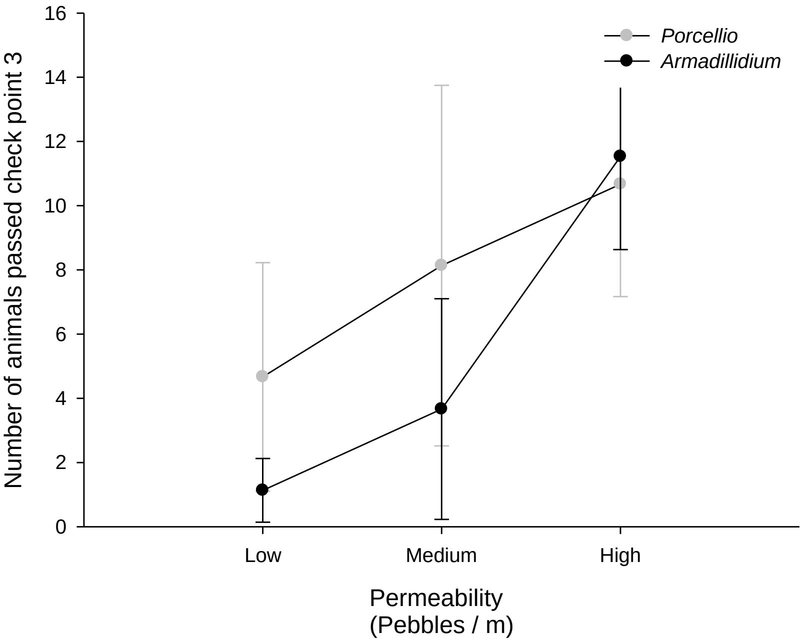


Figure 3-4: Interaction plot of the permeability and species on the number of animals passed the checkpoint 3 (n = 240).

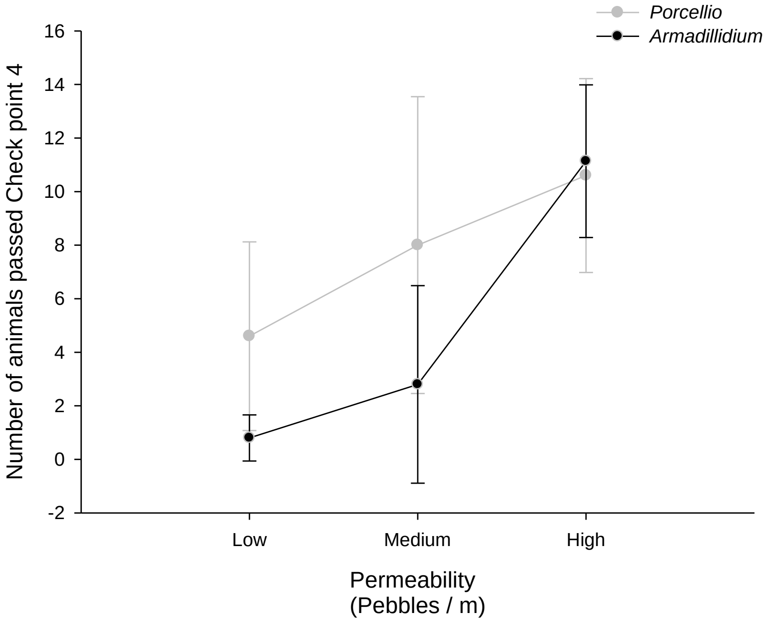
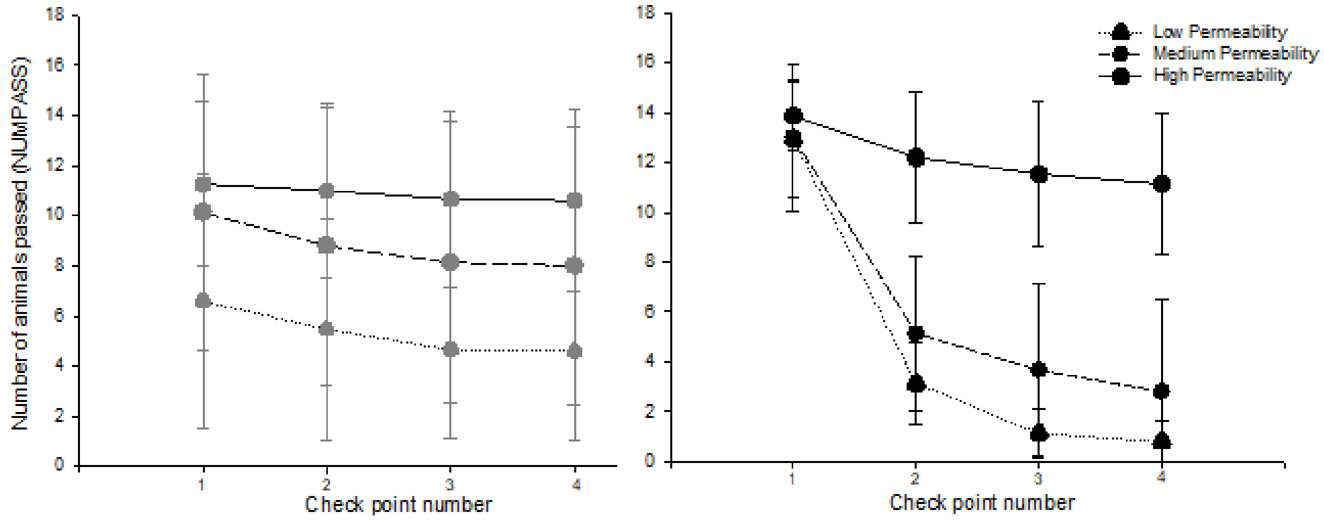


Figure 3-5. Interaction effects of permeability and species on the number of animals passed checkpoint 4.



Porcellio

Armadillidium

Figure 3-6. Mean number of individuals of both species at different checkpoints under three permeability levels (The error bars represent standard deviation from the mean, n = 240).

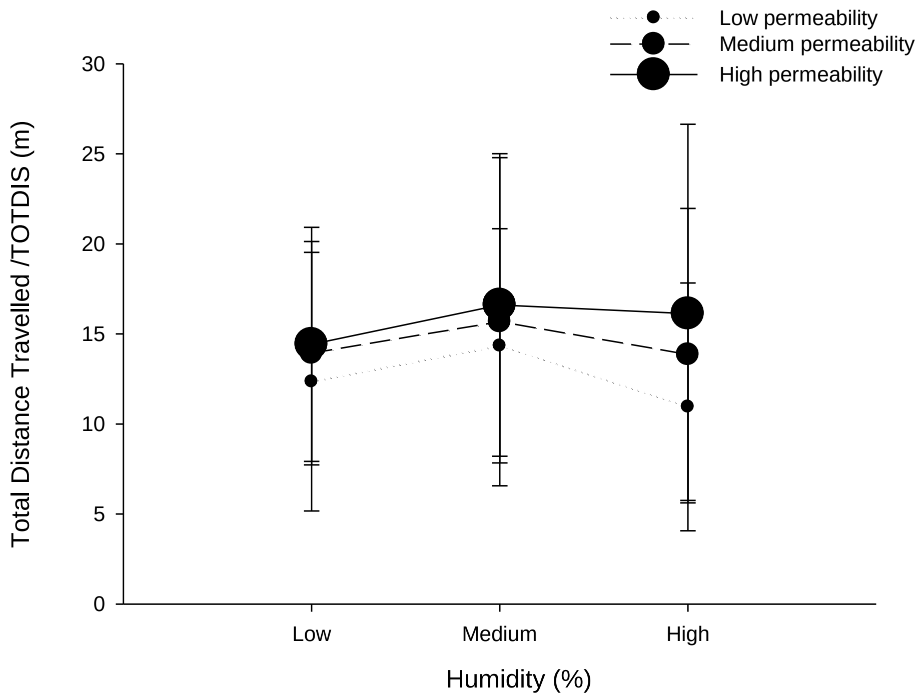


Figure 3-7. Total distance travelled by both species under different humidity and permeability combinations (n = 160).

occurred under low permeability and high humid corridors (x̄ = 10.95 ± 6.88m) followed by low permeable low humid corridors (x̄ =12.35 ± 7.18m). No effects from the treatments or their interactions were seen for both the first-foray distance and the longest-foray distance metrics. Mean foray distances performed by each individual also dropped under low permeability corridors (F = 37.49, df = 2,1416, *P* < 0.001). Additionally the two species also displayed a significant difference in this metric (F = 67.52, df = 2,1416, *P* <0.001) with the mean distance travelled by individual *Porcellio* being higher (4.47 ± SD 2.9 m, n = 720) than in *Armadillidium* (3.3 ± SD 2.29 m, n = 720). Humidity did not have any effect on mean foray distance (F = 0.399, df = 2,1416 *P* = 0.67). For this movement metric, all the interaction effects were statistically insignificant (all *P*s > 0.35).

Total and mean time spent in the corridor (TOTTIME and MEANTIME)

The total time animals spent in the corridor differed only by species (F = 7.013, df = 1,1420, *P* = 0.008), with *Armadillidium* spending significantly more time in the corridor (mean = 6.11 hr, SD = 9.38, n = 720) than *Porcellio* (mean = 3.52 hr, SD = 3.16, n = 720). Humidity, permeability, and their interaction did not affect the total time spent by animals in the corridors (all *P* > 0.24). The mean (average) time that individuals spent in the corridor appeared to have affected only by the species (F = 7.013, df= 1, 1420, *P* = 0.008) where *Armadillidium* spent more time in the corridor (x = 9.38, n = 720) than *Porcellio* (mean = 3.52 hr, SD = 3.16, n = 720). Again humidity, permeability, and their interaction did not affect the mean time spent by animals in the corridors (all *P*s > 0.32).

Speed of the movement (TOTSPEED)

As predicted, the speed of travel for animals in the corridor differed significantly different between species (F= 2.003, df =1,1408, *P* = 0.045), with *Porcellio* averaging 0.17cm/s (SD = 1.39 cm/s, n = 720) and *Armadillidium* 0.13cm/s (SD= 0.44cm/s, n = 720). No significant effects of humidity (f = 0.195, df = 2,1408, *P* = 0.51), permeability (F = 0.513, df = 2,1408, *P* = 0.51) or interactions were detected.

All of the results of this experiment are summarized in Table 3-1.

Measurement	Sig	Direction of effect
No. animals pass each check point (CP)		
No. Check point 1		
Permeability	ns	
Species × Humidity	*	low numbers were recorded by *Porcellio* under low humidity.
No. Check point 2		
Species	***	higher number of *Porcellio* showed up than *Armadillidium*
Humidity × Permeability	**	low numbers appeared at low humid + low permeable corridors and medium humid + low permeable corridors.
No. Check point 3		
Humidity	ns	
Species × Permeability	*	higher no. of *Armadillidium* followed by *Porcellio* were at under high permeability
No. Check point 4		
Species × Permeability	*	higher no. of *Armadillidium* showed up under high humidity
Humidity × Permeability	.	highest numbers were recorded under high humid + high permeable corridors.
Foray Distances		
Species	***	mean foray distance of *Porcellio* is higher than *Armadillidium.*
humidity × permeability	*	total distance travelled under medium humid + high permeability was the highest and high humid + low permeability was the lowest
Total time spent in the corridor		
Humidity	ns	
Food	ns	
Species	**	*Armadillidium.* Spent more time in the corridor than *Porcellio*
Speed of the movement		
Humidity	ns	
Food	ns	
Species	*	*Porcellio* had a greater movement speed than *Armadillidium*

Table 3-1: Summary of species and treatment effects on movement metrics of two isopods, within an experimental microcosm. ns = non-significant, **P*<0.05, ***P*<0.01, ****P*<0.001. Interaction effects not included on this table were insignificant (i.e. all Ps > 0.05). See text for response metric definitions.

DISCUSSION

In this experiment, the two isopod species *Porcellio scaber* and *Armadillidium vulgare* showed significantly different responses for most of the metrics I tested, including; differences in numbers that appeared at each checkpoint, mean foray distances, the total time individuals spent in the corridor, and the movement speed. Low humidity conditions affected the total foray length of the animals and number of animals that initiated leaving home (by passing checkpoint 1) whereas lowering the permeability affected the number of animals progressing towards the destination habitat and the mean foray distance performed by the animals. Additionally, there were interaction effects from the main factors that influenced the number of individuals at each checkpoint as well as the total distance travelled by the individuals. Overall, these results reveal how different species perceive different conditions in the movement corridors and their responses to them.

Contrary to my prediction of *Porcellio* would be mostly affected by the corridor humidity, humidity levels affected only the number of individuals that left the home habitat and total distance travelled by individuals of both species. Hence animals in this study were presumably not “forced” to relocate as they were residing in favorable home environments, it is likely that the individuals initiating exploration out of their home habitats were repulsed by low humidity conditions in the movement corridor. However, once they instigated the exploration, low humidity levels in the corridor did not appear to prevent the advancement of their journey. Some previous work has suggested that lower-quality corridors may actually promote animal movement through a compensatory mechanism (Andreassen *et al.*, 1996; Rosenberg *et al.*, 1998 and Gilliam & Fraser, 2001) such as faster movement through poor habitat increasing the probability of safe passage through a movement corridor. Similarly other studies suggests that animals moving across riskier landscapes alter their behavior in adaptive ways (Yoder *et al.*, 2004 and Bond *et al.*, 2001). For an example, Bakker & Van Vuren (2004) reported that artificially translocated red squirrels move slower in more risky clear cuts than in forested covers and lighter squirrels, which may have lower energetic reserves, are more likely to cross those risky gaps than others. Therefore it is likely that different adaptations of both species must have

produced trade-offs that affect the propensity to move through the low humidity movement corridor specially given that the length of movement corridor was limited only to 3 m.
By altering levels of permeability, I tested the tendency and capability of animals to travel through corridors with different levels of impediment. In keeping with my prediction, the number of animals (of both species) initiating movement out of the home habitats was unaffected, but the number of these continuing to the more-distant checkpoints decreased with lesser permeability, with *Porcellio* appearing less affected by the experimental conditions than *Armadillidium.* The most accentuated decrease in progression of movement occurred under conditions of low permeability (i.e. high resistance), suggesting this caused the animals to return to their home habitat. The number of animals passing each check point after leaving home and the mean foray distance travelled by animals also was directly related to permeability within the corridor.

Although these results are intuitive, they represent a clear demonstration of the direct effects of path/corridor permeability on the movement behaviour of two different animal species with varying mobilities. These observations are consistent with other studies that show movements of animals may decline or differ if they encounter obstacles or less favourable conditions (Crist *et al.*, 1992; Hein, *et al.*, 2003; Cant, *et al.*, 2005 and Castellon & Sieving, 2006) that will ultimately affect their net displacement or dispersal success. Taken together, these studies provide useful information on the dynamics of different environmental parameters in fragmented landscapes because it can predict how landscape variables impact movement patterns of different animals under such circumstances.

The level of ecological specialization of an organism, i.e. its variance in performance across a range of environmental conditions or resources (Devictor *et al.*, 2010), will greatly influence how it reacts to its local environment. Generally, the spatial grain of resources is coarser for habitat specialists than generalists, meaning that the average landscape will be perceived as more fragmented by specialist species (Baguette & Van Dyck, 2007). In this experiment, higher numbers of *Armadillidium* initiated movements out of the home habitat, yet the number of *Armadillidium* travelling further along the corridor dropped off more precipitously than

Porcellio. Perhaps the cost of moving away from familiar habitat for *Porcellio* may be higher than that of *Armadillidium*. *Porcellio,* being more mobile, was less prone to travelling through less-permeable corridors, being able to return more easily to their home/familiar habitat whereas the greater cost of travel by *Armadillidium* resulted in a greater tendency to remain in the destination habitat. Again the fact that *Porcellio* is capable of faster travel than *Armadillidium*, would seem to explain differences in time spent in the corridor. Therefore, we can expect movement behaviour to be counter-selected in specialists when movement costs (both direct and indirect) are important.

Understanding how habitat structure within a patchy matrix influences permeability to animal movement is an important key to managing complex landscapes for conservation. Results of my study demonstrated that connectivity between two patches is a function of both the environmental features of the movement corridor and the abilities of different species to tolerate conditions within the corridors. This underscores the importance of managing for habitat in corridors as well as in patches. Additionally this information could also be used in species reintroduction programmes: the familiarity, conditions and level of adaptation to travel within corridors all need to be taken into account to facilitate movement between patches. Further, knowledge on the movement 'rules' of different species could be used in simulation models to generate more accurate predictions on the species-specific dispersal capacity and survival in complex landscapes.

My results demonstrate that single-factor effects may exert less of (or no) response to corridor travel, but interaction effects between factors may be strong, and affect differently even closely-related species. Such effects will be difficult to detect i*n situ*, because natural variation of ecosystems allow for many possible confounding factors (Vinnedge and Gaffin, 2015). Although movements in this study were measured on a very fine scale, they still indicate that even closely-related species may demonstrate different levels of response to connections between habitats, and the environmental conditions therein. Similar to my study, Marvier *et al*., (2004) and Webala *et al*., (2011) showed the impacts of environmental changes in the movement corridor may vary by species life-history traits, generating costs and benefits according to how species use landscapes differently. In this study, morphological features (and their implications) appear to exert such effects. This illustrates how different environmental conditions weigh into the movement 'decisions' of animals to utilize habitat corridors. Therefore, despite the fact that microcosm studies do not capture the complexity of natural ecosystems, they still can be used to provide insight into how different stimuli may be integrated by animals to generate behavioural responses, and allow more rigorous testing of interaction effects. In the long term, an appropriate combination of field studies, computer modeling and manipulative microcosm studies will allow us to gain a more comprehensive understanding of animal movements within and outside of corridors.

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CHAPTER 4: CONCLUSIONS AND GENERAL DISCUSSIONS

In my first experiment, I used a microcosm environment to examine how the exploratory movements of two terrestrial isopods, *Porcellio scaber and Armadillidium vulgare,* were affected by differences in humidity and levels of food in the home habitat. The results of this study (alteration of home habitat) revealed that both species of isopods for the most part responded predictably to the treatments. *Porcellio* showed a relatively greater response to the treatments, demonstrating a greater tendency to move in response to low humidity and low food availability at home habitat. Perhaps more interestingly, both species appeared to be influenced by interaction effects of low humidity and low food availability at home habitat which led them to be away from their familiar home.

In a second experiment, I tested how differences in humidity and permeability of the movement corridor affected the two isopod species *after* they had entered movement corridors. Unlike the pervious experiment, low humidity in the corridor did not have significantly negative effect on *Porcellio* and overall it had a lesser impact on the movement metrics I measured. On the other hand, as predicted, permeability of the movement corridor had a greater effect on movement behaviour of both species particularly in terms of low permeability limiting the activity of *Armadillidium*. Further, interaction effects of inhospitable conditions in the movement corridors and species performance also showed *Porcellio* was coping better with the harsh conditions in the movement corridor.

In general, these results bear out my predictions that low humidity and low food levels in the home habitat would increase movement tendencies of two isopod species and the low humidity and low permeability levels in the movement corridor would decrease the movement tendencies of two isopod species. Therefore the results of my work indicate, animal movement is affected by conditions in the existing habitat (home environment) as well as conditions in the matrix connecting the habitat patches (movement corridors). A number of *insitu* studies conducted on movement out from familiar habitats and travel through different movement corridors by single species or multiple species have reported similar findings (Crist *et al.*, 1992; Monkkonen & Mutanen, 2003; Hein *et al.*, 2003; Hamilton & Vollrath, 2005; Webala *et al*., 2011 and Segers &

Broders, 2014). Movement decisions of animals are based on the intensity of the changes in the environmental parameters. More importantly, my results showed, though both species showed similar movement patterns throughout the experiments, different movement capabilities and environmental tolerances of two species, resulted in them displaying different degrees of movement behaviours under different conditions in the home habitat and in the movement corridors.

Experimental studies often require a simplification of the real, natural world, by controlling variability of a number of environmental factors. Therefore, in my Chapter 2 experiment, I altered factors that could affect survival of animals in their home environment (humidity and amount of food) thereby prompting (in theory) individuals to leave. In Chapter 3, I altered factors that would affect the movement between habitats. Using more than one species in these experiments allowed me to evaluate how different morphological and physiological features would alter the ‘assessment’ of the environment by the animal, and in turn, their response with respect to movement. By conducting a microcosm study, I could easily isolate the effects of the specific factors in this experiment, and this revealed a few direct effects and a large number of interaction effects influenced the movement behaviour of the two isopods species. The fact that combined effects of more than one factor can exert pressure on animals to alter their movement decisions suggests that the results of my study could relate to natural ecosystem where changes in environmental parameters (eg. temperature, water availability) often trigger concomitant changes in the others, hence requiring animals to respond to interaction effects.

Through my two complimentary experiments, my research has provided a better understanding of the factors generating movements out of familiar habitats into a connecting matrix. The collective results of the two experiments showed that both species were more responsive to changes in the home environment than the changes in the movement corridor. For example, when low humidity was present in the home habitat, both species showed marked increases in home departures, whereas when entering corridors presented with the same low humidity condition, neither species showed a marked decrease in movement. This may be because both species are capable of withstanding low humidity (Quinlan and Hadley, 1983; Smigel & Gibbs

2008 and Edney, 2012) for the period of time they spent exploring the corridor (given the corridor length was limited to 3 m). Additionally, previous studies show that individual animals are not adverse to moving through areas lacking suitable habitat (a typical matrix environment) and the relative use of the matrix as movement habitat depends on the degree to which it contrasts with patch habitat (Rosenberg *et al.*, 1997; Kindvall, 1999; Haddad *et al*., 2003 and Hein *et al*., 2003).

Terrestrial isopods have been employed as study species in numerous animal movement / dispersal studies including, costs and benefits of natal dispersal (Baker & Rao 2004), species area relationships (Gentile & Argano 2005), effect of natal experiences and conspecific cues on dispersal (Robinson *et al*., 2011) and dispersal through heterogeneous landscapes (Sterzynska *et al*., 2015). In this study, I selected these animals to work with as they operate at manageable scales. Both isopod species I used in this study are relatively long-lived, slow-moving, and tractable. Using the same species, as the next step, it would be instructive to use longer movement corridors and / or more than one destination habitat with varying levels of hospitability to study animal movement behaviour. In the current experiments, after individuals decided to leave their familiar home habitat, they had limited choices either to continue travelling towards the destination habitat or turn back and return home. Therefore it would be interesting to explore the movement strategies of both species if they had more choices to explore which would be closer to natural scenario in any fragmented landscape.

A key question relating to any microcosm study, including my own, is: How do the results of the study relate to natural ecosystems and the animal species within them? In accordance with animal space-use models, the results of my study revealed that these two isopod species direct their movements in a way that (presumably) increases fitness (by having access to food and avoiding difficult paths) and minimizes risk of desiccation. Because the results of my experiment revealed fine- scale movement patterns of terrestrial isopods, it exemplifies that even closely-related species can display different magnitudes of movements according to their level of ecological specialization. Hence, these results could be extrapolated to fragmented natural ecosystems that contain several different species and several different environmental conditions.

Additionally, understanding ecological parameters and how they affect different species for efficient resource utilization and survival of animals is essential for improved species reintroduction programmes (Burns, 2005; Russel *et al.*, 2010 and Berger-Tal and Avgar, 2012). Species-based movement models based on data such as those provided by this study could be used for mapping predicted movements, estimating how functional connectivity may change under future land use alterations, or predicting changes in ecological parameters associated with changing land use practices. More importantly, the study demonstrated the combined effects of marginally unfavorable conditions in both home habitat and / or in the movement path could have a greater influence on movement behaviour of animals, making the results of my study more applicable to heterogeneous landscapes. The ability of animals to disperse from one habitat to another under unfavourable or marginally unfavourable ecological conditions, is an important aspect in conservation ecology given expected range shifts with climate change (McLaughlin *et al.*, 2002). Therefore, predicting the consequences of habitat loss and fragmentation for different animal populations is important for the conservation and management of species (Nupp & Swihart, 2000). A better theoretical and empirical understanding of decision-making during dispersal will help design spatially-explicit simulations that better describe the dispersal patterns of real animals (Roitberg & Mangel, 1997 and Russell, *et al*., 2003).

Admittedly, the applicability of my findings directly to larger landscapes and other organisms has limitations (as do all microcosm studies), yet my results provide valuable insight into the factors that govern inter-patch movement behaviour of different species, under different conditions. One of the advantages of small-scale experiments is that links can be made between the mechanisms of individual behaviors and their consequences for population redistribution and dynamics (Ims *et al*., 1993 and Wiens *et al*., 1993). Well-designed experiments will continue to provide valuable insight into pattern-process relationships in similar systems, within natural ecosystems. Experimental studies in conjunction with field studies will reveal how different environmental conditions in the home habitat and in the transit route affect movement behaviour of different species of animals.

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