

## ABSTRACT

SNIDER, SUNNY BROOKE. Towards a Movement Ecology: Modeling the Behavioral Response of Invasive Snails to Resources and Competition. (Under the direction of James F. Gilliam.)

The movement of individuals is one of the fundamental components of contemporary ecological problems such as metapopulation theory, epidemic models, competitive coexistence, and invasion dynamics. Advection-diffusion models, sometimes with a reaction term, have been usefully applied to such problems. For this dissertation, I broadened this approach by seeking to understand the effects of certain biotic and abiotic factors on movement ecology, and asking how to incorporate flexible behavioral responses into classical advection-diffusion models. I asked how resources, competitive environment, and habitat structure, interacting with body size or not, affect the movement behaviors of two coexisting invasive snails (*Melanoides tuberculata* and *Tarebia granifera*), and whether including the behavioral response to these factors improves advection-diffusion models of movement. I also made natural history observations regarding the snail system to provide a biological context for my empirical work. To address these questions, I conducted replicated experiments and observational studies, extended advection-diffusion models, and arbitrated among candidate models using AIC (Akaike's Information Criterion) model selection. Specific studies included (1) behavioral response to phenotypic and resource heterogeneities, and their interaction, (2) behavioral response to intraspecific and interspecific competition, and (3) behavioral response to spatially uniform versus spatially heterogeneous environments. In summary, this dissertation provides insights into modeling movement behaviors, using two coexisting invasive snails as the model system. I advocate for a behaviorally informed modeling framework that integrates sentient responses of individuals

in terms of movement, improving our ability to accurately model ecological processes that depend on movement ecology.

Towards a Movement Ecology: Modeling the Behavioral Response of Invasive Snails to  
Resources and Competition

by

Sunny B. Snider

A dissertation submitted to the Graduate Faculty of  
North Carolina State University  
In partial fulfillment of the  
Requirements for the degree of  
Doctor of Philosophy

Zoology

Raleigh, NC

October 25, 2007

Approved by:

---

Jay F. Levine

---

Kevin Gross

---

Nick M. Haddad

---

James F. Gilliam  
Chair of Advisory Committee

## DEDICATION

This one goes out to the ladies: Suzanne B. Snider, Nicole Cardello Deziel, Alesia Read, Meaghan Darcy, Jun Yoshizaki, Shelley Piner Rhudy, Beth Cresante Hart, Sarah E. Lester, Debby Gilliam, Lisa Shull, Frances Rostant, Indra Sinanan, Sandy Levine, Becky Bartel, Kayde Brownlee, Christina Durham, Grandmother Snider, and (in loving memory of) Granny Brooks.

“Well-behaved women seldom make history.”

-Laurel Thatcher Ulrich

## BIOGRAPHY

Sunny was born on March 20, 1976 in West Palm Beach, Florida and moved to North Carolina in 1981. She graduated from Mooresville High School in the top 2% of her class in 1994. In 1998, she graduated from the University of North Carolina at Chapel with a Bachelor of Science in Public Health in Environmental Sciences and Engineering and a minor in Marine Sciences. As an undergraduate, Sunny studied environmental policy and ecology at the University of East Anglia in Norwich, England and worked as a Sea Turtle intern at Mote Marine Laboratory on the west coast of Florida. Sunny's professional experiences include performing risk assessments as a research assistant with the Carolina Environmental Program at UNC and conducting environmental assessments as a scientist at Environmental Investigations, Inc. in Durham, NC. In 2001, Sunny returned to graduate school at North Carolina State University. During her tenure at N.C. State, Sunny conducted multiple field experiments in Trinidad, West Indies; taught three undergraduate laboratory courses; presented research findings locally and at international conferences; published in peer-reviewed scientific journals; and served as President, Vice President, and Graduate Student Symposium Coordinator for the Zoology Graduate Student Association. Beyond academic pursuits, her hobbies include running, hiking, traveling, reading contemporary fiction, painting, yoga, and spending time with friends and family.

## ACKNOWLEDGMENTS

First and foremost I would like to thank my adviser Jim Gilliam for providing guidance and support throughout my years in graduate school. Jim's enthusiasm for ecology, scientific research, and Trinidad streams has been an inspiration to me, and I aspire to maintain in my career the level of rigorous scientific investigation that Jim promotes and practices. I would also like to thank my committee members, Nick Haddad, Jay Levine, and Kevin Gross. Each of these talented scientists has provided me with mentorship and support from the start of my graduate career, through the stress of preliminary examinations, to the final dissertation. The Department of Zoology staff including Susan Marschalk, Chris Smith, Dollie Moore, Dawn Newkirk, and Meredith Henry have made administrative tasks easy, and I have enjoyed working with each of them. I also thank Thurman Grove, George Hess, and Don Francisco for their mentorship and friendship. In addition to those mentioned in the dedication, I would like to express my gratitude to fellow graduate students at NC State, especially Jake Brimlow, Darren Parsons, Geoff Bell, Trevor Yip-Hoi, Jessica Thompson, and Ellen Damschen. Garrick Skalski, my ecological older brother, also provided guidance and contributed to a great field season in 2005. Matt Levine, my friend forever, encouraged me throughout my graduate school career, and always helped me keep life in perspective. I thank Steve Levine for humorous advice that helped during the final stages of writing. And finally, I would like to thank my mother and father who nurtured my love for the natural world, influencing my career path from a very young age.

## TABLE OF CONTENTS

List of Tables .....	viii
List of Figures.....	ix
<b>Chapter 1: Movement ecology: size-specific behavioral response of an invasive snail to changes in food resource availability .....</b>	<b>1</b>
Abstract .....	2
Introduction.....	4
Model .....	6
Methods.....	9
Results.....	13
Discussion .....	18
Acknowledgements.....	24
Literature Cited .....	25
Figure Legends.....	34
<b>Chapter 2: Competition affects the movement behaviors of two coexisting exotic species .....</b>	<b>39</b>
Abstract.....	40
Introduction.....	42
Model .....	44
Methods.....	46
Results.....	51
Discussion .....	54
Acknowledgements.....	59
Literature Cited .....	60
Figure Legends.....	66
<b>Chapter 3: Advective movement by two invasive snails: a comparison in homogeneous and heterogeneous environments .....</b>	<b>73</b>
Abstract.....	74
Introduction.....	75
Model .....	76
Methods.....	79
Results.....	81
Discussion .....	84
Acknowledgements.....	87
Literature Cited .....	88
Figure Legends.....	94

<b>Chapter 4: Comparative ecology of the two coexisting species: some field observations and experiments</b> .....	100
Abstract .....	101
Introduction .....	102
Methods .....	103
Results .....	108
Discussion .....	110
Acknowledgements .....	113
Literature Cited .....	114
Figure Legends .....	118

## LIST OF TABLES

### **Chapter 1**

Table 1. Parameter combinations that make up the <i>a priori</i> set of candidate models .....	31
Table 2. Characteristics of the movement distribution produced at high and low resources .....	32
Table 3. Top ranking candidate models selected by AIC .....	33

### **Chapter 2**

Table 1. Parameter combinations that make up the <i>a priori</i> set of candidate models .....	64
Table 2. Top ranking candidate models selected by AIC .....	65

### **Chapter 3**

Table 1. Characteristics of the movement distributions produced by each species in each habitat type.....	91
Table 2. Top ranking candidate models selected by AIC for the first model selection.....	92
Table 3. Top ranking candidate models selected by AIC for the second model selection .....	93

## LIST OF FIGURES

### Chapter 1

Figure 1. Movement distributions produced by snails in the experimental stream facility ....	36
Figure 2. The relationship between distance moved and body size.....	37
Figure 3. Model predictions.....	38

### Chapter 2

Figure 1. Exploitative competition in terms of individual growth rates .....	68
Figure 2. Species-specific behavioral response to different levels of interspecific and intraspecific competition.....	69
Figure 3. Intraspecific competition affects variance of distance moved .....	70
Figure 4. Kurtosis of movement distributions .....	71
Figure 5. Movement distributions produced by snails at three levels of competitor density over 24 hours.....	72

### Chapter 3

Figure 1. <i>T. granifera</i> exhibited species-specific habitat-dependent movement behaviors.....	96
Figure 2. <i>M. tuberculata</i> exhibited species-specific habitat-dependent movement behaviors.....	97
Figure 3. The relationship between distance moved and body size for <i>T. granifera</i> in homogeneous and heterogeneous environments.....	98

Figure 4. The relationship between distance moved and body size for *M. tuberculata* in homogeneous and heterogeneous environments.....99

**Chapter 4**

Figure 1. Movement distributions produced by each species in Ramdeen Stream .....119

Figure 2. The presence or absence of riparian canopy affected the local distribution and abundance of exotic snails .....120

Figure 3. Differences in the role of primary production versus detritus-based resources for the two study species in a competitive environment .....121

CHAPTER 1

**Movement ecology: size-specific behavioral response of an invasive snail to changes in  
food resource availability**  
(to appear in *Ecology*)

## ABSTRACT

Immigration, emigration, migration, and redistribution describe processes that involve movement of individuals. These movements are an essential part of contemporary ecological models, and understanding how movement is affected by biotic and abiotic factors is important for effectively modeling ecological processes that depend on movement. I asked how phenotypic heterogeneity (body size) and environmental heterogeneity (food resource level) affect the movement behavior of an aquatic snail (*Tarebia granifera*), and whether including these phenotypic and environmental effects improve advection-diffusion models of movement. I postulated various elaborations of the basic advection-diffusion model as *a priori* working hypotheses. To test these hypotheses I measured individual snail movements in experimental streams at high and low food resource treatments. Using these experimental movement data, I examined the dependency of model selection on resource level and body size using Akaike's Information Criterion (AIC). At low resources, large individuals moved faster than small individuals, producing a platykurtic movement distribution, and including size dependency in the model improved model performance. In stark contrast, at high resources individuals moved upstream together as a wave, and body size differences largely disappeared. The model selection exercise indicated that population heterogeneity is best described by the advection component of movement for this species, as the top ranked model included size dependency in advection, but not diffusion. Also, all probable models included resource dependency. Thus population and environmental heterogeneities both influence individual movement behaviors and the population level distribution kernels, and their interaction may drive variation in movement behaviors in terms of both advection rates and

diffusion rates. A behaviorally informed modeling framework will integrate the sentient response of individuals in terms of movement and enhance the ability to accurately model ecological processes that depend on animal movement.

## INTRODUCTION

The movement of individuals is a fundamental component of contemporary ecological problems such as metapopulation theory, epidemic models, competitive coexistence, and other spatial models. However, despite the vital role that movement plays in these conceptual models, understanding of the ecology of movement behaviors remains limited. Immigration, emigration, migration, and redistribution (e.g. within a population or community) provide connections between habitats, populations, etc. via movement of individuals. Often modeled as constants in metapopulation models, or as a function of distance between sites, these movements are also affected by biotic and abiotic conditions in the vicinity of the focal animal and may be phenotype-specific (Gilliam and Fraser 2001). In face of environmental changes (e.g. land use change, climate change, habitat loss, species extirpations, and species additions) individuals may alter their movement behaviors in response to changing biotic and abiotic conditions. Understanding behavioral response to such factors will often be crucial to effectively modeling ecological processes that depend on individual movement ecology.

Previous research has shown that environmental heterogeneities affect movement (Grosholz 1996, Shigesada and Kawasaki 1997) via factors such as habitat quality (Lubina and Levin 1988, Zabel et al. 1998, Haddad 1999b, Williamson and Harrison 2002, Fraser et al. 2006) and resource availability (Kareiva and Odell 1987, Arditi and Dacorogna 1988, Grunbaum 1998, Fryxell et al. 2004). I was interested in how these ecologically important factors will affect movement behaviors, and I considered how resource availability might

change individual movement. For example, movement rates of individuals might hypothetically decrease through areas of higher resource level, as in an area-restricted search; however movement rates might also hypothetically increase through areas with greater resource availability as individuals sense resource gradients via taxis or some other behavioral response. In addition, individuals' responses to factors such as resource availability may be phenotype-specific. For example, population heterogeneity is known to influence movement behaviors via the effects of body size (Skalski and Gilliam 2000, Zabel 2002, Skalski and Gilliam 2003). Further, the effect of a phenotypic trait (body size) can interact with habitat characteristics (predation regime) producing site-specific patterns of movement that differ among habitat types (Fraser et al. 2006). Thus, not only do population and environmental heterogeneities influence movement behaviors, but their interaction may drive variation in movement behavior as well, requiring integration of these effects into ecological models that depend on movement ecology.

Here I examined how both phenotypic variation and environmental variation affect movement behaviors in populations of exotic freshwater snails using an advection-diffusion framework. My interest lies both in (1) how local movement behaviors are affected by population heterogeneity, in terms of individual body size, and environmental heterogeneity, in terms of resource level, and their interaction, and, (2) which components of the advection-diffusion modeling framework reflects and incorporates these behaviors. I proposed, *a priori*, a set of alternative movement models based on the advection-diffusion model (Okubo and Levin 2001). These alternative models represent hypotheses regarding the effects of body size and food availability on movement behaviors. I chose these factors to represent

environmental and population heterogeneities as past research suggested that body size and food availability may impact movement behaviors of gastropods (DeNicola and McIntire 1991). Using experimental movement data, I evaluated these models using information criteria (Hilborn and Mangel 1997, Burnham and Anderson 2001, 2002). Finally I discuss the implications of these findings in regards to previous studies of movement and ecological processes that depend on movement.

## MODEL

### *Classical advection-diffusion model*

Advection-diffusion models have been used extensively to describe movement and predict population spread including that of invasive species (Skellam 1951, Andow et al. 1990, Liebhold et al. 1992, van den Bosch et al. 1992, Shigesada and Kawasaki 1997, Okubo and Levin 2001). The classic advection diffusion equation

$$\frac{\partial P}{\partial t} = D \left( \frac{\partial^2 P}{\partial x^2} \right) - \beta \frac{\partial P}{\partial x} \quad (1)$$

predicts the changes in density of individuals  $P$  through space  $x$  and time  $t$ , via solution of the above partial differential equation where  $\beta$  is advection and  $D$  is diffusion. Advection describes the change in the mean of a population, or bias in some direction (Okubo and Levin 2001), e.g., bias downstream, downwind, with or against current. Diffusion describes the variance around that mean. For this study I sought to understand how these two components, advection and diffusion, are affected by population heterogeneity and environmental

heterogeneity. First I asked whether differences in movement among different body sizes, if any, were manifested via the advection component, the diffusion component, or both. Then I asked if resource level should be considered in the model or not. In this way, I discerned which components of the advection-diffusion equation, if any, are affected by and should incorporate population heterogeneity, with or without environmental heterogeneity, in a parsimonious model.

### *Population heterogeneity*

I tested for the influence of population heterogeneity, in terms of snail length, on the advection and diffusion components of movement. I incorporated snail length in the models in both the advection term,

$$\beta_i = \beta_0 + (\beta_{length} \times length_i), \quad (2)$$

and the diffusion term,

$$D_i = D_0 + (D_{length} \times length_i), \quad (3)$$

where  $i$  represents an individual. For the set of models, I consider all combinations of advection and diffusion. Advection options include: (1) advection without size-dependency ( $\beta$ ), and (2) advection with size-dependency (Eq. 2). Diffusion options include: (1) diffusion without size-dependency ( $D$ ), and (2) diffusion with size-dependency (Eq. 3). Using the four possible combinations I can determine whether one or both of the parameters depend on body size.

### *Environmental heterogeneity*

To test for the effect of environmental heterogeneity on the variability in snail movement behaviors, I consider resource level as a treatment. In this case I estimate diffusion and advection parameters considering resource levels or not. Thus I compare models that estimate separate diffusion and separate advection terms for different resource levels, where H=high resources and L=low resources, versus models without resource dependency in which the same advection rate and the same diffusion rate are estimated across resource treatments.

### *General model structure*

The most general model structure for estimating advection in my experiment is described below, where  $I_1$ ,  $I_2$ , and  $I_3$  are indicator variables:

$$\beta = [\beta_0 + \beta_0^H I_1 I_3] + [(\beta_1 + \beta_1^H I_1 I_3) \text{length} I_2]. \quad (4)$$

$$I_1 : \text{Resources high?} \begin{cases} 0 & \text{If no} \\ 1 & \text{If yes} \end{cases}$$

$$I_2 : \text{Is length included in the model?} \begin{cases} 0 & \text{If no} \\ 1 & \text{If yes} \end{cases}$$

$$I_3 : \text{Are resources included in the model?} \begin{cases} 0 & \text{If no} \\ 1 & \text{If yes} \end{cases}$$

Similarly, the model structure for estimating diffusion is as below, using the same notation for its indicator variables:

$$D = [D_0 + D_0^H I_1 I_3] + [(D_1 + D_1^H I_1 I_3) length I_2]. \quad (5)$$

The set of candidate models is comprised of combinations of advection and diffusion with or without phenotypic heterogeneity (body length), and with or without environmental heterogeneity (resource level), yielding a set of 20 *a priori* candidate models (Table 1). Using these combinations I identified which parameters, with resource-dependency or not, depend on phenotype to describe movement behaviors for this species.

## METHODS

### *Study system*

I focus on the movement of an aquatic snail that has been introduced to habitats throughout the tropics and portions of the subtropics. The study species, *Tarebia granifera*, was introduced to Trinidad, West Indies, at an unknown date, presumably 10 - 20 years ago, and I confirmed its presence in six rivers within three drainages of the Northern Range Mountains in 2001 (S. Snider, unpublished data). This parthenogenetic snail is native to Asia and India (Abbott 1952) and has been introduced accidentally (presumably via the aquarium trade) through much of the tropics, and also purposefully to out-compete the snail intermediate host for schistosomiasis, *Biomphalaria glabrata* (Pointier 2001). As the intermediate host for a variety of trematodes, *T. granifera* is important to both ecosystem and public health, adversely impacting native species (Mitchell et al. 2000) and, in some cases,

positively influencing human health (Pointier 1999, Pointier and Giboda 1999, Pointier 2001).

I collected snails from the Arima River (a fourth-order stream), which drains portions of the southern slope of the Northern Range Mountains of Trinidad, and Ramdeen Stream (a second-order stream), one of its tributaries (10°41'32" N, 61°17'36" W). At sampling sites, both streams are shallow, clear, fast-flowing, with clear pool-riffle development and varied canopy cover.

#### *Experimental facility*

The circulating experimental stream facility consisted of six 17-m long streams constructed of six-inch diameter PVC rain gutters. A 125-L reservoir at the downstream end of the facility contained guppies (*Poecilia reticulata*) collected from Ramdeen Stream for mosquito control. The water was recirculated using a ¼ horsepower submersible pump and distributed through a manifold; flow rate was maintained at 1.9 cm/s to 2.3 cm/s in each of the six replicate streams. A canopy of green agricultural mesh provided partial shade, both to mimic a partial canopy and to prevent overheating of the water.

The experimental stream facility is located within 0.5 km of both the Arima River and Ramdeen Stream. I used local water pumped from the Arima River and substrates from the river to reasonably mimic the natural environment. Each stream contained a 1.5 cm layer of rinsed river sand and flat river stones, approximately 7 cm by 10 cm. I placed stones in the center of each stream every 1.0 m to inoculate streams with algae and other stream

organisms, and provide natural substrate. Experimental streams flowed for 2 weeks prior to applying treatments.

### *Experimental design*

I used a completely randomized design to assign two resource treatments to the six streams within the experimental facility. Experimental treatments consisted of “low” (grazed) resource treatments and “high” (not grazed) resource treatments. I created these contrasting resource levels by allowing, or not allowing, conspecifics to graze resources prior to conducting the experiment. A barrier separated the treatment portion of the streams (the top 12 m) from the staging portion of the streams (the lower 5 m). For low resource treatments, 20 snails (the “grazers”) were placed in the treatment portion of each stream and allowed to graze for three days. If grazers reached the upstream end of the system, they were returned to the downstream end of the treatment zone. I moved any such grazers from the upstream end to the downstream end just after sunrise (6:00 AM) and just before sunset (6:00 PM). High resource treatments were simply allowed to continue building food resources in the absence of grazers. These treatments provided visually obvious differences in algal cover (green and brown layers of algae on substrate in high resources treatment streams vs. “clean” substrates in grazed/low resource treatments), but I did not quantify the resource levels. Grazers creating the low resources treatments were removed 24 hours prior to running the experiment.

I created individual marks using different color combinations of fingernail polish on the outer shell of each snail. Snails ranged from 9 mm to 26 mm long, and were sorted into

three size classes (“small, medium, large”) prior to random assignment of snails within each size class to each stream, with a total of twenty snails per stream, to assure a range of sizes in each stream. These snails were placed in the staging portion of each stream and allowed to adjust to their environment for 24 hours. After this adjustment period I recorded locations for each snail and removed the barrier into treatments. I then recorded the locations of each individual after three, four, and five hours, the five-hour limit reflected termination of the experiment when the first snail reached the upstream end of one experimental stream. I used only the data collected after five hours for the analysis and model selection. I used the data collected after three and four hours to assess the fit of the best model to empirical data.

### *Analysis of models*

I estimated advection and diffusion parameters for each of the 20 models in the model set via maximum likelihood estimation using Microsoft Excel Solver. I used the general likelihood

$$L\{x | D, \beta, t\} = \left( \frac{P_0}{2\sqrt{\pi Dt}} \right) \exp\left( \frac{-(x - \beta t)^2}{4Dt} \right). \quad (6)$$

Eqn. 6 is the solution to the PDE shown in Eqn. 1 and predicts a normal distribution with mean  $\beta t$  and variance  $2Dt$ . To compare my 20 hypotheses, I used the resulting maximum likelihood estimates to calculate Akaike’s Information Criterion (AIC) (Akaike 1973), specifically AICc for small sample size (Burnham and Anderson 2002). I also calculated Akaike weights and evidence ratios to assist in the model selection.

I also examined how a reduced set of the models fit the empirical data by plotting predicted displacements on snail body size. First I demonstrated the fit of the best model from the candidate to the movement data collected after three and four hours (movement data not considered in the model selection). I also chose to show an assessment of the relative model fit by comparing four of the candidate models: (1) the simplest form of the model; (2) a model that incorporates body size but ignores resources; (3) a model that ignores body size but incorporates resources; and (4) a model that incorporates both body size and resources. This analysis allowed for comparisons of model fit given each type of heterogeneity alone and when both heterogeneities are included in the model.

To account for the replicate nature of the experimental facility I added a second set of models to the analysis. Replicate experimental structure is not routinely considered in AIC model selection, so I controlled for the existence of replicate experimental streams by including or not including each experimental stream as a variable in the model for each of the 20 movement models. In this way, I estimated separate advection and diffusion coefficients for each experimental stream. I compared these models with the original set of models using the same method described above.

## RESULTS

### *The empirical results*

Resource level dramatically affected the pattern of upstream movement, changing the qualitative and quantitative pattern of movement. At low resources (Fig. 1 A-C), I observed an upstream bias, and a broad distribution of the upstream population wave (mean distance

moved upstream in 5 hours: 5.51 m, SE=0.61, SD=4.67, pooled across replicates) (Table 2). The movement distributions showed no skewness (-0.05, SE=0.31, n=59, p=0.87) and did show platykurtosis (-1.70, SE=0.61, n=59, p<0.01) (Table 2). In stark contrast, individuals moved in concert as a narrow wave at high resources (Fig. 1 D-F), while still showing the upstream bias also observed at low resources (mean distance moved in 5 hours: 7.26 m, SE=0.25, SD=1.91 m, pooled across replicates) (Table 2). This distribution was negatively skewed (-2.28, SE=0.31, n=60, p<0.01) and leptokurtic (6.49, SE=0.61, n=60, p<0.01) (Table 2). This contrast in pattern was evident across replicates (Fig. 1; Table 2).

By examining the relationship between distance moved and snail length, I saw that the different movement behaviors observed at high and low resources were created by differences in the strength of size-dependency in movement (Fig. 2). At low resources there was a positive relationship between body size and distance moved, with large individuals moving faster than small individuals (Fig. 2 A-C). A decidedly different pattern emerged for the relationship between body size and distance moved at high resources: the narrow wave of movement exhibited in the population-level distributions (described above) arose because individuals moved in concert despite differences in body size (Fig. 2 D-F). It appeared that at high resources larger individuals slowed, and smaller individuals sped up, relative to movement at low resources. Examination of the data on size-specific movement also aids in understanding the platykurtosis observed in the low-resource treatment: summations of multiple approximately normal distributions of approximately equal sample size (one distribution for each snail size or size class) can result in a platykurtic distribution overall. Thus, heterogeneity in advection rates for different size classes can yield platykurtosis. In

contrast, heterogeneity in diffusion rates produce leptokurtic distributions (Skalski and Gilliam 2000, Rodriguez 2002). The skew at high resources results from a few of the smallest snails failing to maintain the upstream pace of the rest of the snails.

#### *Alternative movement models*

Of the candidate models, the top ranked model (Model 10) incorporated size dependency in advection rates, but not diffusion rates, across both resource levels (Table 3). Therefore, these data reflect population heterogeneity in advection, but not diffusion. This model also specified that advection rates and diffusion rates be estimated separately for different resource levels. Thus, the model includes a size-dependent advection rate for movement at low resources (2 parameters), a size-dependent advection rate for movement at high resources (2 parameters), a diffusion rate (size-independent, 1 parameter) for movement at low resources, and a diffusion rate (size independent, 1 parameter) for movement at high resources (6 parameters total).

Although Model 10 is the top ranking model in the analysis, according to evidence ratios, this model had only 2.52 times more support than the next most likely model (Model 18) and only 2.59 times more support than Model 9 (Table 3). Going beyond the top three ranked models, there is a distinct jump in the support for the first three models (Models 10, 18, and 9) relative to the remaining ranked models, which received much less support in terms of evidence ratios. Due to model selection uncertainty, I accepted the top three ranking models ( $\Delta AICc < 3$ ) as plausible (Burnham and Anderson 2002). Size dependency and resource dependency are supported across the plausible models. Models that did not

incorporate size dependency into some aspect of advection received no support. More specifically, models that did not incorporate a size-dependent advection rate at low resources received no support. I also rejected all models that were not resource-dependent. Size dependency in diffusion received only weak support (Model 18, for low resources). Overall, the three top models collectively support the top ranked model: size-dependent advection that depends on resources, and size-independent diffusion that depends on resources.

In Fig. 3, I examine how Model 10 captures features of the data that simpler models do not, and also how Model 10 fits data from previous time periods. At the completion of the experiment ( $t = 5$  hours), it is clear that although none of the models appears to totally characterize the variation in movement, Model 10 is certainly the best of this set as it provides for patterns of movement resulting from an interaction of body size and response to resource level: one pattern at high resources where individuals move upstream together regardless of body size, and one at low resources where there is a positive relationship between predicted distance moved and body size. The other models presented here cannot capture that interaction between phenotype and environment, because they include at most one of those factors. In my view, Model 10, which was fit only with data for  $t=5$ , also reasonably modeled the data for  $t=3$  and  $t=4$ , as the patterns seen for  $t=5$  are developed. However, these plots also reveal a phenomenon that none of the candidate models could capture: the apparent trend towards a bimodal distribution in the low resource environment, generating the positive kurtosis values observed in the movement distributions. Model 10 did capture the fact that the largest snails tended to move upstream (all snails  $>21$  mm moved strongly upstream), and that the smallest snails did not, via the modeling of advection as a

linear function of body size. However, none of the *a priori* candidate models had the flexibility to incorporate the apparent development of a bimodal distribution that developed at low resources, with some individuals not moving upstream, and others doing strongly so, in contrast to the high resource treatment, in which almost all individuals moved upstream in concert. The mechanism(s) leading to development of that bimodality at low resources but not high resources is worthy of further investigation, but here I restrict myself to assessment of the *a priori* model set.

When I included “stream effects”, i.e., the effects of using replicate experimental streams to collect data, in the models, AIC scores were lower than when I did not incorporate these effects despite a much higher number of parameters under penalty in AIC. Hence, including replicate structure in AIC model selection provided some amount of improved fit of the models to the data. The movement patterns observed across replicates in Fig. 1 and Fig. 2 appear very similar for each resource treatment, suggesting that this model selection process was sensitive even to very slight differences in movement patterns (i.e., deviations of one or two individuals from the prevailing pattern) across replicates. Remarkably, including stream effects in the models had little effect on the ultimate model choice in terms of the parameters of interest (Table 3). Of the candidate models in this case, the top ranking model is still the one that is resource dependent and includes size dependency in advection rates. Model 10 also had 20 times more support than Model 9 in this case, and I therefore accept only Model 10 as plausible in this analysis.

## DISCUSSION

### *Patterns from empirical data*

By changing the way that phenotype (body size) responded to the environment (food resources), different resource levels created strikingly different movement patterns for *T. granifera*. At low resources, I observed a clear correlation between size and mean distance moved (Fig. 2, A-C), contributing to a broad and distinctly platykurtic distribution of movement by the population as a whole (Fig. 1, A-C; Table 2). At high resources, in contrast, the effect of body size disappeared and individuals moved upstream together at a similar rate, as a narrow wave (Fig. 2, D-F). The environment-phenotype interaction I found involving resources and body size has also been shown to be important to the movement behavior of a tropical killifish, *Rivulus hartii*, under different predation regimes (Gilliam and Fraser 2001, Fraser et al. 2006) and in migrating salmon (Zabel 2002). In the predator-prey study, researchers showed that body size can interact with level of predation threat, changing movement behaviors in different habitat types (Gilliam and Fraser 2001, Fraser et al. 2006). Similarly, Zabel (2002) modeled travel time, or migration duration, of chinook salmon. Results of his study indicated that both body size and current velocity, and their interaction, were contributors to the variability of animal movement patterns (Zabel 2002). Predation, current velocity and a host of other biotic and abiotic factors not addressed in this study also may affect movement behavior in natural settings.

The narrow wave of movement at high resources occurred because smaller individuals moved faster, and larger individuals moved more slowly, than individuals of equivalent size at low resources. I have not yet studied the micro-scale, behavioral

mechanisms producing this pattern. One possibility is an area-restricted search, in which larger individuals slow down given high food resources, and small individuals speed up through areas where food resources have been reduced, *sensu* Kareiva and Odell (1987). Previous studies have shown that this foraging behavior can result in resource-mediated grouping behaviors predicted theoretically (Wilson and Richards 2000) or “density dependent migratory waves” illustrated with large-scale empirical data (Fauchald et al. 2006). Given the strong directional bias in this species, I am reluctant to assume an area-restricted search hypothesis with turning rate as its mechanism, but some behavioral response to resource gradients, with steeper or more detectable gradients in the high resource case, would appear to be involved. While this model depicts movement by snails as independent of other snails, a different model incorporating interaction via resources is worthy of attention.

Since low resource treatments were previously grazed, but high resource treatments were not, the empirical results may have implications for understanding movement behavior at the front of an invading population. I can label the high resource treatment as an “uninvaded” habitat and the low resource treatment as a “previously invaded” habitat. Viewed in this context, this species exhibited a behavioral response at the front of the invasion in the “uninvaded” habitat, resulting in a narrow population wave for a broad array of sizes at the invasion front when compared to movement in the “previously invaded” habitat. Given previous work showing sensitivity of invasion speed to demography at the edge of the invasion (Neubert and Caswell 2000), attention to behavioral influences on population composition at the edge of a spreading population should improve predictive

models of invasive spread. Also, based purely on population dynamics without heterogeneity in phenotype or flexible behavior, Sherratt et al. (Sherratt et al. 1997, Sherratt 2001) has shown production of periodic traveling waves as an invading predator interacts with a prey population. The changes in the width of the wave I observed occurred purely due to behavioral response to different levels of resources (prey) without involving population dynamics, while Sherratt et al. (1997, 2001) found waves purely due to population dynamics without considering flexible behavior. Linking these two phenomena, and asking when and how the two processes interact, could also improve predictive capacity in spatially interacting predator-prey systems. I do not know what role, if any, chemical cues would play in the grazed or “previously invaded” treatments.

*Phenotype- and environment- specific behavior is needed in movement models*

My findings showed that not only does population heterogeneity impact movement behaviors (Price et al. 1994, Oriain et al. 1996, Paradis et al. 1998, Skalski and Gilliam 2000, Fraser et al. 2001, Gilliam and Fraser 2001, Langellotto and Denno 2001, Rodriguez 2002, Zabel 2002, Skalski and Gilliam 2003, Coombs and Rodriguez 2007), but it may impact components of movement models in different ways. The model selection exercise indicated that the effect of population heterogeneity is best described via the advection component of movement: the top ranked model was one that included size-dependency in the advection rate, but not in the diffusion rate. For any given species, predictions about the impact of population heterogeneity on movement patterns will depend on which component(s) of movement are most affected by phenotypic variation. Further, the role that population heterogeneity plays in structuring population-level patterns of movement in an advection-

diffusion framework may interact with environmental heterogeneity, as found here. Given that a separate advection coefficient should be used for these data at high and low resources, and given the size-dependency in the advection rates, the magnitude of the influence of population heterogeneity was context-dependent. Thus population and environmental heterogeneities both influence movement behaviors and their interaction may drive variation in movement behavior in terms of both advection rates and diffusion rates.

Finally, I emphasize the importance of the advection component for modeling movement of these exotic snails when using an advection-diffusion framework. In this species I observed a strong upstream bias in the movement distributions that is reflected in the model selection results. This upstream bias also occurs in natural streams, as revealed by mark-recapture studies (S. Snider, unpublished data). While neither advection nor diffusion terms could be considered constant across all sizes and environments, the size-dependent advection rate was consistent across the top-ranked models in the set, suggesting that the observed movement patterns are consistently influenced by the advection component in this framework. Further research addressing the consequences of different advection rates relative to diffusion, and the impact of other biotic and abiotic factors on advection, would be helpful for accurately modeling the movement ecology of this species.

#### *On the utility of simple advection-diffusion models*

The simple diffusion model is often criticized for its simplicity, yet it has been used extensively to model and, perhaps, to understand movement in the context of invasive spread (Holmes 1993, Shigesada and Kawasaki 1997, Okubo and Levin 2001). Following earlier

work by Fisher (1937) and Skellam (1951), it has been utilized to describe the spread of many different organisms in various environments (Lubina and Levin 1988, Andow et al. 1990, Liebhold et al. 1992, Holmes 1993, Skalski and Gilliam 2000, Okubo and Levin 2001, Zabel 2002, Fryxell et al. 2004). Although there is a substantial scientific literature that expands on the simple diffusion model (van den Bosch et al. 1990, van den Bosch et al. 1992, Holmes 1993, Kot et al. 1996, Neubert and Caswell 2000) and related approaches using random walks (Morales et al. 2004, Jonsen et al. 2006), I chose to focus on understanding how population and environmental heterogeneities are incorporated into the two components of this simple, yet arguably elegant, form of the model.

The simple advection-diffusion equation is criticized because, in part, its assumptions are not achievable by any organism (Turchin 1998). First, the model arose from a mathematical derivation that assumes that dispersal occurs randomly at an infinite velocity throughout every stage of an organism's life. This assumption is never met; not only is movement not infinitely rapid, but also many organisms have life stages or phenotypes that differ in dispersal rate, and animal dispersal follows from behavioral decisions rather than non-sentient wandering (van den Bosch et al. 1992, Holmes 1993, Shigesada and Kawasaki 1997). Although the common criticisms discussed above are cited against the simple diffusion model, and I have shown that the simplest model performs poorly, I do not advocate eliminating this basic modeling framework from the set of tools used to understand and model movement behaviors and population spread. In many cases, and for particular purposes, even the simplest advection-diffusion model has been shown to provide satisfactory estimations of population redistribution for many species (Skellam 1951, Kareiva

1983, Lubina and Levin 1988, Andow et al. 1990, Okubo and Levin 2001) and the assumptions of the model are not as severe as they appear. Holmes (1993) points out that the assumptions are valid only on “infinitesimal scales,” and that on a more practical level the consequences of the assumptions are slight. Comparing telegraph models with the simplest advection-diffusion model, Holmes (1993) concluded that for particular parameter values and for some classical examples of invasive spread, the simple advection-diffusion model performed as well as the more complicated alternative. Also, the random walk assumption does not necessarily require that individuals move randomly; rather, it requires that at the population level, movement distributions mimic the distribution produced by randomly moving individuals, and this relaxation of the assumption can sometimes allow for navigation or intelligent moves by individuals (Lubina and Levin 1988). Finally, the homogeneous form of the advection-diffusion equation predicts a Gaussian distribution, but modeling the total population as mixtures of normal distributions can produce leptokurtic or other distributions often observed in nature (Skalski and Gilliam 2000, Okubo and Levin 2001, Morales 2002) Therefore the basic model is flexible enough to consider population heterogeneities via extensions.

One final criticism of the simple advection diffusion model is that it does not predict long distance moves. Modeling has indicated that rare long distance dispersal events ultimately determine invasion speed (Kot et al. 1996, Clark 1998, Neubert and Caswell 2000). However, diffusion models with population heterogeneity in behavior easily produce arbitrarily strongly leptokurtic dispersal kernels (e.g., Skalski and Gilliam 2000), allowing use of the diffusion approach or any of several alternatives in many cases (Coombs and

Rodriguez 2007), while explicitly modeling individual differences in behavior rather than treating dispersal kernels as a purely phenomenological component of the model. In the present study, I chose to focus on movement over a short spatial scale, and how advection and diffusion reflect animal behavior within that scale. Expanding such studies to larger spatial and temporal scales to explore and compare the usefulness of advection-diffusion or other approaches in behaviorally informed models remains a useful area of research.

#### ACKNOWLEDGMENTS

I thank Brett Albanese, Jose Rodriguez, and Vicki Albanese for help in the field, the Ramdeen family for access to Ramdeen Stream, and Ronni Hernandez and Simla Biological Field Station for providing space and support for the experimental facility. Lori Davias made insightful comments on the manuscript. I thank the National Science Foundation (NSF/DEB 0108439) for financial support.

## LITERATURE CITED

- Abbott, R. T. 1952. A study of an intermediate snail host (*Thiara granifera*) of the Oriental lung fluke (*Paragonimus*). *Proceedings of the United States National Museum* **102**:71-116.
- Akaike, H. 1973. Information theory as an extension of the maximum likelihood principle. Pages 267-281 *in* B. N. Petran and F. Csaki, editors. *Second International Symposium on Information Theory*. Akademiai Kiado, Budapest.
- Andow, D., P. Kareiva, S. Levin, and A. Okubo. 1990. Spread of invading organisms. *Landscape Ecology* **4**:177-188.
- Arditi, R., and B. Dacorogna. 1988. Optimal foraging on arbitrary food distributions and the definition of habitat patches. *American Naturalist* **131**:837-846.
- Burnham, K. P., and D. R. Anderson. 2001. Kullback-Leibler information as a basis for strong inference in ecological studies. *Wildlife Research* **28**:111-119.
- Burnham, K. P., and D. R. Anderson. 2002. *Model selection and multimodel inference: a practical information-theoretic approach*, 2nd edition. Springer-Verlag New York, Inc., New York.
- Clark, J. S. 1998. Why trees migrate so fast: Confronting theory with dispersal biology and the paleorecord. *American Naturalist* **152**:204-224.
- Coombs, M. F., and M. A. Rodriguez. 2007. A field test of simple dispersal models as predictors of movement in a cohort of lake-dwelling brook charr. *Journal of Animal Ecology* **76**:45-57.

- DeNicola, D. M., and C. D. McIntire. 1991. Effects of hydraulic refuge and irradiance on grazer-periphyton interactions in laboratory streams. *Journal of the North American Benthological Society* **10**:251-262.
- Fauchald, P., M. Mauritzen, and H. Gjosaeter. 2006. Density-dependent migratory waves in the marine pelagic ecosystem. *Ecology* **87**:2915-2924.
- Fisher, R. A. 1937. The wave of advance of advantageous genes. *Annals of Eugenics* **7**:353-369.
- Fraser, D. F., J. F. Gilliam, B. W. Albanese, and S. B. Snider. 2006. Effects of temporal patterning of predation threat on movement of stream fish: evaluating an intermediate threat hypothesis. *Environmental Biology of Fishes* **76**:25-35.
- Fraser, D. F., J. F. Gilliam, M. J. Daley, A. N. Le, and G. T. Skalski. 2001. Explaining leptokurtic movement distributions: Intrapopulation variation in boldness and exploration. *American Naturalist* **158**:124-135.
- Fryxell, J. M., J. F. Wilmshurst, and A. R. E. Sinclair. 2004. Predictive models of movement by Serengeti grazers. *Ecology* **85**:2429-2435.
- Gilliam, J. F., and D. F. Fraser. 2001. Movement in corridors: enhancement by predation threat, disturbance, and habitat structure. *Ecology* **82**:258-273.
- Grosholz, E. D. 1996. Contrasting rates of spread for introduced species in terrestrial and marine systems. *Ecology* **77**:1680-1686.
- Grunbaum, D. 1998. Using spatially explicit models to characterize foraging performance in heterogeneous landscapes. *American Naturalist* **151**:97-115.
- Haddad, N. M. 1999. Corridor use predicted from behaviors at habitat boundaries. *American Naturalist* **153**:215-227.

- Hilborn, R., and M. Mangel. 1997. The ecological detective: confronting models with data. Princeton University Press, Princeton.
- Holmes, E. E. 1993. Are diffusion models too simple: a comparison with telegraph models of invasion. *American Naturalist* **142**:779-795.
- Jonsen, I. D., R. A. Myers, and M. C. James. 2006. Robust hierarchical state-space models reveal diel variation in travel rates of migrating leatherback turtles. *Journal of Animal Ecology* **75**:1046-1057.
- Kareiva, P. 1983. Local movement in herbivorous insects: applying a passive diffusion model to mark-recapture field experiments. *Oecologia* **57**:322-324.
- Kareiva, P., and G. Odell. 1987. Swarms of predators exhibit "preytaxis" if individual predators use area-restricted search. *American Naturalist* **130**:233-270.
- Kot, M., M. A. Lewis, and P. VanDenDriessche. 1996. Dispersal data and the spread of invading organisms. *Ecology* **77**:2027-2042.
- Langellotto, G. A., and R. F. Denno. 2001. Benefits of dispersal in patchy environments: Mate location by males of a wing-dimorphic insect. *Ecology* **82**:1870-1878.
- Liebhold, A. M., J. A. Halverson, and G. A. Elmes. 1992. Gypsy moth invasion in North America: a quantitative analysis. *Journal of Biogeography* **19**:513-520.
- Lubina, J. A., and S. A. Levin. 1988. The spread of a reinvading species: range expansion in the California sea otter. *American Naturalist* **131**:526-543.
- Mitchell, A. J., M. J. Salmon, D. G. Huffman, A. E. Goodwin, and T. M. Brandt. 2000. Prevalence and pathogenicity of a heterophyid trematode infecting the gills of an endangered fish, the fountain darter, in two central Texas spring-fed rivers. *Journal of Aquatic Animal Health* **12**:283-289.

- Morales, J. M. 2002. Behavior at habitat boundaries can produce leptokurtic movement distributions. *American Naturalist* **160**:531-538.
- Morales, J. M., D. T. Haydon, J. Frair, K. E. Holsiner, and J. M. Fryxell. 2004. Extracting more out of relocation data: Building movement models as mixtures of random walks. *Ecology* **85**:2436-2445.
- Neubert, M. G., and H. Caswell. 2000. Demography and dispersal: Calculation and sensitivity analysis of invasion speed for structured populations. *Ecology* **81**:1613-1628.
- Okubo, A., and S. A. Levin. 2001. Diffusion and ecological problems: modern perspectives, 2nd edition. Springer-Verlag New York, Inc., New York.
- Oriain, M. J., J. U. M. Jarvis, and C. G. Faulkes. 1996. A dispersive morph in the naked mole-rat. *Nature* **380**:619-621.
- Paradis, E., S. R. Baillie, W. J. Sutherland, and R. D. Gregory. 1998. Patterns of natal and breeding dispersal in birds. *Journal of Animal Ecology* **67**:518-536.
- Pointier, J. P. 1999. Invading freshwater gastropods: Some conflicting aspects for public health. *Malacologia* **41**:403-411.
- Pointier, J. P. 2001. Invading freshwater snails and biological control in Martinique Island, French West Indies. *Memorias Do Instituto Oswaldo Cruz* **96**:67-74.
- Pointier, J. P., and M. Giboda. 1999. The case for biological control of snail intermediate hosts of *Schistosoma mansoni*. *Parasitology Today* **15**:395-397.
- Price, M. V., P. A. Kelly, and R. L. Goldingay. 1994. Distances moved by Stephens kangaroo-rat (*Dipodomys-Stephensi* Merriam) and implications for conservation. *Journal of Mammalogy* **75**:929-939.

- Rodriguez, M. A. 2002. Restricted movement in stream fish: The paradigm is incomplete, not lost. *Ecology* **83**:1-13.
- Sherratt, J. A. 2001. Periodic travelling waves in cyclic predator-prey systems. *Ecology Letters* **4**:30-37.
- Sherratt, J. A., B. T. Eagan, and M. A. Lewis. 1997. Oscillations and chaos behind predator-prey invasion: mathematical artifact or ecological reality? *Philosophical Transactions of the Royal Society of London Series B-Biological Sciences* **352**:21-38.
- Shigesada, N., and K. Kawasaki. 1997. *Biological invasions: theory and practice*. Oxford University Press, Oxford.
- Skalski, G. T., and J. F. Gilliam. 2000. Modeling diffusive spread in a heterogeneous population: a movement study with stream fish. *Ecology* **81**:1685-1700.
- Skalski, G. T., and J. F. Gilliam. 2003. A diffusion-based theory of organism dispersal in heterogeneous populations. *American Naturalist* **161**:441-458.
- Skellam, J. G. 1951. Random dispersal in theoretical populations. *Biometrika* **38**:196-218.
- Turchin, P. 1998. *Quantitative analysis of movement: measuring and modeling population redistribution in animals and plants*. Sinauer Associates, Inc., Sunderland.
- van den Bosch, F., R. Hengeveld, and J. A. J. Metz. 1992. Analysing the velocity of animal range expansion. *Journal of Biogeography* **19**:135-150.
- van den Bosch, F., J. A. J. Metz, and O. Diekmann. 1990. The velocity of spatial population expansion. *Journal of Mathematical Biology* **28**:529-565.
- Williamson, J., and S. Harrison. 2002. Biotic and abiotic limits to the spread of exotic revegetation species. *Ecological Applications* **12**:40-51.

Wilson, W. G., and S. A. Richards. 2000. Consuming and grouping: resource-mediated animal aggregation. *Ecology Letters* **3**:175-180.

Zabel, R. W. 2002. Using "travel time" data to characterize the behavior of migrating animals. *American Naturalist* **159**:372-387.

Zabel, R. W., J. J. Anderson, and P. A. Shaw. 1998. A multiple-reach model describing the migratory behavior of Snake River yearling chinook salmon (*Oncorhynchus tshawytscha*). *Canadian Journal of Fisheries and Aquatic Sciences* **55**:658-667.

Table 1. Parameter combinations that make up the *a priori* set of candidate models.

		Candidate Models	
Model no.	No resource dependency		
	Low resources	High resources	
1	$\beta, D$		
2	$\beta$ size-depdt, $D$		
3	$\beta, D$ size-depdt		
4	$\beta$ size-depdt, $D$ size-depdt		
5	$\beta, D$	$\beta, D$	
6	$\beta, D$	$\beta$ size-depdt, $D$	
7	$\beta, D$	$\beta, D$ size-depdt	
8	$\beta, D$	$\beta$ size-depdt, $D$ size-depdt	
9	$\beta$ size-depdt, $D$	$\beta, D$	
10	$\beta$ size-depdt, $D$	$\beta$ size-depdt, $D$	
11	$\beta$ size-depdt, $D$	$\beta, D$ size-depdt	
12	$\beta$ size-depdt, $D$	$\beta$ size-depdt, $D$ size-depdt	
13	$\beta, D$ size-depdt	$\beta, D$	
14	$\beta, D$ size-depdt	$\beta$ size-depdt, $D$	
15	$\beta, D$ size-depdt	$\beta, D$ size-depdt	
16	$\beta, D$ size-depdt	$\beta$ size-depdt, $D$ size-depdt	
17	$\beta$ size-depdt, $D$ size-depdt	$\beta, D$	
18	$\beta$ size-depdt, $D$ size-depdt	$\beta$ size-depdt, $D$	
19	$\beta$ size-depdt, $D$ size-depdt	$\beta, D$ size-depdt	
20	$\beta$ size-depdt, $D$ size-depdt	$\beta$ size-depdt, $D$ size-depdt	

Table 2. Characteristics of movement distributions at high and low resources. Estimates of skewness and kurtosis (with standard error and sample size [n] reported in parentheses), mean, and variance of the movement distributions produced by snails in each experimental stream, and pooled across replicate experimental streams.

Resource level	Replicate	Skewness (1 SE, <i>n</i> )	Kurtosis (1 SE, <i>n</i> )	Mean±SD	Variance
Low	1	0.33 (0.51, 20)	-1.72 (0.99, 20)	4.95±4.99	24.87
	2	-0.77 (0.52, 19)	-1.06 (1.01, 19)	7.02±4.28	18.34
	3	0.19 (0.51, 20)	-1.73 (0.99, 20)	4.63±4.58	20.95
	Combined	-.05 (0.31, 59)	-1.70 (0.61, 59)	5.51±4.67	21.83
High	1	-2.27 (0.51, 20)	4.15 (0.99, 20)	5.7±2.21	4.87
	2	-2.39 (0.51, 20)	4.97 (0.99, 20)	8.11±1.16	1.35
	3	-2.11 (0.51, 20)	5.17 (0.99, 20)	7.96±1.27	1.13
	Combined	-2.28 (0.31, 60)	6.49 (0.61, 60)	7.26±1.91	3.64

Table 3. Top ranking candidate models for the effects of body size and resource level on animal movement in an advection-diffusion framework. Clearly, a size-dependent advection rate is consistent across the top ranked models in this set.

Model no.	Model Description		log(L)	K	AIC <sub>c</sub>	Δ <sub>i</sub> AIC <sub>c</sub>	w <sub>i</sub>	Evidence ratio	Rank
	Low Resources	High Resources							
<b>10</b>	<b>β size-depdt, D</b>	<b>β size-depdt, D</b>	<b>-285.46</b>	<b>6</b>	<b>583.67</b>	<b>0.00</b>	<b>0.489</b>	<b>1.00</b>	<b>1</b>
<b>18</b>	<b>β size-depdt, D size-depdt</b>	<b>β size-depdt, D</b>	<b>-285.25</b>	<b>7</b>	<b>585.52</b>	<b>1.85</b>	<b>0.194</b>	<b>2.52</b>	<b>2</b>
<b>9</b>	<b>β size-depdt, D</b>	<b>β, D</b>	<b>-287.52</b>	<b>5</b>	<b>585.57</b>	<b>1.91</b>	<b>0.189</b>	<b>2.59</b>	<b>3</b>
17	β size-depdt, D size-depdt	β, D	-287.32	6	587.38	3.71	0.076	6.40	4
12	β size-depdt, D	β size-depdt, D size-depdt	-287.26	7	589.53	5.86	0.026	18.76	5
Experimental unit as variable									
<b>10</b>	<b>β size-depdt, D</b>	<b>β size-depdt, D</b>	<b>-259.76</b>	<b>18</b>	<b>562.36</b>	<b>0.00</b>	<b>0.937</b>	<b>1.00</b>	<b>1</b>
9	β size-depdt, D	β, D	-266.85	15	568.35	5.99	0.047	20.03	2

Notes: log(L) is the log likelihood estimate, K is the number of parameters, and AIC<sub>c</sub> is the corrected Akaike’s Information Criterion; ΔAIC<sub>c</sub> is the difference in between the lowest AIC<sub>c</sub> score and the AIC<sub>c</sub> score of each model (model i); the Akaike’s weight (w<sub>i</sub>) is the weight of evidence in favor of model i; the evidence ratio is the amount of times more likely the top selected model is relative to model i (e.g., model 1 is 2.52 times more likely than model 2).

## FIGURE LEGENDS

Figure 1. Movement distributions produced by snails in the experimental stream facility over 5 hours at low and high resources. The data are presented per experimental stream to illustrate the consistency of results within each unit. (A-C) Distance moved at low resources showing an upstream bias and population spread around the mean. (D-F) Distance moved at high resources, showing a distinctly narrower upstream wave.

Figure 2. The relationship between distance moved and body size (length, mm) for each of the experimental units. (A-C) At low resources, there is a positive relationship between distance moved and body size (Slopes of each of regression line are different from zero: A,  $P < 0.01$ ; B,  $P < 0.05$ ; C,  $P < 0.05$ ). (D-F) At high resources, most individuals moved upstream at a similar rate despite differences in body size, resulting in the narrower wave seen in Fig. 1 (Slopes of two of three regression lines are different from zero: D,  $P < 0.05$ ; E,  $P < 0.01$ ; F,  $P > 0.05$ ).

Figure 3. Model predictions overlaid on the relationship between distance moved and body size after 3 (A), 4 (B), and 5 (C) hours and pooled across replicate streams. Closed circles indicate low resource treatments and open circles represent high resource treatments. Lines represent model predictions for four models from the *a priori* set of models. Models that are resource dependent produce two prediction lines, one for low resources (L) and one for high resources (H). Model 1 is the simplest form of the model, predicting that all snails move upstream the same amount despite differences in body size and resource level. Model 2 represents model predictions from a model that incorporates body size in advection,

illustrating a positive relationship between distance moved and body size, but no discrimination for resource level. Model 5 predictions illustrate the effect of adding resources to the model; snails at a particular resource level move the same distance despite differences in body size. Finally, Model 10, the best model in the set, shows predictions given size-dependent advection and resource dependency. Clearly, there is an interaction between resources and body size at each time, and, out of this set of models, Model 10 provides the best fit to the empirical data.

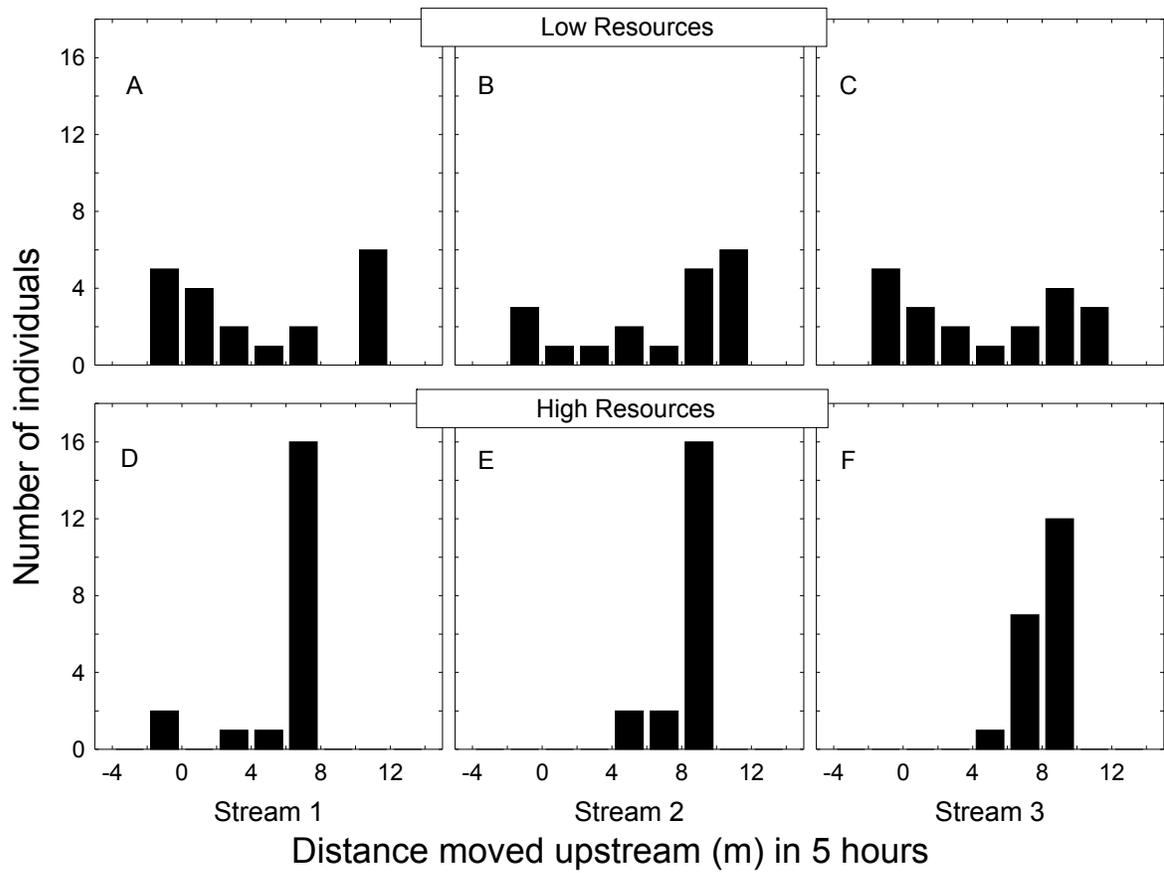


Figure 1. Movement distributions produced by snails in the experimental stream facility

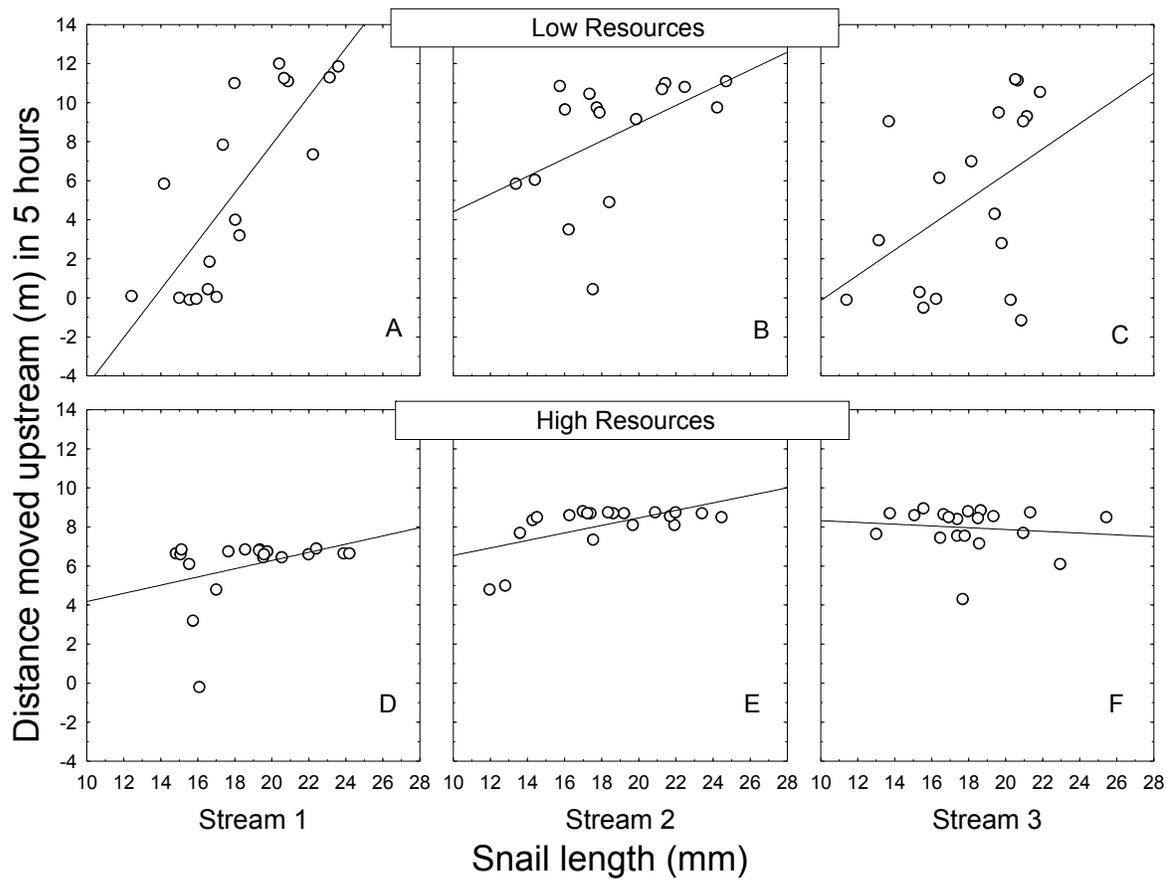


Figure 2. The relationship between distance moved and body size

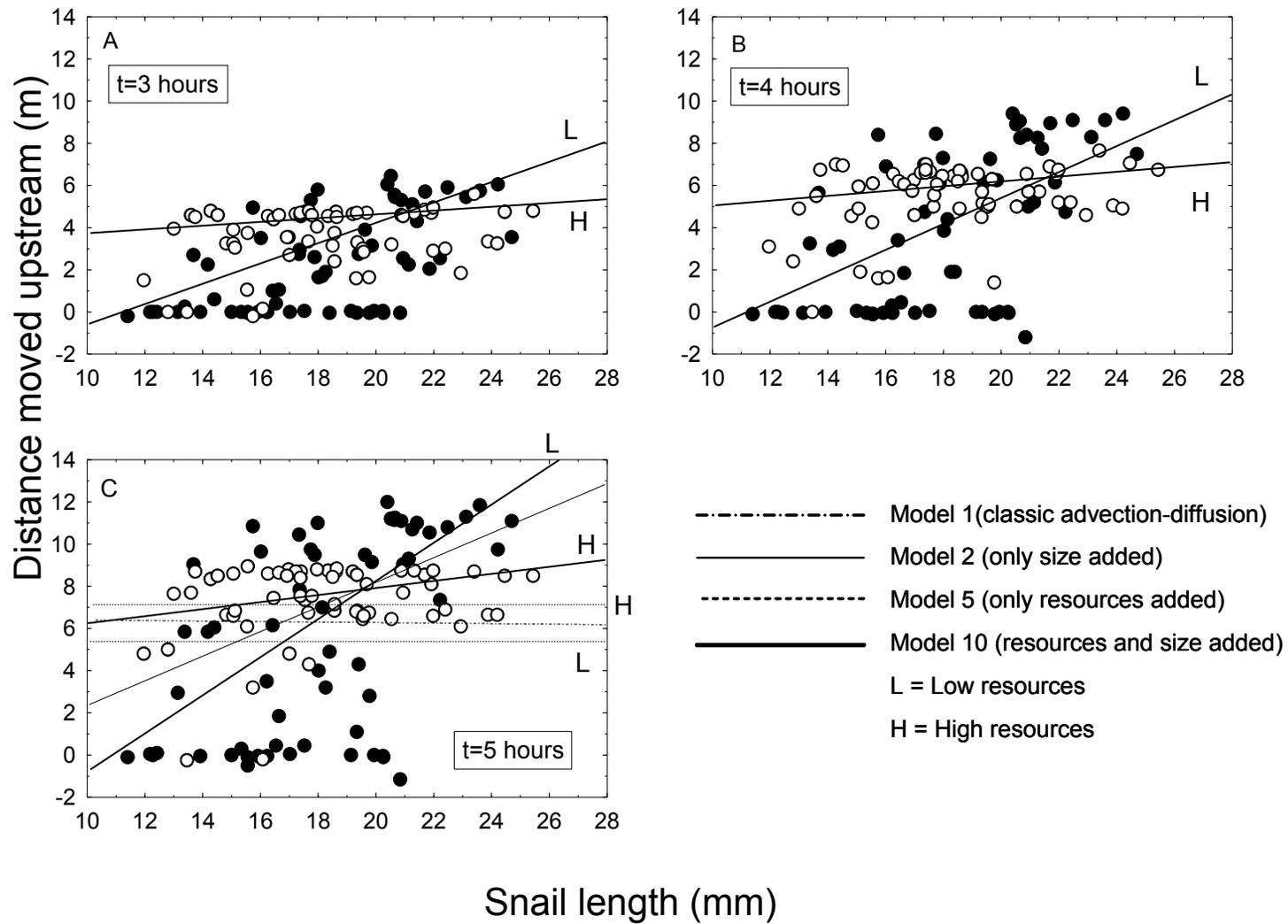


Figure 3. Model predictions

## CHAPTER 2

### **Competition affects the movement behaviors of two coexisting exotic species**

## ABSTRACT

Dating to classical work by Fisher and Skellam, population spread has typically been modeled as a function of both population growth and individual movement at the edge of the population. Density dependence within a species and competition between species have also been incorporated into these models via population growth functions, but the population movement component of spread has been considered only in single-species models. Here, I extend these models to include a flexible behavioral response in terms of individual movement due to exploitative competitive interactions. I asked how both interspecific and intraspecific competition between two coexisting invasive gastropod species affects their movement behaviors, and if including density of conspecifics and heterospecifics improves advection-diffusion models of movement. I proposed various modifications of the advection-diffusion model that include competitive interactions as *a priori* hypotheses. To test these hypotheses, I measured movement rates of both species at different density treatments. Using these experimental movement data, I examined individual and population level movement behaviors by testing for differences in the movement distributions at different density combinations. Competition had a dramatic affect on the movement behaviors of one of the study species, *Melanoides tuberculata*, changing individual and population level movement behaviors. In stark contrast, competition had no affect on the movement behaviors of a second invader, *Tarebia granifera*. *M. tuberculata* movement rates increased with increasing density of snails of either of the study species. Moreover, at the population level, there was a distinct shift from a leptokurtic movement distribution at low levels of competition (or higher resources) to a platykurtic movement distribution at high levels of

competition (low resources). These patterns were also reflected in the model selection results, as both the advection and diffusion parameters showed dependency on density of conspecifics and heterospecifics. Clearly, competition induced a behavioral change in terms of movement behaviors for one of the study species. Models that predict rates of population spread may include competition in their growth function, but have not been extended to include flexible behaviors that result from competition in terms of movement.

## INTRODUCTION

Diffusion models that describe population spread incorporate both population movement and population growth via a diffusion approximation, with or without advection and based on a random walk, and a growth function. Density-dependence and species interactions have been included in models of spread, but are typically incorporated in the growth function via simple density-dependent growth (e.g., logistic growth) and Lotka-Volterra principles (Okubo et al. 1989, Shigesada and Kawasaki 1997, Okubo and Levin 2001). However, density of conspecifics and heterospecifics also has the potential to affect the movement component of population spread, though this effect is often ignored when modeling spread and predicting rate of spread. I found one example in the literature in which diffusion depended on density of conspecifics (Aronson 1980, Okubo and Levin 2001). I did not find any examples in which models incorporate species interactions into the advection term, nor have I found a derivation for rate of spread in which species interactions are included in the diffusion and advection terms of the equation.

Despite being deficient in theoretical explorations, empirical research has indicated that movement rates and patterns are influenced by density-dependence (Kareiva 1983) and other species interactions, such as predation and interspecific competition. A study by Fraser and others (2006) indicates that a predator can change the movement behaviors of prey in a stream fish community. In this study, nocturnal piscivore, *Hoplias malabaricus*, speeds the movement of its prey, *Rivulus hartii*, through hostile corridors. Keeley (2001) showed that juvenile steelhead trout showed a higher probability of emigration as researchers increased

per capita competition with cutthroat trout. Thus, in both these cases, negative biotic interactions enhanced movement of stream fishes. However, a study examining the effects of an exotic brown trout species on a native cutthroat trout species, indicated that the exotic species reduced, at the population level, movement of the native species via some native-exotic species interaction (McHugh and Budy 2006). These few studies illustrate two things: (1) species interactions can and do affect individual movement behaviors and, (2) species interactions can have different net effects on movement behaviors. Obviously, there are other species interactions that affect movement behaviors, e.g., predators follow prey, and prey move away from predators, but I focused the current discussion on competition.

I examined how competitive interactions affect the movement behaviors of two exotic freshwater snail species in an advection-diffusion framework. Objectives included (1) asking whether inter- and intra- specific competition affects the individual growth rates of both species to assess the magnitude of competition using a more traditional response variable, (2) determining how intra- and inter- specific competition can affect individual movement behaviors, (3) determining if intra- and inter- specific competition impacts population level distribution kernels, (4) examining which components of the advection-diffusion modeling framework best reflect competitive interactions, and (5) exploring the potential implications for models of population spread and rate of spread. I predicted potential outcomes for the effects of competition on movement in an advection-diffusion framework. For advection, effects on competition included: increased advection rates (i.e. density dependent movement rates), no effect on advection rates, or decreased advection rates. Effects on the process of diffusion are also possible, where competition results in higher or lower variance of distance

moved, or no effect. Using experimental movement data, I examined movement behaviors under different levels of competition and tested competing advection-diffusion hypotheses.

## MODEL

### *Classical advection-diffusion model*

Reaction advection-diffusion models have played an important role in predicting and describing population spread (Skellam 1951, Andow et al. 1990, Liebhold et al. 1992, van den Bosch et al. 1992, Shigesada and Kawasaki 1997, Okubo and Levin 2001). The solution to the reaction advection-diffusion equation

$$\frac{\partial P}{\partial t} = D \left( \frac{\partial^2 P}{\partial x^2} \right) - \beta \frac{\partial P}{\partial x} + f(P) \quad (1)$$

predicts the change in density of individuals  $P$  through space  $x$  and time  $t$ , where  $\beta$  is advection,  $D$  is diffusion, and  $f(P)$  is a general population growth function. Advection and diffusion are the movement components of this equation, as described in Chapter 1. For this study, I chose to examine how these two components, advection and diffusion, are affected by intraspecific and interspecific competition.

I asked if effects of intraspecific competition and interspecific competition on movement among different body sizes were manifested in advection, diffusion, or both components of movement. Thus, I determined whether density dependence and/or competition should be incorporated into one or both of the components of the advection-diffusion equation, if either, in a parsimonious model. I also considered population

heterogeneity, in terms of snail length, in the diffusion and advection components of movement, as a relationship with body size was found to be important in previous work (Chapter 1). I incorporated density of competitors and snail length in the models in both the advection term,

$$\beta_i = \beta_0 + (\beta_{length} \times length_i) + (\beta_{intra} \times intra_i) + (\beta_{inter} \times inter_i), \quad (2)$$

and the diffusion term,

$$D_i = D_0 + (D_{length} \times length_i) + (D_{intra} \times intra_i) + (D_{inter} \times inter_i), \quad (3)$$

where  $i$  represents an individual. For the set of models, I consider combinations of advection and diffusion. Advection options include: (1) only size-dependent advection (heretofore referred to as “constant” with respect to the effects of competition), (2) advection linearly related to the number of intraspecific competitors, (3) advection linearly related to density of interspecific competitors, and (4) advection linearly related to both the number of intra and inter specific competitors (i.e., total density and species matter) (Eq. 2). Diffusion options are the same options as described for advection (Eq. 3). Using these hypotheses for advection and diffusion, I can determine whether one or both of the parameters depend on density of competitors, density of intra- or inter-specific competitors, or density of both intra- and inter- specific competitors.

### *General model structure*

The most general model structures for estimating advection and diffusion are

described below, where  $I_1$  and  $I_2$  are indicator variables:

$$\beta = \beta_0 + \beta_1 length + \beta_2 intra I_1 + \beta_3 inter I_2 \quad (4)$$

$$D = D_0 + D_1 length + D_2 intra I_1 + D_3 inter I_2. \quad (5)$$

$I_1$  : Does intraspecific competition matter?  $\begin{cases} 0 & \text{If no} \\ 1 & \text{If yes} \end{cases}$

$I_2$  : Does interspecific competition matter?  $\begin{cases} 0 & \text{If no} \\ 1 & \text{If yes} \end{cases}$

The set of candidate models is determined by all combinations of the four advection and four diffusion hypotheses, yielding a set of 16 *a priori* candidate models (Table 1).

Using these combinations, I identified which parameter(s) requires incorporation of competition to describe movement behaviors for each of the two species.

## METHODS

### *Study system*

I used two aquatic snail species, *Tarebia granifera* and *Melanoides tuberculata*, that have been introduced to tropical and subtropical habitats around the world. In Trinidad streams both species coexist; *M. tuberculata* occurs primarily along the edges of the stream

whereas *T. granifera* is found throughout the entire stream (Snider, unpublished data). This pattern is consistent with observations in other riverine systems (Pointier et al. 1994, Samadi et al. 1997). When occurring alone, however, *T. granifera* is observed utilizing mostly edge habitats (Samadi et al. 1997). These patterns suggest a competitive interaction between the two species.

### *Experimental facility*

The circulating experimental stream facility consisted of 36 6-m long “movement streams” constructed of six-inch PVC rain gutters that were used for movement experiments and 36 25cm x 30cm “growth streams” constructed of plastic tubs that were used for growth experiments. There was a 3785-L water holding tank at the upstream end of the facility and two 1892-L collecting tanks at the downstream end of the facility. The water was recirculated using a ½ horsepower sump pump resulting in an average flow rate of 0.61 cm/s for each movement stream. A canopy of agricultural mesh provided partial shade, both to mimic a partial canopy and to prevent overheating of the water.

The experimental stream facility is located within 0.5 km of both the Arima River and Ramdeen Stream. I used local water and substrates to reasonably mimic the natural environment. Each stream contained a 1.5 cm layer of rinsed river sand and flat river stones, approximately 7 cm by 10 cm. In movement streams, I placed stones in the center of each stream every 1.0 m to inoculate streams with algae and other stream organisms, and provide natural substrate. In growth streams, I placed one stone and one cacao leaf (*Theobroma cacao*) in the center of each stream to inoculate streams with algae and other stream

organisms, and provide natural substrate. The cocoa leaves were collected in Ramdeen Stream and were covered in a visible layer of algae and detritus. Each stone and each leaf placed in each stream were of approximately equal area. New rocks and cocoa leaves were rotated in and out of the growth streams every 48 hours during the experiment to provide enough algae and detritus for snails to survive. Experimental streams flowed for 2 weeks prior to applying treatments.

### *Experimental design*

I used a response surface experimental design in which the density of individuals of each of the two species was varied independently. I used a wide range of density treatments, including densities that were near the maximum, minimum, and average densities observed in the field (Inouye 2001). Thus, for my design, I used three target densities with four species combinations per density, resulting in a total of twelve density treatments, with 3 replicates of each treatment. I calculated maximum and minimum densities for *T. granifera* and *M. tuberculata* by estimating mean and maximum densities in both Ramdeen Stream and the Arima River (Snider unpublished data). Based on these estimates, I considered average density to be approximately 100 snails/m<sup>2</sup>, maximum density >200 snails/m<sup>2</sup> and minimum density <50 snails/m<sup>2</sup>. I collected all snails from the Arima River and Ramdeen Stream.

The 36 movement streams received the following density treatments, where M designates *M. tuberculata* and T designates *T. granifera*: (1) a low density treatment with sixteen snails per stream consisting of density combinations 0M and 16T, 16M and 0T, 6M and 10T, 10M and 6T, (2) an average density treatment with 48 snails per stream consisting

of density combinations 0M and 48T, 48M and 0T, 16M and 32T, 32M and 16T, and (3) a high density treatment with 144 snails per stream consisting of density combinations 0M and 144T, 144M and 0T, 48M and 96T, 96M and 48T. For each replicate, snails of each species were sorted into three size classes (“small, medium, large”), and snails within each size class randomly assigned to each stream in the appropriate density combination. Due to upstream bias of both species, I moved individuals from upstream end to downstream end to keep snails distributed throughout the stream.

For the movement trials, I applied the density treatments to each replicate movement stream and allowed the snails to create the treatments for 19 days before starting the movement experiment. After the 19-day conditioning period, a newly collected and individually marked set of snails were sorted into three size classes (“small, medium, large”), and snails within each size class randomly assigned to each stream, for a total of 20 *M. tuberculata* and 20 *T. granifera* per replicate, to assure a range of sizes in each stream. An 8 AM point release of snails occurred at 0.5 m in the downstream end of each stream. I then recorded the locations of each marked individual after 2, 4, 8, and 24 hours. The experiment ran for 24 hours to include one day and one night, as I have observed that *M. tuberculata* show greater activity at night (Snider and Gilliam unpublished data). Snails were individually marked with different color combinations of fingernail polish.

The 36 growth streams received the following density treatments, where M designates *M. tuberculata* and T designates *T. granifera*: (1) a low density treatment with four snails per stream consisting of density combinations 0M and 4T, 4M and 0T, 1M and 3T, 3M and 1T, (2) an average density treatment with 12 snails per stream consisting of density

combinations 0M and 12T, 12M and 0T, 4M and 8T, 8M and 4T, and (3) a high density treatment with 36 snails per stream consisting of density combinations 0M and 36T, 36M and 0T, 12M and 24T, 24M and 12T. To illustrate competition in a traditional way, I measured individual growth rates of all individuals at each of the density treatments after 19 days. I measured change in total length of individually marked snails. Snails were individually marked with different color combinations of fingernail polish.

### *Analysis*

To assess the effects of competition on individual growth rates, I calculated instantaneous growth rate for each individual snail based on changes in snail body length after 19 days. Then I plotted the average individual growth rate for each replicate on a response surface and used a general linear model to test for the effects of interspecific and intraspecific competition (number of *M. tuberculata*, number of *T. granifera*, and initial body length as predictor variables) on individual growth rates for each density treatment for each species (STATISTICA 6.0).

I calculated distance moved for each individual snail after 24 hours. I used a general linear model to test for the effects of interspecific and intraspecific competition (number of *M. tuberculata*, number of *T. granifera*, and body length as predictor variables) on replicate mean distance moved and replicate variance of distance moved for each density treatment for each species. I also tested for the effects of total snail density (regardless of species) of competitors on mean distance moved and variance of distance moved for both species using ANOVA. All analyses were performed using STATISTICA 6.0.

I calculated kurtosis and p-values for kurtosis based on a t distribution for each species. I plotted these kurtosis values vs. total snail density of each replicate or treatment using EXCEL. Finally, I used ANOVA to test for differences in kurtosis values at different snail densities.

### *Analysis of movement models*

For each of the models in the model set, I estimated diffusion and advection parameters via maximum likelihood estimation (Microsoft Excel Solver) based on the general likelihood

$$L\{x | D, \beta, t\} = \left( \frac{P_0}{2\sqrt{\pi Dt}} \right) \exp\left( -\frac{(x - \beta t)^2}{4Dt} \right). \quad (6)$$

Eqn. 6 is the solution to the PDE shown in Eqn. 1 (ignoring the growth function) and predicts a normal distribution with mean  $\beta t$  and variance  $2Dt$ , where  $\beta$  and  $D$  are functions of length and possibly density of heterospecifics and/or conspecifics, depending on the model. To compare the 16 hypotheses, I used the resulting maximum likelihood estimates to calculate Akaike's Information Criterion (AIC) (Akaike 1973, Burnham and Anderson 2002). I also calculated Akaike weights and evidence ratios to assist in the model selection.

## RESULTS

### *Empirical results*

Individual growth rates of both species were reduced by competition (Fig. 1).

Individual growth rates of *M. tuberculata* were reduced by interspecific competition ( $F_{1,23}=12.13$ ,  $p=0.002$ ) and by intraspecific competition ( $F_{1,23}=29.16$ ,  $p<0.001$ ). Likewise, individual growth rates of *T. granifera* were reduced by interspecific competition ( $F_{1,23}=9.42$ ,  $p=0.005$ ) and by intraspecific competition ( $F_{1,23}=17.01$ ,  $p<0.001$ ). Both species experienced exploitative competition in this system, providing the impetus for the second experiment in which I predicted that competition will induce a behavioral response in terms of individual movement.

Mean distance moved (advection) by the edge-dwelling species, *M. tuberculata*, was enhanced by increased snail densities (Fig. 2A), both by interspecific competition ( $F_{1,32}=11.28$ ,  $p=0.003$ ) and by intraspecific competition ( $F_{1,31}=19.22$ ,  $p<0.001$ ). Mean variance of distance moved over the same 24 hour time period was also enhanced by intraspecific competition ( $F_{1,31}=5.47$ ,  $p=0.03$ ), but the effect of interspecific competition, suggested in Fig. 3A, was not statistically significant at the  $\alpha=0.05$  level ( $F_{1,31}=3.68$ ,  $p=0.06$ ). In contrast, the movement behavior of *T. granifera* was, for the most part, not affected by competition (Figs. 2B and 3B). Mean distance moved was not affected by interspecific competition ( $F_{1,31}=1.44$ ,  $p=0.24$ ) or intraspecific competition ( $F_{1,31}=0.06$ ,  $p=0.81$ ). There was a significant effect of intraspecific competition on the mean variance of distance moved for this species ( $F_{1,31}=8.69$ ,  $p=0.006$ ), but no effect on mean variance by interspecific competition ( $F_{1,31}=2.46$ ,  $p=0.12$ ). These data indicate a species specific response to competition in terms of movement behavior.

This species-specific response was mimicked at the population level. Interspecific and intraspecific competition affected movement at the population level by changing the

shape of the distribution kernel for *M. tuberculosis* (Fig. 4A), but had no effect on population level movement behaviors of *T. granifera* (consistent with individual level behavior) (Fig. 4B). At high density of both inter and intra specific competitors, *M. tuberculosis* exhibited a platykurtic distribution of movement. At low density of competitors, kurtosis values were much higher and leptokurtic. The movement distributions produced at these different densities illustrate the population level movement patterns (Fig. 3).

#### *Model selection results*

For *M. tuberculosis*, competition, both intraspecific and interspecific, was reflected in both the advection and diffusion components of the model. Model 16 is the top ranking model in the analysis, and according to evidence ratios, this model had 12.31 times more support than the next most likely model (Model 8) (Table 2). Clearly, both advection and diffusion are affected by intraspecific and interspecific competition for *M. tuberculosis* as Model 16 was unambiguously the top ranking model relative to the remaining models in the set.

In stark contrast, *T. granifera* showed a lack of response to competitive interactions and consequently, the top ranked model in this analysis ignores competition altogether (Model 1). However, this model received only 1.48 times more support than Model 3 with interspecific competition in advection, 1.73 times more support than Model 9 with interspecific competition in diffusion, and 2.07 times more support than Model 2 with intraspecific effects in advection. Due to model selection uncertainty, I accepted these top four ranking models ( $\Delta AIC < 3$ ) as plausible (Burnham and Anderson 2002). This result is

consistent with the empirical data in that there is relatively little relationship with the presence of competitors at any density, but indicates that there is some sort of behavioral response to both interspecific and intraspecific competition that was not entirely discernible at the scale or level of this study. Given these ambiguities, I quantified the evidence in support of each of the three variables across the entire model set by calculating relative variable importance (Burnham and Anderson 2002) for each of the variables to both advection and diffusion. Burnham and Anderson (2002) define relative variable importance as the sum of Akaike weights across all models that include the variable of interest. For advection, intraspecific competition had the highest relative variable importance (intra=0.34, inter=0.32). For diffusion, interspecific competition had the highest relative variable importance (intra=0.30, inter=0.36). The relative importance of both variables is about one third, and therefore it remains unfeasible to discern whether one of these variables is more likely to be included in the model without more data.

## DISCUSSION

### *Patterns from empirical data*

Competition had a dramatic affect on the movement behaviors of *M. tuberculata*, changing individual and population level movement behaviors. In stark contrast, competition had little effect on the movement behaviors of *T. granifera*. Movement by *M. tuberculata* was promoted by increasing density of both interspecific competition and intraspecific competition, increasing mean distance moved to convergence with that of *T. granifera* (Fig. 5). Furthermore, at the population level, there is a distinct shift from a leptokurtic movement

distribution at low levels of competition (or higher resources) to a platykurtic movement distribution at high levels of competition (low resources).

To create leptokurtosis a few individuals move long distances, resulting in a distribution with a high peak and heavy tails. For platykurtosis, fewer individuals move long distances relative to the mean, leaving less density in the tails of the distribution. In terms of diffusion, this shift suggests that at low levels of competition there is intrapopulation variability in movement behaviors. However, at high levels of competition, or low resources, the probability of movement for a given individual changes so that intrapopulation variability in movement is reduced. This result has implications for rate of population spread if the rate of spread is dependent on rare, long-distance movement events (Kot et al. 1996, Neubert and Caswell 2000, Caswell et al. 2003) and resource availability or competition can change the probability of a rare long distant move, or can change the number of individuals making long distance movements. The shape of the dispersal kernel also influences the ability to accurately predict invasion speeds. Long distance movers make the leading edge of a leptokurtic distribution more variable and, thus, invasion speed less predictable (Lewis 1997).

Other researchers have demonstrated how changes in individual level behaviors are reflected in population level movement distributions. In such studies, empirical and theoretical evidence most commonly produce leptokurtic distribution kernels (Lewis 1997) attributable to population heterogeneity ((Kareiva 1983, Fraser et al. 2001, Skalski and Gilliam 2003) and habitat boundaries (Morales 2002), and sometimes producing platykurtic distribution kernels (Kareiva 1983) due to the interaction of resource availability and body

size (Chapter 2). A complete understanding of when and why these different types of distributions arise for spreading populations will have implications for many sorts of contemporary models in ecology.

*Implications for models that describe population spread*

That both intra- and inter- specific competition can change local movement behaviors for some species has implications for multiple population and community models that depend on movement. For instance, population spread is typically modeled as arising from local population growth plus individual movement, so factors that affect both population growth and movement behaviors in turn affect population spread. Thus, the net effect of variation in a given biotic or abiotic factor on population spread will reflect effects on each of these two processes. For example, management of invasive species and agricultural pests often target local population growth rates of exotic species or agricultural pests and/or seek to limit rates of dispersal. If a control practice was implemented that reduced population growth in an area, but promoted movement out of that area, the reduction in spread by depressed growth could theoretically be overcome by movement rates, in effect negating the desired outcome of the control and instead promoting spread of the pest species.

*Making advection and diffusion dependent on species interactions*

Our results show that, when it matters, density of competitors is reflected in both the diffusion and advection components of advection-diffusion models. I was unable to assess whether or not I must specify interspecific and intraspecific levels of competition, but it is obvious that total density of competitors changes movement behaviors. There are few

models that incorporate density-dependence into the diffusion term (Aronson 1980, Okubo and Levin 2001) and no existing models that I have found that incorporate density of heterospecifics into the diffusion term. Furthermore, I have not encountered any models that consider density of conspecifics and/or heterospecifics in the advection component of movement.

Including this type of flexible behavior in movement models may then be extended to models that predict rate of population spread. I can then explore the potential implications for rate of spread, or invasion speed ( $c^*$ ). The invasion speed solution is a traveling wave solution at the leading edge of an invasion in the form of

$$c^* = 2\sqrt{rD} + \beta \quad (7)$$

In this equation,  $r$  is the intrinsic rate of population growth,  $D$  is the diffusion coefficient, and  $\beta$  is the advection rate. Therefore conceptually, the invasion rate is made up of a growth and a movement component. This solution is for a traveling wave at the edge of an invasion, where the effects of density dependence are minimal, and a model with exponential growth is approximately the same as the equation with logistic growth. Shigesada and Kawasaki (1997) extend this traveling wave solution for invasion by competing species. In this case, invasion occurs into an area occupied by a resident species and the two species compete. A set of two interacting equations, that are extensions of Eqn. 1 without advection, describe this scenario:

$$\frac{\partial n_1}{\partial t} = D_1 \frac{\partial^2 n_1}{\partial x^2} + (\varepsilon_1 - \mu_{11}n_1 - \mu_{12}n_2)n_1, \quad (8)$$

$$\frac{\partial n_2}{\partial t} = D_2 \frac{\partial^2 n_2}{\partial x^2} + (r_2 - \mu_{21}n_1 - \mu_{22}n_2)n_2, \quad (9)$$

where  $n_1(x,t)$  is the population of the resident species (species 1) and  $n_2(x,t)$  is the population density of the invading species (species 2) at position  $x$  and time  $t$ . The second term is the growth term with coefficients  $\mu_{ii}$  and  $\mu_{ij}$  ( $i, j = 1, 2$ ) representing intraspecific competition and interspecific competition in a simple Lotka-Volterra fashion, where  $\mu_{ii}=(r_i/K_i)$  and  $\mu_{ij}=(r_i\alpha_{ij}/K_i)$  ( $K$  is carrying capacity and  $\alpha$  is a competition coefficient). The solution for the speed of the invader into the area occupied by the resident species is

$$c_2^* = 2\sqrt{r_2 D_2 (1 - r_1 \mu_{21} / r_2 \mu_{11})}. \quad (10)$$

In this case we see that competitive interactions with a resident species will slow the rate of invasion by species 2. My data suggest that to estimate population spread we should include an advection term and incorporate competition into both the diffusion parameter and the advection rate. Following the result of Shigesada and Kawasaki (1997) shown in Eqn. 10, I surmise that competitive interactions in diffusion and advection might change the solution for invasion speed. However, including competition in either advection or diffusion results in a non-linear reaction diffusion equation. The mathematics required to derive an analytical solution to this problem are currently beyond the scope of this work, and there may or may not be an analytical solution for the traveling wave speed with competition in diffusion and advection. I intend to pursue this problem further as I believe that finding a solution would provide valuable insights into the role of flexible behavior in terms of how competition affects invasion dynamics.

## ACKNOWLEDGMENTS

I thank Chip Small, Wayne Rostant, Debby Gilliam, Nikhil Seeraj, Matthew Madoo, and David Swan, and several undergraduates from the University of Dundee DUNATS 2004 Expedition for help in the field, the Ramdeen family for access to Ramdeen Stream, Robin Sinnanan for plumbing assistance, and the Sinnanan family for space to construct the experimental facility. I thank the National Science Foundation (NSF/DEB 9208102, NSF/DEB 9509585, NSF/DEB 0108365, NSF/DEB 0108439) for financial support.

## LITERATURE CITED

- Akaike, H. 1973. Information theory as an extension of the maximum likelihood principle. Pages 267-281 *in* B. N. Petran and F. Csaki, editors. Second International Symposium on Information Theory. Akademiai Kiado, Budapest.
- Andow, D., P. Kareiva, S. Levin, and A. Okubo. 1990. Spread of invading organisms. *Landscape Ecology* **4**:177-188.
- Aronson, D. G. 1980. Density-dependent interaction-diffusion systems. Pages 161-176 *in* W. E. Stewart, W. H. Ray, and C. C. Conley, editors. Dynamics and modelling of reactive systems: proceedings of an advanced seminar conducted by the Mathematics Research Center. Academic Press, New York-London.
- Burnham, K. P., and D. R. Anderson. 2001. Kullback-Leibler information as a basis for strong inference in ecological studies. *Wildlife Research* **28**:111-119.
- Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach, 2nd edition. Springer-Verlag New York, Inc., New York.
- Caswell, H., R. Lensink, and M. G. Neubert. 2003. Demography and dispersal: Life table response experiments for invasion speed. *Ecology* **84**:1968-1978.
- Fraser, D. F., J. F. Gilliam, B. W. Albanese, and S. B. Snider. 2006. Effects of temporal patterning of predation threat on movement of stream fish: evaluating an intermediate threat hypothesis. *Environmental Biology of Fishes* **76**:25-35.

- Fraser, D. F., J. F. Gilliam, M. J. Daley, A. N. Le, and G. T. Skalski. 2001. Explaining leptokurtic movement distributions: Intrapopulation variation in boldness and exploration. *American Naturalist* **158**:124-135.
- Hilborn, R., and M. Mangel. 1997. *The ecological detective: confronting models with data*. Princeton University Press, Princeton.
- Inouye, B. D. 2001. Response surface experimental designs for investigating interspecific competition. *Ecology* **82**:2696-2706.
- Kareiva, P. 1983. Local movement in herbivorous insects: applying a passive diffusion model to mark-recapture field experiments. *Oecologia* **57**:322-324.
- Keeley, E. R. 2001. Demographic responses to food and space competition by juvenile steelhead trout. *Ecology* **82**:1247-1259.
- Kot, M., M. A. Lewis, and P. VanDenDriessche. 1996. Dispersal data and the spread of invading organisms. *Ecology* **77**:2027-2042.
- Lewis, M. A. 1997. Variability, patchiness, and jump dispersal in the spread of an invading population. Pages 46-69 *in* D. Tilman and P. Kareiva, editors. *Spatial ecology: the role of space in population dynamics and interspecific interactions*. Princeton University Press, Princeton, N.J.
- Liebhold, A. M., J. A. Halverson, and G. A. Elmes. 1992. Gypsy moth invasion in North America: a quantitative analysis. *Journal of Biogeography* **19**:513-520.
- McHugh, P., and P. Budy. 2006. Experimental effects of nonnative brown trout on the individual- and population-level performance of native Bonneville cutthroat trout. *Transactions of the American Fisheries Society* **135**:1441-1455.

- Morales, J. M. 2002. Behavior at habitat boundaries can produce leptokurtic movement distributions. *American Naturalist* **160**:531-538.
- Neubert, M. G., and H. Caswell. 2000. Demography and dispersal: Calculation and sensitivity analysis of invasion speed for structured populations. *Ecology* **81**:1613-1628.
- Okubo, A., and S. A. Levin. 2001. *Diffusion and ecological problems: modern perspectives*, 2nd edition. Springer-Verlag New York, Inc., New York.
- Okubo, A., P. K. Maini, M. H. Williamson, and J. D. Murray. 1989. On the spatial spread of the grey squirrel in Britain. *Proceedings of the Royal Society of London Series B-Biological Sciences* **238**:113-125.
- Pointier, J. P., R. N. Incani, C. Balzan, P. Chrosciechowski, and S. Prypchan. 1994. Invasion of the rivers of the littoral central region of Venezuela by *Thiara granifera* and *Melanoides tuberculata* (Mollusca: Prosobranchia: Thiaridae) and the absence of *Biomphalaria glabrata*, snail host of *Schistosoma mansoni*. *Nautilus* **107**:124-128.
- Samadi, S., C. Balzan, B. Delay, and J. P. Pointier. 1997. Local distribution and abundance of thiarid snails in recently colonized rivers from the Caribbean area. *Malacological Review* **30**:45-52.
- Shigesada, N., and K. Kawasaki. 1997. *Biological invasions: theory and practice*. Oxford University Press, Oxford.
- Skalski, G. T., and J. F. Gilliam. 2003. A diffusion-based theory of organism dispersal in heterogeneous populations. *American Naturalist* **161**:441-458.
- Skellam, J. G. 1951. Random dispersal in theoretical populations. *Biometrika* **38**:196-218.

van den Bosch, F., R. Hengeveld, and J. A. J. Metz. 1992. Analysing the velocity of animal range expansion. *Journal of Biogeography* **19**:135-150.

Table 1. Parameter combinations that make up the *a priori* set of candidate models.

Model no.	Candidate Models	
	Advection ( $\beta$ )	Diffusion (D)
1	constant	constant
2	intra	constant
3	inter	constant
4	intra and inter	constant
5	constant	intra
6	intra	intra
7	inter	intra
8	intra and inter	intra
9	constant	inter
10	intra	inter
11	inter	inter
12	intra and inter	inter
13	constant	intra and inter
14	intra	intra and inter
15	inter	intra and inter
16	intra and inter	intra and inter

Table 2. Top ranking candidate models for the effects of competition on animal movement in an advection-diffusion framework. Clearly, competition-dependent diffusion and advection is consistent across the top ranked models for *M. tuberculosis*. However, pattern is not discernible for *T. granifera*, and competitive interactions may or may not be important at this scale for this species.

Model no.	Model Description		log(L)	K	AIC	$\Delta_i$ AIC	$w_i$	Evidence ratio	Rank
	Advection	Diffusion							
<i>M. tuberculosis</i>									
<b>16</b>	<b>intra and inter</b>	<b>intra and inter</b>	<b>-696.91</b>	<b>8</b>	<b>1409.83</b>	<b>0.00</b>	<b>0.887</b>	<b>1.00</b>	<b>1</b>
8	intra and inter	intra	-700.42	7	1414.85	5.02	0.072	12.31	2
<i>T. granifera</i>									
<b>1</b>	<b>constant</b>	<b>constant</b>	<b>-735.30</b>	<b>4</b>	<b>1478.60</b>	<b>0.00</b>	<b>0.202</b>	<b>1.00</b>	<b>1</b>
<b>3</b>	<b>inter</b>	<b>constant</b>	<b>-734.69</b>	<b>5</b>	<b>1479.39</b>	<b>0.78</b>	<b>0.137</b>	<b>1.48</b>	<b>2</b>
<b>9</b>	<b>constant</b>	<b>inter</b>	<b>-734.85</b>	<b>5</b>	<b>1479.70</b>	<b>1.10</b>	<b>0.117</b>	<b>1.73</b>	<b>3</b>
<b>2</b>	<b>intra</b>	<b>constant</b>	<b>-735.03</b>	<b>5</b>	<b>1480.06</b>	<b>1.46</b>	<b>0.098</b>	<b>2.07</b>	<b>4</b>
5	constant	intra	-735.41	5	1480.81	2.21	0.067	3.01	5

Notes: log(L) is the log likelihood estimate, K is the number of parameters, and AIC is Akaike’s Information Criterion;  $\Delta$ AIC is the difference in between the lowest AIC score and the AIC score of each model (model i); the Akaike’s weight ( $w_i$ ) is the weight of evidence in favor of model i; the evidence ratio is the amount of times more likely the top selected model is relative to model i (e.g., for *M. tuberculosis*, model 16 is 12.31 times more likely than model 8).

## FIGURE LEGENDS

Figure 1. Both species experienced exploitative competition in terms of individual growth rates. Open circles represent instantaneous growth rates for individual snails, calculated over 19 days, for each species at each density treatment. Instantaneous growth rates declined with increasing density of both conspecifics and heterospecifics for both (A) *M. tuberculata* (interspecific competition:  $p=0.002$ ; intraspecific competition:  $p<0.001$ ) and (B) *T. granifera* (interspecific competition:  $p=0.005$ ; intraspecific competition:  $p<0.001$ ). The surface represents a linear fit to the data.

Figure 2. Species-specific behavioral response to different levels of interspecific and intraspecific competition. Open circles represent distance moved (m) by (A) *M. tuberculata* and (B) *T. granifera* over 24 hours at the twelve density treatments. (A) Distance moved (advection) by *M. tuberculata* was enhanced by competition (interspecific:  $p=0.003$ ; intraspecific:  $p<0.001$ ). (B) In contrast, the movement behavior of *T. granifera* was, for the most part, not affected by competition (interspecific:  $p=0.24$ ; intraspecific:  $p=0.81$ ). However, visual inspection of the data in (B) suggests that there may be a slight reduction in mean distance moved at high levels of interspecific competition. The surface represents a linear fit to the data.

Figure 3. Intraspecific competition affects variance of distance moved. Open circles represent replicate variance distance moved by (A) *M. tuberculata* and (B) *T. granifera* over 24 hours at each of the twelve density treatments. (A) Variance of distance moved by *M.*

*tuberculata* was enhanced by intraspecific competition ( $p=0.03$ ), and an effect of interspecific competition was suggested, but not statistically significant at the  $\alpha=0.05$  level ( $p=0.06$ ). (B) For *T. granifera* there was also a significant effect of intraspecific competition on variance of distance moved ( $p=0.006$ ), but no effect on variance by interspecific competition ( $p=0.12$ ). The surface represents a linear fit to the data.

Figure 4. Kurtosis of movement distributions for (A) *M. tuberculata* and (B) *T. granifera* at three density treatments. For *M. tuberculata*, kurtosis values decreased with increasing density of competitors, indicating leptokurtosis at low competition and platykurtosis at the highest level of competition. In contrast, *T. granifera* showed no differences in kurtosis of the movement distributions across these density treatments.

Figure 5. Movement distributions produced by snails at three levels of competitor density over 24 hours. The data are presented across density combinations to illustrate the population level patterns. (A-C) Distance moved by *M. tuberculata* showing a leptokurtic movement distribution at the lowest density of competitors (A) and a platykurtic movement distribution at the highest density of competitors (C). (D-F) Distance moved by *T. granifera*, showing no differences in the movement distributions across the three levels of competition.

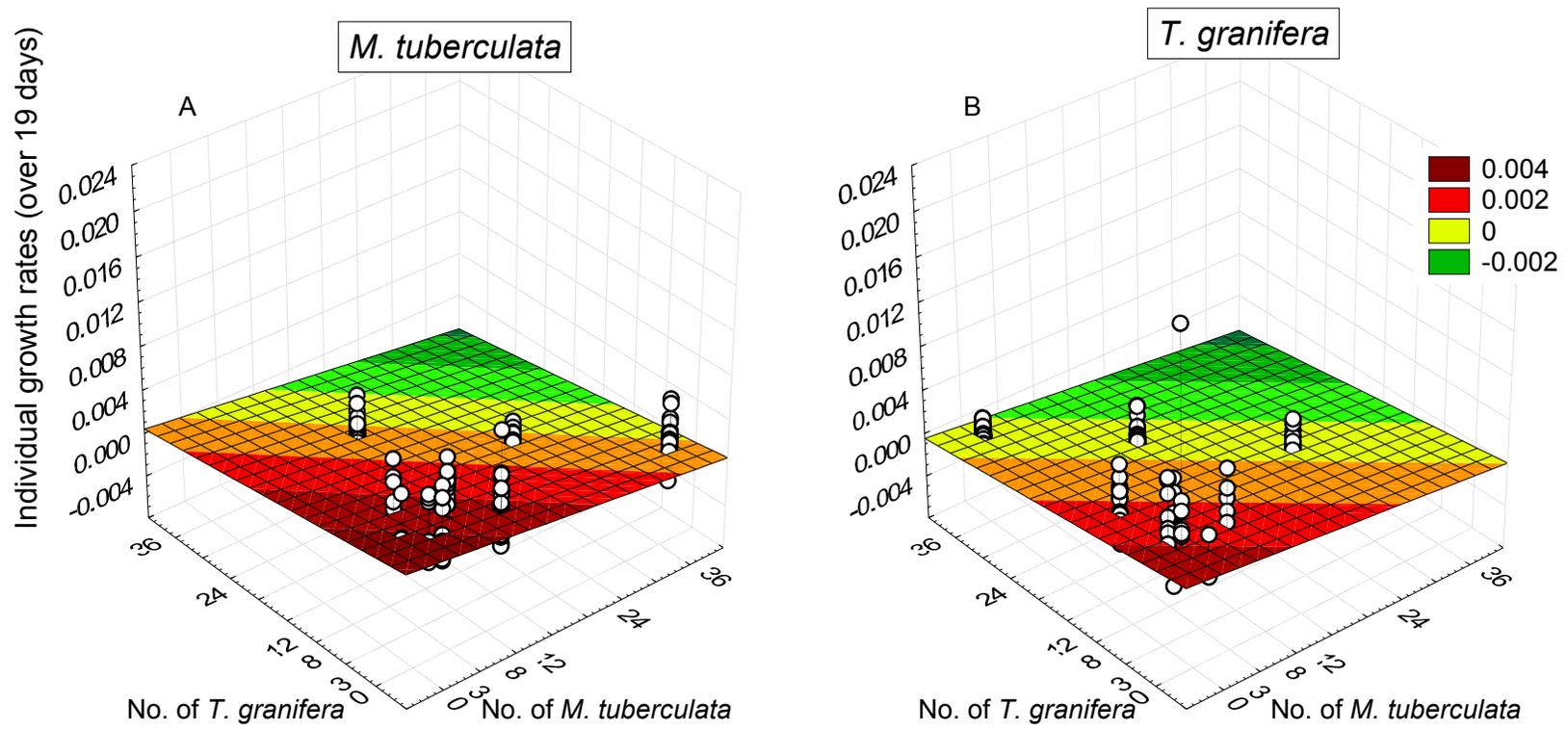


Figure 1. Exploitative competition in terms of individual growth rates

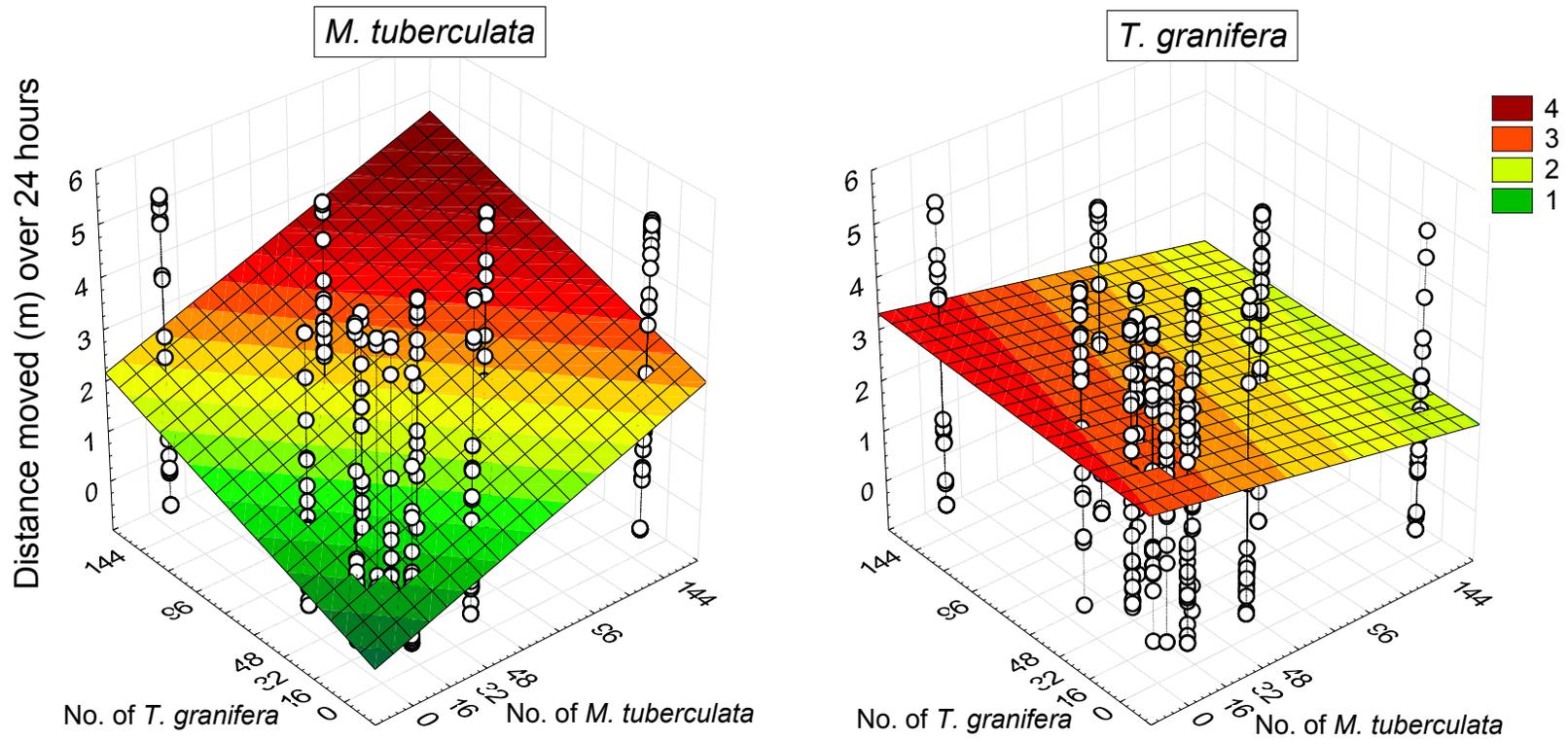


Figure 2. Species-specific behavioral response to different levels of interspecific and intraspecific competition

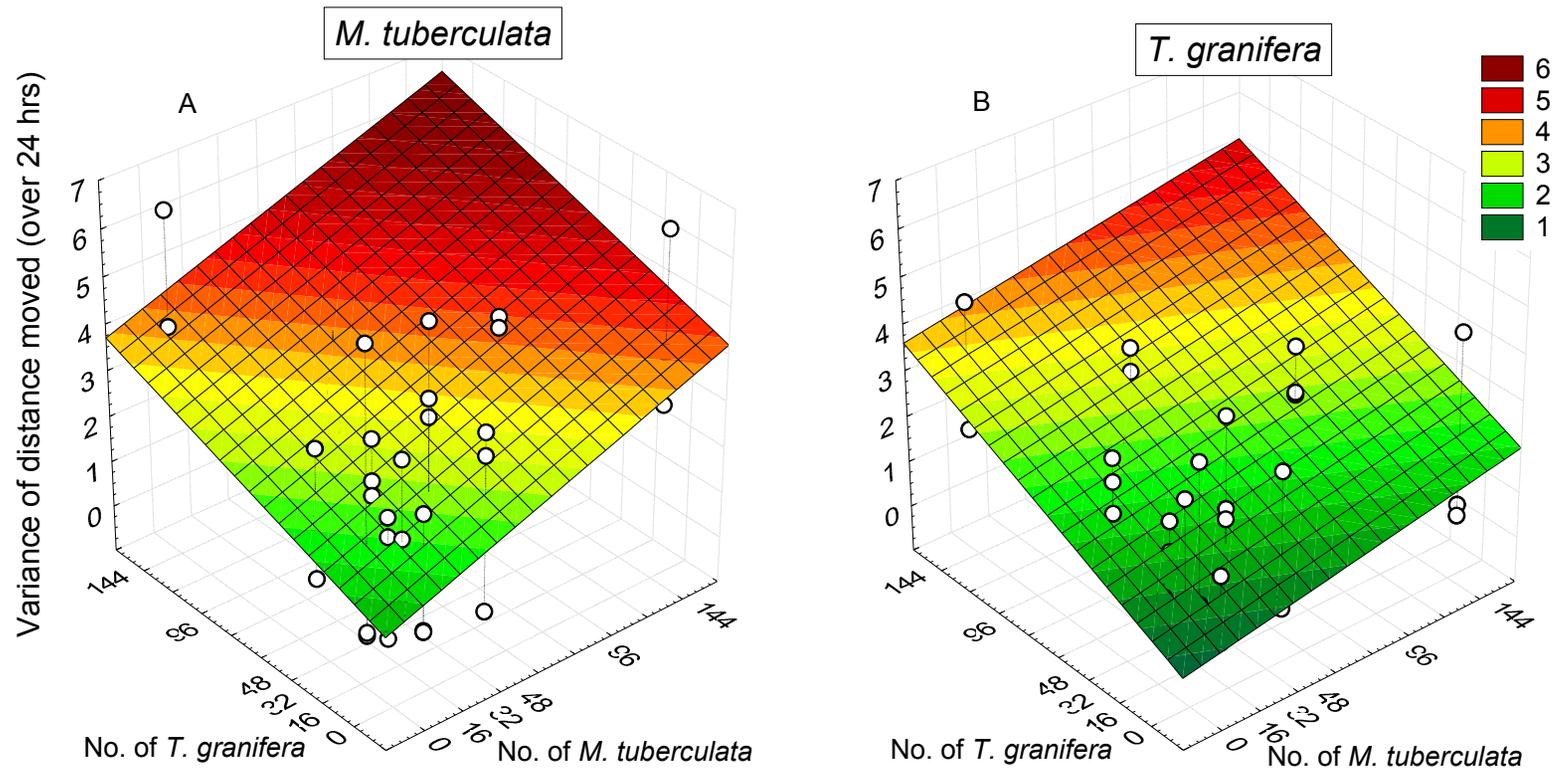


Figure 3. Intraspecific competition affects variance of distance moved

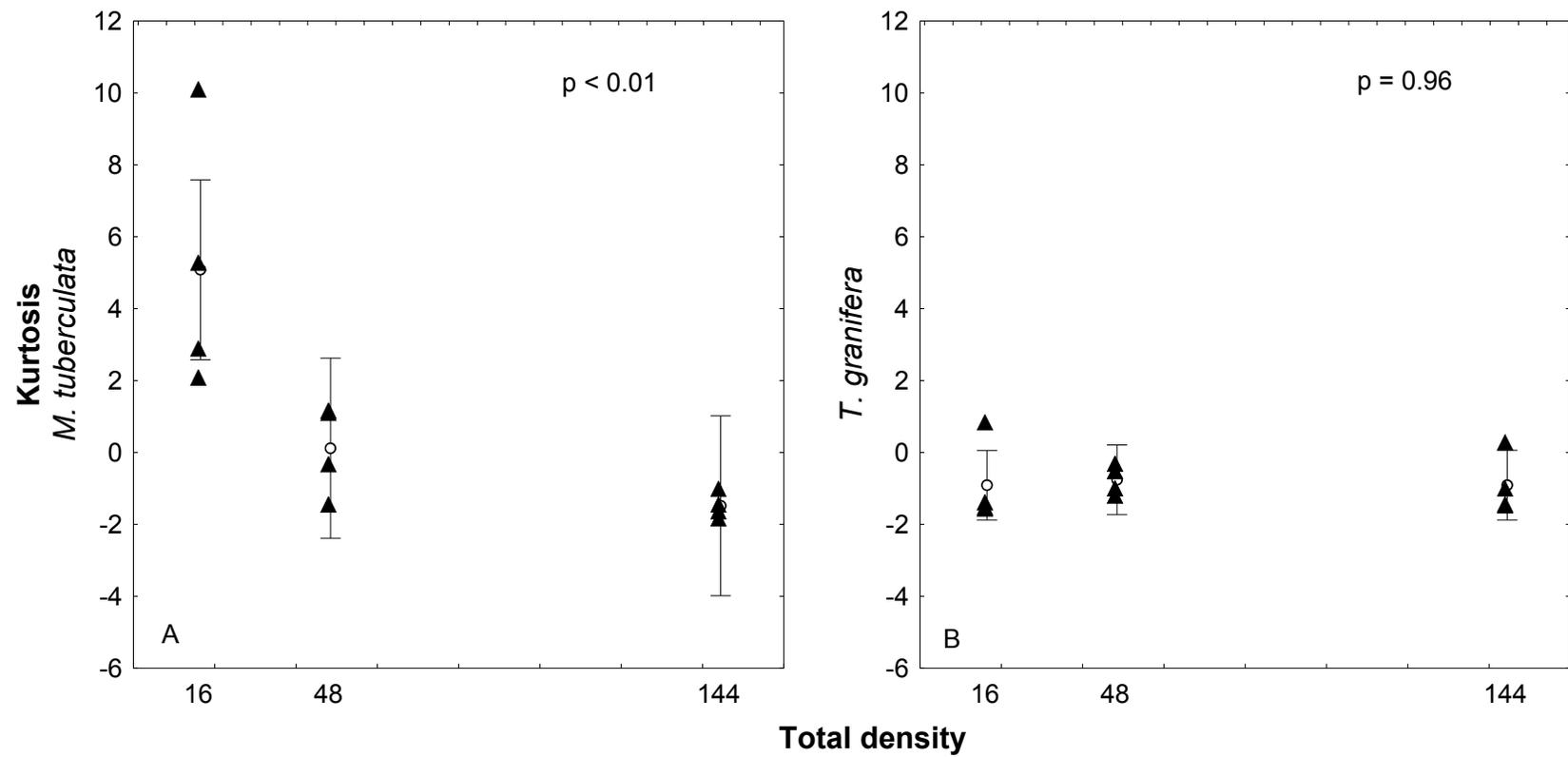


Figure 4. Kurtosis of movement distributions

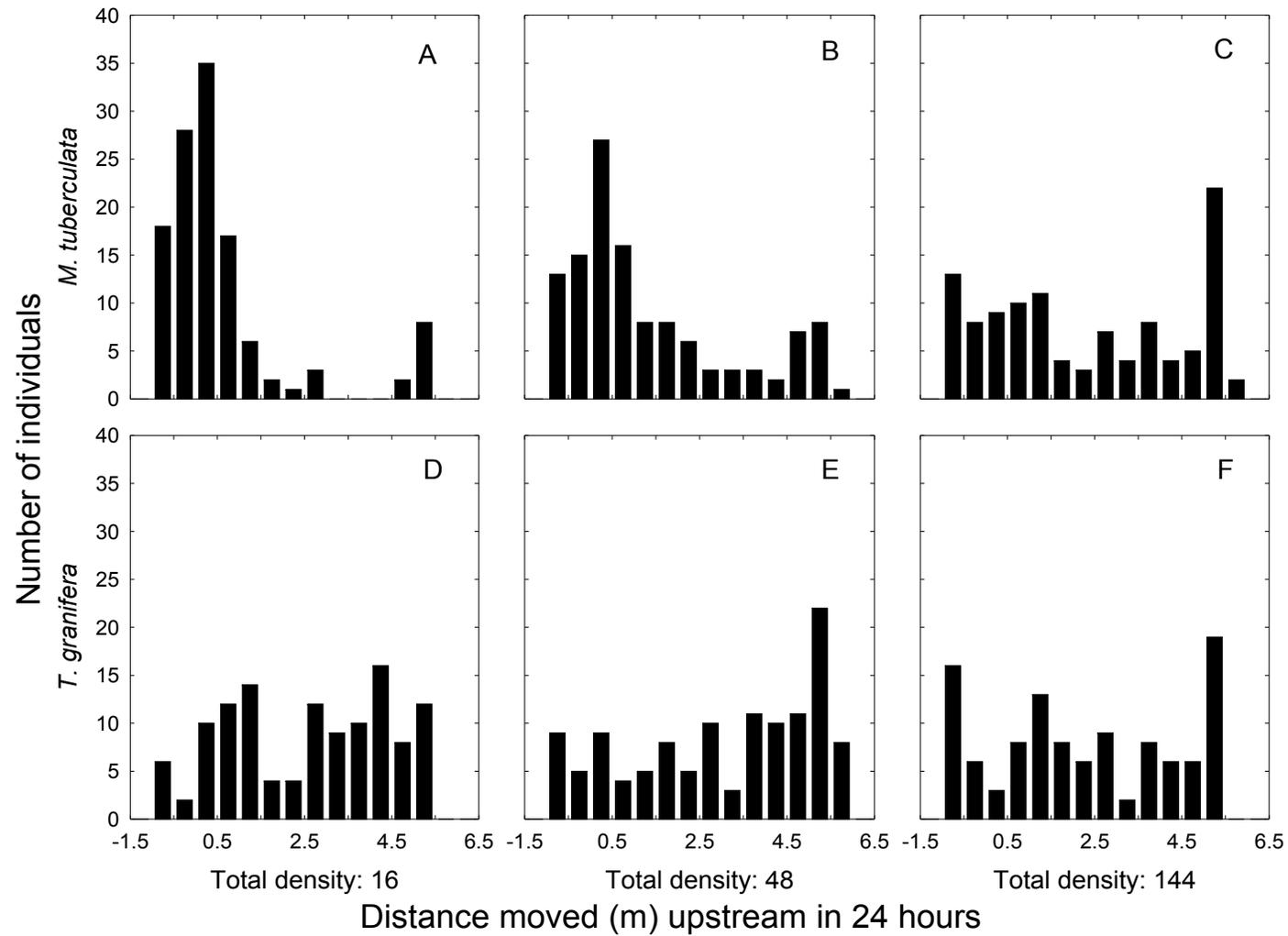


Figure 5. Movement distributions produced by snails at three levels of competitor density over 24 hours

## CHAPTER 3

### **Advective movement by two invasive snails: a comparison in homogeneous and heterogeneous environments**

## ABSTRACT

Habitat heterogeneity is an inherent characteristic of natural landscapes that affects many ecological processes, including movement, at multiple spatial scales. Habitat types, and the presence of boundaries separating different habitat types, may affect movement behaviors. Using a snail system that consists of two coexisting invasive species, in which advective movement plays an important role, I compared the effects of homogeneous and heterogeneous environments on movement behaviors. I also asked whether including habitat-specific movement behaviors improves advection-diffusion movement models and if such habitat-dependency can be averaged across a heterogeneous environment. I found an effect of habitat type on movement when comparing spatially uniform environments, and assessed alternative candidate models applicable to the spatially heterogeneous environment.

## INTRODUCTION

Classical ecological models often do not consider habitat heterogeneity even though it is an inherent characteristic of natural landscapes. Current ecological research is thus faced with the challenge of understanding the effects of heterogeneity on ecological processes, and finding appropriate methods for including these effects in ecologically relevant models. Movement rates are no exception to this pattern, as habitat-dependent movement rates have been documented in multiple systems (Lubina and Levin 1988, Grosholz 1996, Shigesada and Kawasaki 1997, Williamson and Harrison 2002).

Indeed, my own research (Chapters 1 and 2) documented behavioral responses to resource, population, and competitive heterogeneities. The effects of these heterogeneities were demonstrated by comparing movement behaviors for different treatments that remained homogeneous within a treatment. Once habitats become heterogeneous within a treatment, individuals are faced with multiple habitat types, and the boundaries that separate them. These boundaries also have the potential to affect animal movement patterns (Wiens et al. 1993, McIntyre and Wiens 1999a, b, Collinge and Palmer 2002). In a diffusion and/or random walk framework, researchers have proposed modifications in diffusive behavior at habitat edges (Cantrell and Cosner 1999). However, I know of no application of these ideas to a system in which advection plays a prominent role, as in the snail model system used in this dissertation. Thus, for this chapter I sought to demonstrate habitat-dependent movement rates and to understand how movement behaviors might change when faced with a mixture of

habitat types and their associated boundaries, especially in light of the strong advective component of movement in this system.

Objectives included (1) asking if snails exhibited different movement behaviors in different habitat types (using two treatments and homogeneous within a treatment), and if the two species varied in their response to the different habitat types; (2) modeling this response in an advection-diffusion framework to determine which component(s) of movement, advection and/or diffusion, is affected by habitat type; (3) asking how a heterogeneous environment, created by alternating both habitat types, with multiple habitat boundaries, affects movement behaviors for each species; and (4) using the model selection results for the single habitat types to determine if movement in alternating habitat types can be described by models that reflect the proportional change in habitat, or if there is an additional penalty for crossing boundaries and/or moving through multiple habitat patches. In the alternating patch habitat, I hold both patch shape and the number of edges per length of stream constant in order to assess the potential additive effects of habitat-dependent movement behaviors.

## MODEL

### *Classical advection-diffusion model*

I described advection-diffusion models and their use in predicting movement and population spread including (Skellam 1951, Andow et al. 1990, Liebhold et al. 1992, van den Bosch et al. 1992, Shigesada and Kawasaki 1997, Okubo and Levin 2001) in Chapters 1 and 2. The classic advection diffusion equation without a population growth function

$$\frac{\partial P}{\partial t} = D \left( \frac{\partial^2 P}{\partial x^2} \right) - \beta \frac{\partial P}{\partial x} \quad (1)$$

is described in Chapter 1. In the work leading to this chapter, I sought to understand how the two movement components of this modeling framework, advection and diffusion, are affected by differences in habitat type, and whether parameters estimated in each of two habitat types can be averaged to predict movement behaviors through an environment consisting of a mixture of the two habitat types.

*Initial model selection: habitat-specific advection and diffusion*

I asked whether possible differences in movement due to habitat type were manifested via the advection component, the diffusion component, neither, or both. In this way, I discerned which components of the advection-diffusion equation, if any, should be estimated on a per habitat basis in a parsimonious model. I also considered population heterogeneity, in terms of snail length, in the diffusion and advection components of movement, as a relationship with body size was found to be important in previous work (Chapter 1). I incorporated habitat type and snail length in the models in both the advection term,

$$\beta_i = Q \left( \beta^A_0 + \left( \beta^A_1 \times length_i \right) \right) + (1 - Q) \left( \beta^B_0 + \left( \beta^B_1 \times length_i \right) \right), \quad (2)$$

and the diffusion term,

$$D_i = Q \left( D^A_0 + \left( D^A_1 \times length_i \right) \right) + (1 - Q) \left( D^B_0 + \left( D^B_1 \times length_i \right) \right), \quad (3)$$

where  $i$  represents an individual, A represents habitat type A, B represents habitat type B, and  $Q$  is the proportion of Habitat A in the environment. For the initial set of models, I consider combinations of alternative advection and diffusion components for the cases  $Q=1$  and  $Q=0$  (pure A habitat and pure B habitat). Advection options include: (1) only size-dependent advection (heretofore referred to as “constant” with respect to the effects of habitat), and (2) size-dependent advection rates estimated as different values for each habitat (heretofore referred to as “habitat-dependent”) (Eq. 2). Diffusion options are the same options as described for advection (Eq. 3). Using these hypotheses for advection and diffusion, I can determine which parameters, if any, are habitat-dependent by conducting experiments and modeling results for the cases  $Q=1$  and  $Q=0$  (e.g., for a given snail size, does a common value of  $\beta$  suffice for both habitat types?). This set of candidate models is determined by all combinations of the two advection and two diffusion hypotheses, yielding a set of 4 *a priori* candidate models (e.g., Model 1: a common  $\beta$  and a common  $D$  suffices for both habitat types; Model 2: a common  $\beta$  suffices but not a common  $D$ , etc.).

*Second model selection: habitat-specific advection-diffusion through alternating patches*

To examine the case of alternating habitat types (experimentally, setting  $Q=0.5$ ), I postulated extensions that could be applied to the model selected as best in the first modeling exercise. The initial selection resulted in a model with habitat-specific  $\beta$ , but a common  $D$  across habitat types (presented in results), hence I considered a set of further models in which habitat-dependent  $\beta$ s are additive in the heterogeneous landscape in a way that is (Model 2-1) proportional to the amount of each habitat (here,  $Q=0.5$ ); (Model 2-2) acceptably modeled as

a linear weighting of the two habitat types, but as an “effective proportion”:  $Q_e \neq Q$ , rather than  $Q$  itself; (Model 2-3) proportional to the amount of habitat ( $Q$ ), but with a penalty based on edge density  $E$  (units: edges per distance, where an edge occurs at a change between habitat type) and an estimated parameter  $\beta_E$  (units: time per edge) depicting a time cost of encountering edges; or (Model 2-4) proportional to the amount of habitat ( $Q$ ) and requiring a penalty based on edge density  $E$  and penalty  $\beta_E$  that is size-dependent (i.e., small snails treat edges differently from larger snails).

I incorporated habitat type and snail length in the models in both the advection term and/or the diffusion term (results in the same specification for  $D$  as shown below for  $\beta$ ),

$$\beta_i = \left( Q(\beta^A_0 + (\beta^A_1 \times length_i)) + (1 - Q)(\beta^B_0 + (\beta^B_1 \times length_i)) \right) - \left( \frac{1}{\beta_E * E} \right), \quad (4)$$

where  $i$  represents an individual, and  $A$  and  $B$  represent two different habitat types. In Model 2-1, the final term is absent. In Model 2-2, the final term is absent plus  $Q$  is replaced by  $Q_e$ , the “effective proportion”. In Model 2-3, the equation is written as above. In Model 2-4,  $\beta_E$  as an estimated parameter is replaced by  $\beta_E(\text{length}) = \beta_{0E} + \beta_{1E} * \text{length}$ , with  $\beta_{0E}$  and  $\beta_{1E}$  estimated in the model.

## METHODS

### *Examining habitat-specific movement behaviors: experimental stream study*

To examine habitat-dependent movement behaviors, I measured movement rates of both species in different types of substrates: sand versus rock. I conducted these experiments

in three of the movement streams in the experimental facility described in detail in Chapter 2. For these experiments I constructed substrates to create three treatments: a sand habitat, a rock habitat, and a combination habitat consisting of alternating sand and rock habitats. Twenty individually marked snails were placed in the center of the stream at 1.5 m in each of the treatments (at the boundary of a sand and rock habitat in the combination habitat). In the alternating habitat treatment, each portion of habitat was 0.5-m long, i.e.,  $E=2.0$  edges/m. The most downstream end of the experimental stream consisted of a 0.5 m sand habitat, followed by a 0.5 meter rock habitat, and so on.

Each snail was individually marked with different color combinations of nail polish, and length of each snail was measured prior to conducting the experiments. Each experiment was terminated when a snail reached the upstream limit of the mesocosm, resulting in 12-hr *T. granifera* trials and 24-hr *M. tuberculata* trials. *M. tuberculata* was used as the experimental species in one trial (n=20 snails), and *T. granifera* was used in two trials on consecutive days (n=40 snails per treatment).

### *Analysis*

To analyze these data, I examined movement distributions for each species in each habitat type. I calculated mean, variance, kurtosis, and skewness of the movement distributions to determine population level patterns for each species in each habitat type. I also considered the relationship between total distance moved (m) per time and body size for each habitat type.

## *Analysis of movement models*

I estimated diffusion and advection parameters for each of the models in the model set via maximum likelihood estimation using the Solver tool in Microsoft Excel. I used the general likelihood

$$L\{x | D, \beta, t\} = \left( \frac{P_0}{2\sqrt{\pi Dt}} \right) \exp\left( \frac{-(x - \beta t)^2}{4Dt} \right). \quad (6)$$

Eqn. 6 is the solution to the PDE shown in Eqn. 1 and predicts a normal distribution with mean  $\beta t$  and variance  $2Dt$ , where  $\beta$  and  $D$  are functions of length and possibly habitat type. To compare the 4 initial models of movement in single-habitat treatments, and to compare the 4 additional models for movement in the patchy habitat treatment, I used the resulting maximum likelihood estimates to calculate Akaike's Information Criterion (AIC) (Akaike 1973), specifically AICc for small sample size (Burnham and Anderson 2002). I also calculated Akaike weights and evidence ratios to assist in model selection.

## RESULTS

### *Empirical results*

Both species exhibited species-specific habitat-dependent movement behaviors. For *T. granifera*, movement rates were lower through the rock and combination habitats (Table 1, Fig. 1). In both of these habitats, movement distributions are platykurtic (rock: -0.81, SE=0.75, n=38, p=0.003; combination: -1.08, SE=0.73, n=40, p<0.001) but not skewed. In contrast, the movement distribution in the sand habitat produced a negatively skewed

distribution (-0.93, SE=0.38, n=38, p=0.001) (Table 1). For *M. tuberculata*, the mean distance moved was highest in the rock habitat (Table 1, Fig. 2). The movement distribution in the rock habitat was platykurtic (-1.95, SE=0.99, n=20, p=0.001), but showed no skewness (-0.25, SE=0.51, n=20, p=0.33). In contrast, the movement distributions for this species in the sand habitat and the combination habitat were both positively skewed (sand: 1.26, SE=0.52, n=19, p=0.008; combination: 1.76, SE=0.52, n=19, p<0.001), and in the combination habitat leptokurtic (1.71, SE=1.10, n=19, p<0.001) (Table 1).

The relationship between distance moved and body size for *T. granifera* also differs across the three habitat types (Fig. 3). There is a positive relationship between distance moved and body size in sand habitat (linear fit:  $R^2 = 0.22$ , slope>0, p=0.003), and a suggestion of a positive relationship between distance moved and body size in rock habitat, though not statistically significant at  $\alpha=0.05$  (linear fit:  $R^2 = 0.09$ , p=0.07). In contrast, there is no relationship between distance moved and body size in the alternating sand and rock habitat (linear fit:  $R^2 = 0.008$ , p=0.59). It appears that the presence of rock habitat, whether patchy or not, reduced and even eliminated the effects of body size on movement rates for *T. granifera*.

I also observed remarkable differences in the relationship between distance moved and body size for *M. tuberculata* across the three habitat types (Fig. 4). There is a positive relationship between distance moved and body size in the sand habitat (linear fit:  $R^2 = 0.30$ , slope>0, p=0.02), but no relationship between distance moved and body size in the rock habitat (linear fit:  $R^2 = 0.03$ , p=0.48). Though not statistically significant at  $\alpha=0.05$ , there is a suggestion of a positive relationship between distance moved and body size in the alternating

sand and rock habitat (linear fit:  $R^2 = 0.17$ ,  $p = 0.08$ ). It appears that the rock habitat promoted upstream movement by individuals of all sizes and there may even be a bimodal distribution of movement behaviors in this habitat type; none of my a priori models encompassed possible bimodality. In the alternating sand and rock habitat, it is important to note that most individuals were recorded in sand habitats, and most snails remained in one of the downstream sand habitats.

#### *Model selection results*

In the spatially uniform habitats, *T. granifera* demonstrated habitat-specific movement rates that were reflected in the advection component of the AIC best model (Model 1-3). This model received 43.53 times more support than the next best model, Model 1-1. Thus, in this case, I only accepted Model 1-3 as plausible (Burnham and Anderson 2002). *M. tuberculata* responded similarly to habitat and, consequently, the top ranked model for spatially uniform habitats is the same for this species. Model 1-3 is the top ranking model in the selection, but according to evidence ratios, this model had only 2.22 times more support than the next most likely model (Model 1-1) (Table 2). Given model selection uncertainty, I accepted these top two ranking models ( $\Delta AIC < 3$ ) as plausible (Burnham and Anderson 2002). The patterns observed in the empirical data offer additional support for a model that includes habitat-dependency, thus I chose to work with Model 1-3 as the best candidate model in subsequent analyses.

For the second model selection, I extended Model 1-3 to account for the spatially heterogeneous environment with respect to edge density and proportion of each habitat in the

alternating sand and rock environment (Table 3). For both species, Models 2-2, 2-3, and 2-4 were plausible models. Model 2-2 was the top ranked model for *T. granifera*, with 2.29 times more support than Model 2-3 and 2.87 times more support than Model 2-4. Model 2-3 was the top ranked model for *M. tuberculata*, with 2.38 and 2.87 times more support than Models 2-2 and 2-4, respectively. Obviously, arbitrating among this model set proved to be more difficult, though we gained valuable insights from the process. The only candidate model in the set that receives no support (for both species), is the model that assumes that advection rates for the two habitat types can be averaged according to the proportion of each habitat type (Model 2-1). In other words, snails are not simply adjusting their upstream movement rates to those estimated in the spatially uniform environments as they move through the alternating habitats.

## DISCUSSION

Habitat type induced behavioral responses in both study species (Figs. 1, 2, 3, and 4), and, in an advection-diffusion framework, this response was manifested via separate estimates for advection, and common estimates for diffusion, through each of the habitat types (Table 2). However, I also found that these habitat-dependent estimates for advection, given the two habitat types, are not simply additive in the heterogeneous landscape in a way that is proportional to the amount of each habitat in the landscape. Instead, there is some sort of change in the behaviors (of both species) in the heterogeneous landscape that could be attributable to behaviors that influence the amount of time spent in a particular patch and/or time spent at habitat boundaries. The second model set revealed that some penalty, either by determining and effective proportion of habitat or by including an index of edginess, is

necessary to more accurately describe movement across changing habitats, or at habitat edges. The index of edginess I assigned was a function of edge density ( $E$ ) and time per edge (estimated parameter  $\beta_E$ ), portraying a time cost of encountering edges. This index is expressed as “time removed” due to encountering an edge, but might actually include mean “time taken” at an edge, and/or changes in movement rates within a patch, while not at an edge.

The second set of models exploring the spatially heterogeneous environments, and the penalties I imposed in these models, were, for the most part, phenomenological. However, they motivate future studies on this type of edge index, specifically conducting simulations that explore the performance of the penalty at different levels of “edginess”, and investigating mechanistic models that address the behavior of individuals at the edge. Focusing on how ecological processes are affected by boundaries, sometimes called “edge-mediated effects”, provides insights into both basic and applied ecological questions (Fagan et al. 1999). Fagan and colleagues (1999) review empirical and theoretical studies addressing the effects of edges on species interactions and community dynamics, and the mechanisms underlying these effects. Indeed, our work in Chapter 2 indicated that competition changes the movement behaviors of one of our study species. Among others, hypotheses regarding the interaction between competitive effects and edge effects on movement behaviors emerge for this system.

One of the characteristics of boundaries that is usually considered important to movement behaviors is patch shape (Stamps et al. 1987, Wiens et al. 1993, Collinge and Palmer 2002). For example, ratio of patch edge to patch area has been shown to influence

movement rates across boundaries (Turchin 1998, Okubo and Levin 2001). Though I do not investigate shape of patch in the current analysis (our patches are of equal size and shape), nor do we explicitly examine other edge characteristics such as edge permeability (Stamps et al. 1987), these are interesting and important factors. Furthermore, though boundaries between habitats can be important characteristics in heterogeneous landscapes that affect animal movement behaviors (Wiens et al. 1993, McIntyre and Wiens 1999a, b), the result of these effects may have multiple, far-reaching consequences that affect the outcome of species interactions and other ecologically important processes (Fagan et al. 1999). These effects of boundaries and environmental heterogeneities are especially relevant in the context of habitat fragmentation and land use change (Haddad 1999a). Small-scale observations of individual snails at boundaries, and between boundaries, could elucidate the mechanisms of the differences I observed in this study, and inform further mechanistic modeling efforts.

At multiple spatial scales, habitat heterogeneity is often an important contributor to movement ecology. Habitat dependent movement rates were postulated for the re-expansion of sea otters along the coast of California. Expansion through rocky, sub-tidal kelp forest habitats occurred at constant speeds from 1938 to 1972. Between 1973 and 1984, upon reaching soft-bottom habitats, rate of spread increased. Researchers suggested that sea otters increased their rate of spread through these inferior habitats (Lubina and Levin 1988). Williamson and Harrison (2002) provide empirical evidence for habitat-dependent rates of spread. In their study, introduced species spread more rapidly into fertile oak woodlands than nutrient poor serpentine soil habitats. In this case, rates of spread increased through superior habitats. Grosholz (1996) found that the speed of invasion of European green crabs

(*Carcinus maenas*) differed for three different geographic regions, California, South Africa, and Canada. Additionally, their model, parameterized for the spread of green crabs in California, did not predict invasion rates at the other two sites. The experimental and modeling approach in the current study, although conducted at a small and experimentally feasible spatial scale, may be germane to obtaining a more general predictive framework of spread rates in contrasting and heterogeneous environments.

#### ACKNOWLEDGMENTS

I thank the Ramdeen family for access to Ramdeen Stream, Robin Sinnanan for plumbing assistance, and the Sinnanan family for space to construct the experimental facility. I thank the National Science Foundation (NSF/DEB 9208102, NSF/DEB 9509585, NSF/DEB 0108365, NSF/DEB 0108439) for support.

## LITERATURE CITED

- Akaike, H. 1973. Information theory as an extension of the maximum likelihood principle. Pages 267-281 *in* F. Csaki, editor. Second International Symposium on Information Theory. Akademiai Kiado, Budapest.
- Andow, D., P. Kareiva, S. Levin, and A. Okubo. 1990. Spread of invading organisms. *Landscape Ecology* **4**:177-188.
- Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach, 2nd edition. Springer-Verlag New York, Inc., New York.
- Cantrell, R. S., and C. Cosner. 1999. Diffusion models for population dynamics incorporating individual behavior at boundaries: Applications to refuge design. *Theoretical Population Biology* **55**:189-207.
- Collinge, S. K., and T. M. Palmer. 2002. The influences of patch shape and boundary contrast on insect response to fragmentation in California grasslands. *Landscape Ecology* **17**:647-656.
- Fagan, W. E., R. S. Cantrell, and C. Cosner. 1999. How habitat edges change species interactions. *American Naturalist* **153**:165-182.
- Grosholz, E. D. 1996. Contrasting rates of spread for introduced species in terrestrial and marine systems. *Ecology* **77**:1680-1686.
- Haddad, N. M. 1999. Corridor and distance effects on interpatch movements: a landscape experiment with butterflies. *Ecological Applications* **9**:612-622.

- Liebhold, A. M., J. A. Halverson, and G. A. Elmes. 1992. Gypsy moth invasion in North America: a quantitative analysis. *Journal of Biogeography* **19**:513-520.
- Lubina, J. A., and S. A. Levin. 1988. The spread of a reinvading species: range expansion in the California sea otter. *American Naturalist* **131**:526-543.
- McIntyre, N. E., and J. A. Wiens. 1999a. How does habitat patch size affect animal movement? An experiment with darkling beetles. *Ecology* **80**:2261-2270.
- McIntyre, N. E., and J. A. Wiens. 1999b. Interactions between habitat abundance and configuration: experimental validation of some predictions from percolation theory. *Oikos* **86**:129-137.
- Okubo, A., and S. A. Levin. 2001. *Diffusion and ecological problems: modern perspectives*, 2nd edition. Springer-Verlag New York, Inc., New York.
- Shigesada, N., and K. Kawasaki. 1997. *Biological invasions: theory and practice*. Oxford University Press, Oxford.
- Skellam, J. G. 1951. Random dispersal in theoretical populations. *Biometrika* **38**:196-218.
- Stamps, J. A., M. Buechner, and V. V. Krishnan. 1987. The Effects of Edge Permeability and Habitat Geometry on Emigration from Patches of Habitat. *American Naturalist* **129**:533-552.
- Turchin, P. 1998. *Quantitative analysis of movement: measuring and modeling population redistribution in animals and plants*. Sinauer Associates, Inc., Sunderland.
- van den Bosch, F., R. Hengeveld, and J. A. J. Metz. 1992. Analysing the velocity of animal range expansion. *Journal of Biogeography* **19**:135-150.
- Wiens, J. A., N. C. Stenseth, B. Vanhorne, and R. A. Ims. 1993. *Ecological Mechanisms and Landscape Ecology*. *Oikos* **66**:369-380.

Williamson, J., and S. Harrison. 2002. Biotic and abiotic limits to the spread of exotic revegetation species. *Ecological Applications* **12**:40-51.

Table 1. Estimates of skewness and kurtosis (with standard error and sample size [n] reported in parentheses), mean, and variance of the movement distributions produced by each species in each habitat type.

Species	Treatment	Skewness (1 SE, <i>n</i> )	Kurtosis (1 SE, <i>n</i> )	Mean±SD	Variance
<i>T. granifera</i>					
	Sand	-0.93 (0.38, 38)*	-0.19 (0.75, 38)	2.84±1.77	3.12
	Rock	0.47 (0.38, 38)	-0.81 (0.75, 38)*	1.56±1.70	2.9
	Combination	0.45 (0.37, 40)	-1.08 (0.73, 40)*	1.27±1.96	3.83
<i>M. tuberculata</i>					
	Sand	1.26 (0.52, 19)*	0.24 (1.01, 19)	0.005±2.05	4.2
	Rock	-0.25 (0.51, 20)	-1.95 (0.99, 20)*	1.92±2.55	6.51
	Combination	1.76 (0.52, 19)*	1.71 (1.01, 19)*	-0.06±2.06	4.23

Notes: The (\*) next to kurtosis and skewness values indicates significance ( $p < 0.05$ ).

Table 2. Top ranking candidate models for the first model selection investigating the effects of habitat type movement in an advection-diffusion framework. Habitat-dependent advection is consistent across the top ranked models for both species, i.e., models included advection estimates for both sand and rock habitats.

Model no.	Model Description		log(L)	K	AICc	$\Delta_i$ AICc	$w_i$	Evidence ratio	Rank
	Advection	Diffusion							
<i>T. granifera</i>									
<b>1-3</b>	<b>habitat-dependent</b>	<b>constant</b>	<b>-143.10</b>	<b>6</b>	<b>299.43</b>	<b>0.00</b>	<b>0.975</b>	<b>1.00</b>	<b>1</b>
1-1	constant	constant	-149.21	4	306.97	7.55	0.022	43.53	2
1-2	constant	habitat-dependent	-149.06	6	311.33666	11.909473	0.0025275	385.57539	3
1-4	habitat-dependent	habitat-dependent	-148.12	8	314.39	14.96	0.001	1773.22	4
<i>M. tuberculata</i>									
<b>1-3</b>	<b>habitat-dependent</b>	<b>constant</b>	<b>-85.94</b>	<b>6</b>	<b>185.10</b>	<b>0.00</b>	<b>0.559</b>	<b>1.00</b>	<b>1</b>
<b>1-1</b>	<b>constant</b>	<b>constant</b>	<b>-89.07</b>	<b>4</b>	<b>186.69</b>	<b>1.60</b>	<b>0.252</b>	<b>2.22</b>	<b>2</b>
1-4	habitat-dependent	habitat-dependent	-84.87	8	187.90	2.80	0.138	4.05	3
1-2	constant	habitat-dependent	-88.34	6	189.89	4.79	0.051	10.97	4

Notes: log(L) is the log likelihood estimate, K is the number of parameters, and AIC<sub>c</sub> is the corrected Akaike’s Information Criterion;  $\Delta$ AIC<sub>c</sub> is the difference in between the lowest AIC<sub>c</sub> score and the AIC<sub>c</sub> score of each model (model i); the Akaike’s weight ( $w_i$ ) is the weight of evidence in favor of model i; the evidence ratio is the amount of times more likely the top selected model is relative to model i (e.g., for *M. tuberculata*, model 3 is 2.22 times more likely than model 1).

Table 3. Top ranking candidate models for the second model selection examining habitat-dependent advection and diffusion through alternating patches.

Model no.	Model Description				log(L)	K	AICc	$\Delta_i$ AICc	$w_i$	Evidence ratio	Rank
	Advection	Diffusion	Proportion habitat	Edge density							
<i>T. granifera</i>											
2-2	habitat-dependent	constant	Yes (estimate)	No	-84.45	1	170.96	0.00	0.559	1.00	1
2-3	habitat-dependent	constant	Yes (=0.5)	Yes	-85.28	1	172.62	1.66	0.244	2.29	2
2-4	habitat-dependent	constant	Yes (=0.5)	Yes (size-dependent)	-84.45	2	173.07	2.11	0.19	2.87	3
2-1	habitat-dependent	constant	Yes (=0.5)	No	-91.14	0	182.27	11.31	0.002	286.17	4
<i>M. tuberculata</i>											
2-3	habitat-dependent	constant	Yes (=0.5)	Yes	-39.63	1	81.31	0.00	0.531	1.00	1
2-2	habitat-dependent	constant	Yes (estimate)	No	-40.50	1	83.04	1.74	0.223	2.38	2
2-4	habitat-dependent	constant	Yes (=0.5)	Yes (size-dependent)	-39.63	2	83.42	2.11	0.185	2.87	3
2-1	habitat-dependent	constant	Yes (=0.5)	No	-42.83	0	85.66	4.35	0.060	8.81	4

Notes: log(L) is the log likelihood estimate, K is the number of parameters, and AIC<sub>c</sub> is the corrected Akaike’s Information Criterion;  $\Delta$ AIC<sub>c</sub> is the difference in between the lowest AIC<sub>c</sub> score and the AIC<sub>c</sub> score of each model (model i); the Akaike’s weight ( $w_i$ ) is the weight of evidence in favor of model i; the evidence ratio is the amount of times more likely the top selected model is relative to model i (e.g., for *M. tuberculata*, model 3 is 2.38 times more likely than model 2).

## FIGURE LEGENDS

Figure 1. *T. granifera* exhibited habitat-dependent movement behaviors. Movement rates were highest through the sand habitat, and the distribution was negatively skewed. Both the rock and the combination habitats were platykurtic, but not skewed.

Figure 2. *M. tuberculata* exhibited habitat-dependent movement behaviors. Mean distance moved over time was highest in the rock habitat, and the distribution was platykurtic. In contrast, the movement distributions for this species in the sand habitat and the combination habitat were both positively skewed. The distribution in the combination habitat was leptokurtic.

Figure 3. Differences in slope of the relationship between distance moved and body size for *T. granifera* in homogeneous and heterogeneous environments. (A) There is a positive relationship between distance moved and body size in sand habitat (slope of linear fit:  $R^2 = 0.22$ ,  $p = 0.003$ ). (B) Though not statistically significant, there is a slight positive relationship between distance moved and body size in rock habitat (grey background indicates rock habitat) (slope of linear fit:  $R^2 = 0.09$ ,  $p = 0.07$ ). (C) There is no relationship between distance moved and body size in the alternating sand and rock habitat (slope of linear fit:  $R^2 = 0.008$ ,  $p = 0.59$ ).

Figure 4. Differences in slope of the relationship between distance moved and body size for *M. tuberculata* in homogeneous and heterogeneous environments. (A) There is a positive relationship between distance moved and body size in sand habitat (slope of linear fit:  $R^2$

=0.30,  $p=0.02$ ). (B) There is no relationship between distance moved and body size in rock habitat (grey background indicates rock habitat) (slope of linear fit:  $R^2=0.03$ ,  $p=0.48$ ). (C) Though not statistically significant, there is a slight positive relationship between distance moved and body size in the alternating sand and rock habitat (slope of linear fit:  $R^2=0.17$ ,  $p=0.08$ ). Notably, most individuals were recorded in sand habitats.

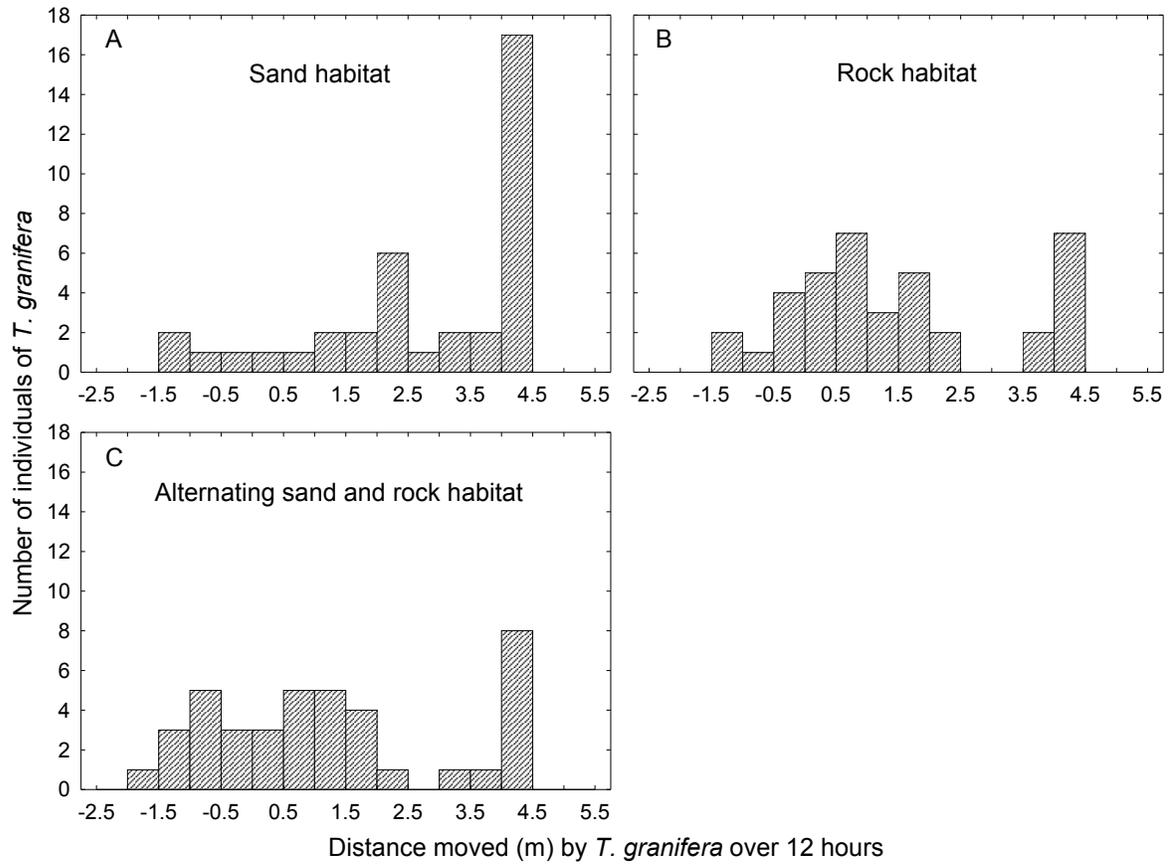


Figure 1. *T. granifera* exhibited species-specific habitat-dependent movement behaviors

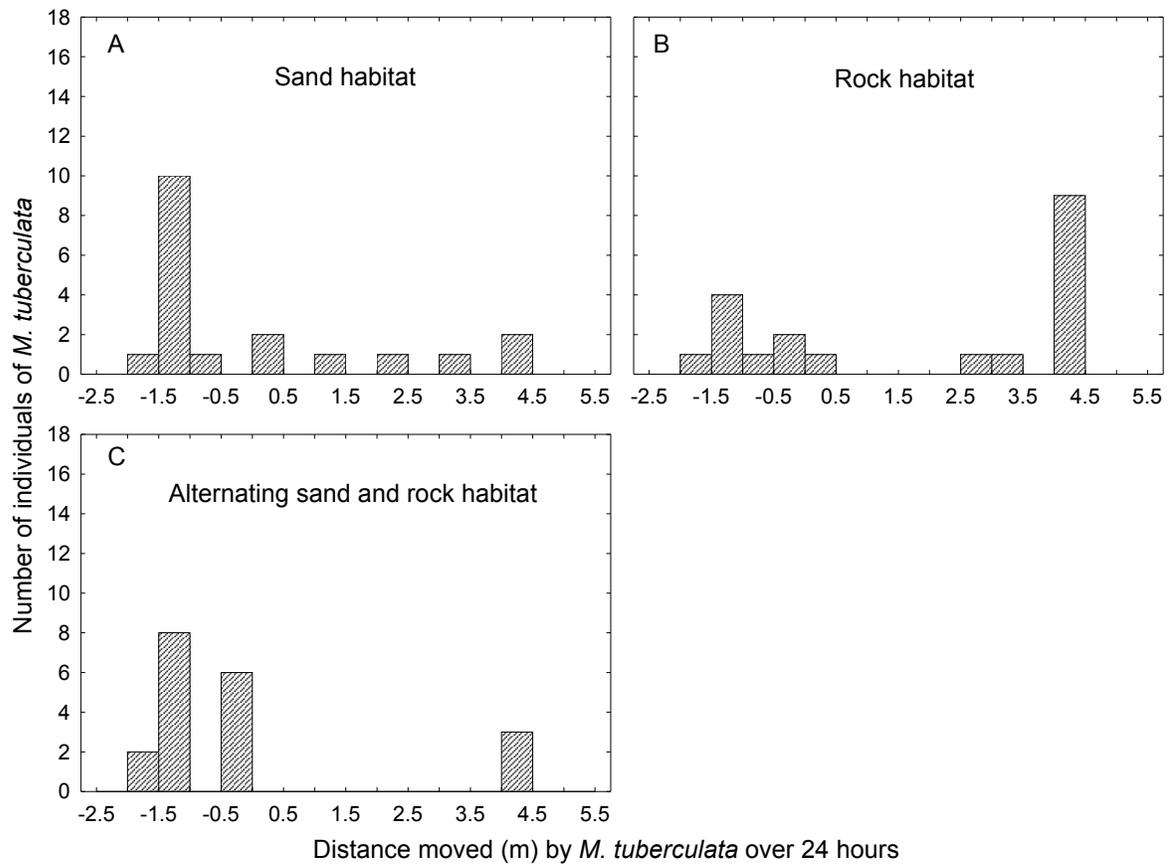


Figure 2. *M. tuberculata* exhibited species-specific habitat-dependent movement behaviors

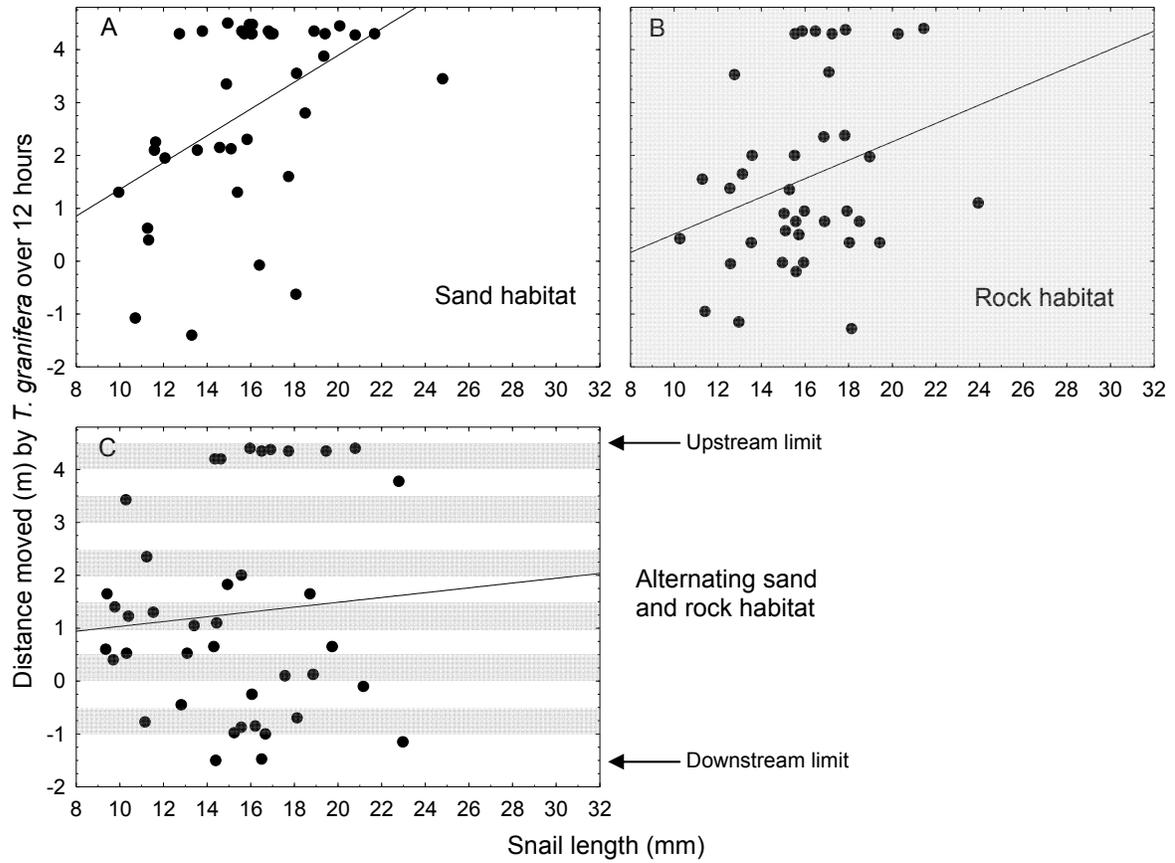


Figure 3. The relationship between distance moved and body size for *T. granifera* in homogeneous and heterogeneous environments

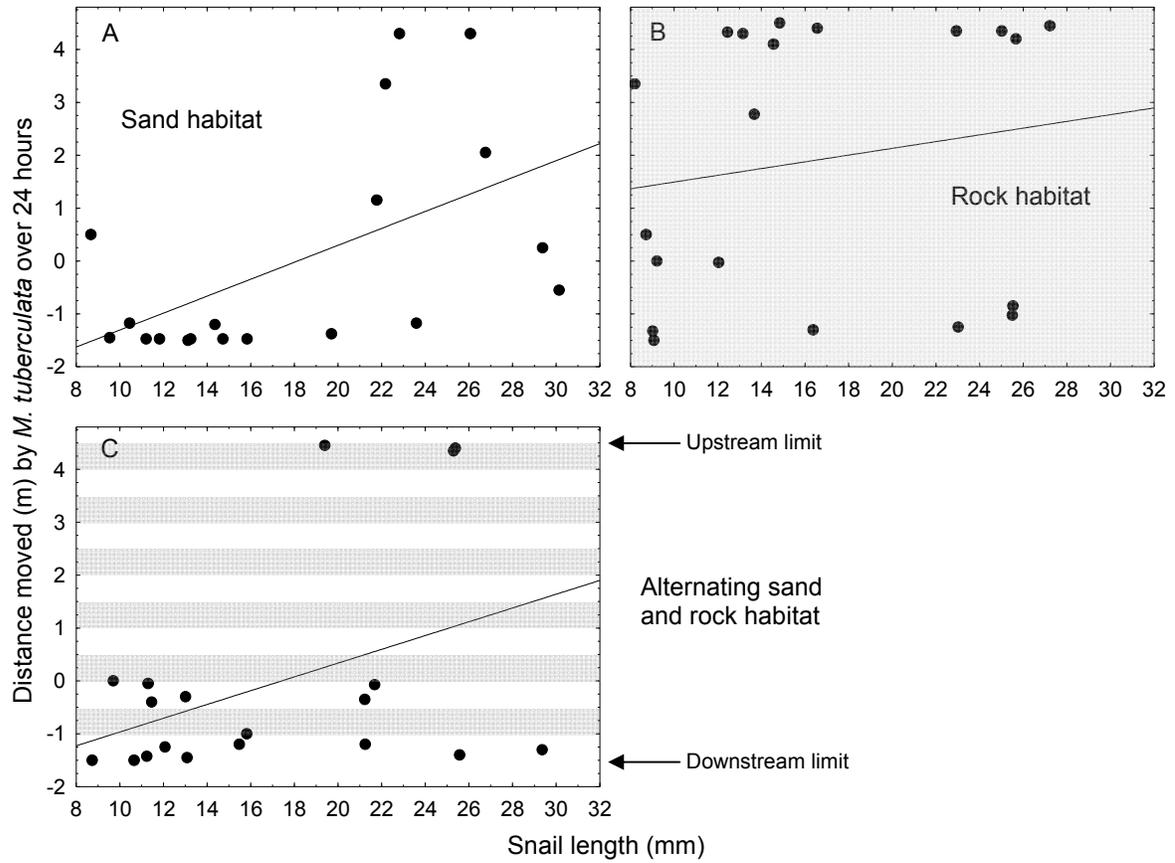


Figure 4. The relationship between distance moved and body size for *M. tuberculata* in homogeneous and heterogeneous environments

## CHAPTER 4

### **Comparative ecology of the two coexisting species: field observations and experiments**

## ABSTRACT

The coexistence of two invasive species provides an excellent background in which to explore characteristics of a multiple species invasion, such as habitat use, resource use, competitive interactions, and movement behaviors that ultimately impact large scale ecological patterns such as population spread and biodiversity. I compared the in-stream movement behaviors and habitat use of two exotic species in Trinidad streams. I found that the two species of invaders have different rates of upstream movement and different local scale distributions within the stream (use of the edge of the stream versus the entire extent of the stream, and in sunny and shady reaches). In light of these habitat differences, I also compared growth of the two species on algal- and detritus-based resources finding that *M. tuberculata* outperforms *T. granifera* on detritus-based resources. These results suggest a biological basis for coexistence and spatially changing relative abundance, processes that are influenced by land use and other anthropogenic changes.

## INTRODUCTION

The spread of invasive species, though one of the most significant threats to biodiversity (Orians and Soule 2001), also provides newly organized systems that act as “natural experiments” (Sakai et al. 2001). Consequently, studying the characteristics of biological invasions contributes to our understanding of basic ecological processes, such as species interactions and community structure, and socially important ecological phenomena, such as the impacts of exotic species, biological control practices, and other related anthropogenic changes (Sax et al. 2005). Studies on the dynamics of exotic species will lead to a better understanding of our past, current, and future ecological communities (Soule 1990).

The presence of two invasive gastropods, *Melanoides tuberculata* and *Tarebia granifera*, throughout streams in Trinidad, West Indies provides a valuable field system in which to examine some characteristics of a multiple invader system. The local spatial distribution of these two invaders raises questions about coexistence and how competitive interactions and dispersal characteristics might be functioning to create observed patterns. Where both species coexist, I observed that *M. tuberculata* is usually found along the edges of the stream, but *T. granifera* utilizes the entire width of the stream (Snider, unpublished data). A similar spatial pattern was found for these two species in other systems (Pointier et al. 1994, Samadi et al. 1997). However, when occurring alone, *T. granifera* was predominantly found in edge habitats (Samadi et al. 1997). At this local scale, these patterns suggest a host of potential mechanisms including, but not limited to, competitive interaction

between the two species, niche differentiation due local habitats that differ in substrates and/or the amount of primary production versus detritus, and differences in movement behaviors.

Factors influencing the distribution and abundance of freshwater snails may include food availability, water velocity (Crowl and Schell 1990, Laamrani et al. 1997), the presence or absence of predators, water chemistry, competition, and other biotic and abiotic factors (Lodge et al. 1987). Moreover, the existence of small-scale spatial structure, such as that caused by biological interactions, may significantly impact population dynamics (Pacala and Levin 1997). To begin studying the factors influencing the spatial pattern and dynamics of invading species, we must first document the nature of the spatial distribution of an invading population. To address some of these potential mechanisms of distribution and coexistence, I compared movement patterns and habitat use of two invasive species in Trinidad streams by comparing (1) the in-stream movement behaviors, (2) local distribution/abundance patterns of both species in different habitat types; and (3) the growth rates of each species in different habitat types. Finally, I discuss the significance of these findings in light of invasion biology, and use these results to motivate future experimental work addressing movement behaviors and competitive interactions.

## METHODS

### *Biology of the two study species*

*Tarebia granifera* and *M. tuberculata* are viviparous prosobranch (gill) snails (Mollusca: Gastropoda: Thiaridae). *T. granifera* is parthenogenetic (Brown 1991), while *M.*

*tuberculata* is reported to be both parthenogenetic (Myers et al. 2000) and sexually reproducing (Livshits and Fishelson 1983). Both species brood young snails in a pouch located posterior to their head (Brown 1991). Also, research on the biology of *M. tuberculata* suggests that females of this species may be able to control the release of hatchlings until conditions exist that are favorable to their survival (Dudgeon 1986).

The morphology of *T. granifera* shells includes axial and spiral sculptures, flattened whorls near the tip of the spire, and rows of nodules on their shells. Typically, the length of the aperture is greater than half the entire length of the shell. *Melanooides tuberculata* has a relatively elongated shell shape with rounded body whorls, spiral grooves, and axial ribs (Pointier et al. 1998). An extensive range of polymorphism is exhibited by this species resulting in the classification of morphs based on shell type (Pointier 1989).

Parthenogenicity may contribute to the rapid colonization of new habitats by both species as an entire population can arise from one female individual. The extensive geographic range of these gastropods may be a function of this property (Dudgeon 1986), and thus compensate for missed advantages of genetic recombination (Smith 1978). However, the idea of local adaptations via “ecophenotypic modification” (Fryer et al. 1983) has been suggested as another contributor to *M. tuberculata*’s successful invasions (Dudgeon 1986). Also, *M. tuberculata* colonizes and survives within numerous habitat types, and populations have been found even in roadside ditches (Myers et al. 2000). Anecdotally, I have noted that at least one, and usually both, of the species appears to occur in all major drainages in Trinidad, West Indies.

*Exploring in-stream movement behaviors and local spatial distributions*

Chapters 1 and 2 both documented a strong advective component to *T. granifera* movement, and a less pronounced upstream tendency in *M. tuberculata*. To assess movement rates and population level movement patterns of each species in nature, I conducted a mark recapture study in Ramdeen Stream. I collected all snails (both species) throughout a 15 meter stretch of stream. Snails were collected by first scanning the area for visible individuals, then looking under rocks, and, finally, scraping the substrate with a dip net until achieving three empty scrapes in a row. Snails were bagged at their locations, and marked flags were left at the location so that snails could be returned to their exact longitudinal location after processing. I also recorded whether snails were found at the edge (operationally, 30 cm from the stream bank) or in the middle of the stream (the remainder of the streambed). I measured the snails with calipers, and individually marked snails with different combinations of fingernail polish dots. Individually marked snails were returned to within 0.05 meters of where they were found, and placed into the substrate to avoid being washed downstream. I collected and marked 79 *M. tuberculata* and 464 *T. granifera*.

Recapture events occurred at 4 and 7 days. On each of these days I searched for marked snails using the same technique described above for collecting snails within the study reach. I also searched downstream and upstream at least 15 meters from where any marked snails were recaptured to avoid distance-biased sampling (Albanese et al. 2003). I recorded longitudinal location in the stream, and if the snail was found utilizing edge habitat, or was found throughout the middle of the stream. I recaptured 33 *M. tuberculata* (42% recapture

rate) and 249 *T. granifera* (54% recapture rate) after four days, and 25 *M. tuberculata* (32% recapture rate) and 221 *T. granifera* (48% recapture rate) after 7 days.

To analyze these data, I examined histograms of distanced moved for each time step. I calculated mean, variance, kurtosis and skewness of the movement distributions to document population level patterns. I also compared mean distance moved upstream by the two species using a general linear model with initial body length as a covariate. I used STATISTICA 6.0 for all statistical analyses. I also calculated the percent of each species that was found in edge habitat.

I also assessed how the presence or absence of a natural riparian canopy affects snail distribution patterns. First I measured the density of *T. granifera* in shaded areas with an intact riparian canopy in Ramdeen Stream relative to that of a sunny area of the stream in which the riparian canopy was removed. Density was estimated by counting and measuring all snails found within six 6-inch wide transects across the streambed (perpendicular to stream flow) in each habitat. Using a length-weight regression (Snider, unpublished data), I calculated density for each type of habitat in mass/m<sup>2</sup>. I then used a 2X2 ANOVA to compare mean density of snails in sunny habitats with mean density of snails in shaded habitats for each species, with contrast of means of interest with a Scheffe test.

#### *Comparing growth rates on different resources: a common garden experiment*

The local spatial distribution of snail species in Trinidad streams (edge versus center, sunny versus shady), suggests possible underlying differences in the role of primary production versus detritus-based resources for these species. Specifically, I hypothesized

that there would be an interaction between resource type and species, in a competitive environment.

To assess growth rates on the different types of resources, I conducted a replicated common garden experiment using experimental mesocosms. The treatments were (1) a bright, algae based treatment, and (2) a dark, detritus based treatment. The mesocosms had a diameter of 60 cm, were filled with local stream water and substrates, and were positioned next to the natural stream to mimic the natural environment as closely as possible. Algal based treatments were stocked with rocks and one cacao leaf (*Theobroma cacao*) gathered from a sunny portion of stream. These treatments were open to natural light levels. Detritus based treatments were stocked with river rocks and one cacao leaf gathered from a heavily shaded portion of the stream. These treatments were completely covered (sides taped) with black plastic to eliminate primary production. I created four replicates of each treatment, and stocked each replicate with five individuals of each species, yielding a total of ten snails per replicate container. Before starting the experiment I measured total length of each snail and individually marked snails (as described above). I categorized snails as small, medium and large, and sorted snails of each size class into each replicate to assure similar size distributions within each replicate. After 14 days, I removed the snails and again measured total length of each individual.

I calculated instantaneous rate of change in length over the 14 day period for each individual. I then tested for differences in growth rates for each species at each treatment using split-plot design with a Scheffe test for contrasting means of interest (STATISTICA 6.0).

## RESULTS

### *Exploring in-stream movement behaviors and local spatial distributions*

Mark-recapture data indicated that *T. granifera* (mean=3.69, SD=2.28, n=220) had a stronger upstream bias than *M. tuberculata* (mean=1.13, SD=1.75, n=23) using a two-sample t-test for unequal variances ( $t(30)=6.46$ ,  $p<0.001$ ), consistent with patterns observed in the experimental facility in Chapter 2 at low density of competitors (Fig. 1). For both species, the movement distributions were neither leptokurtic nor platykurtic (*T. granifera*: 0.17, SE=0.33, n=220; *M. tuberculata*: -1.05, SE=0.93, n=23), and were not skewed (*T. granifera*: 0.25, SE=0.16, n=220; *M. tuberculata*: 0.52, SE=0.43, n=23). The local spatial distribution observed in this study was consistent with previous documentation except perhaps for a substantial presence of *T. granifera* in edge habitats: for the original capture event, 67% of *M. tuberculata* were found at the edge of the stream (57 of 85) more than the 34 individuals that would be expected if the distribution were random, given that 40% of the habitat was classified as edge habitat ( $\chi^2$  (df=1, N=85) = 15.56,  $p<0.005$ ), while 49% of *T. granifera* (227 of 464) were found in the edge habitat, more than the 186 individuals that would be expected if the distribution were random ( $\chi^2$  (df=1, N=464) = 9.23,  $p<0.005$ ). We found a consistent result when we recaptured snails after 7 days: 100% of *M. tuberculata* were found at the edge of the stream (25 of 25), while 37% of *T. granifera* (81 of 221) were found in the edge habitat, more than the 63 individuals that would be expected if the distribution were random, given that 29% of the habitat was classified as edge habitat ( $\chi^2$  (df=1, N=221) = 5.05,  $p<0.025$ ).

I also observed that densities (in mass/m<sup>2</sup>) of both species of invasive snails were higher in open canopy areas of the stream relative to stream reaches with a well-developed riparian canopy (Fig. 2). The 2x2 factorial ANOVA revealed a main effect of habitat ( $F_{1,20}=14.28$ ,  $p<0.001$ ), a main effect of species ( $F_{1,20}=9.37$ ,  $p=0.006$ ), and an interaction ( $F_{1,20}=6.11$ ,  $p=0.02$ ). Density of *T. granifera* is significantly higher (Scheffe test, error df=20,  $p=0.003$ ) in sunny locations where riparian canopy has been removed than in shaded areas where the riparian canopy is intact. In contrast, there was no significant difference between the density of *M. tuberculata* in sunny versus shady areas of the stream ( $p=0.84$ ) (Fig. 2). In shaded areas of the stream, densities of the two species do not differ ( $p=0.98$ ); however, in sunny areas of the stream where riparian canopy has been removed, the density of *T. granifera* far exceeds that of *M. tuberculata* ( $p=0.001$ ) (Fig. 2).

#### *Comparing growth rates on different resources: common garden experiments*

The split-plot revealed an interaction ( $F_{1,70}=8.43$ ,  $p=0.005$ ) between resource type and species. Instantaneous growth rates of *T. granifera* and *M. tuberculata* did not differ in bright, algae-dominated experimental treatments (Scheffe test, error df=70,  $p=0.70$ ), but *M. tuberculata* outperformed *T. granifera* in dark, detritus-based experimental treatments ( $p=0.04$ ) (Fig. 2). Also, *T. granifera* showed higher growth rates consuming an algal based resource relative to consuming detritus based resources ( $p=0.002$ ). In contrast, the performance of *M. tuberculata* did not differ across resource types ( $p=0.99$ ). Notably, *M. tuberculata* had higher growth rates on algae than *T. granifera* had on detritus, though not significant at the  $\alpha=0.05$  level ( $p=0.05$ ).

## DISCUSSION

In this system, there appear to be interactions between the snail species via movement behaviors, habitat use, and resource use. The two species of invaders have different rates of upstream movement, possibly leading to different rates of spread into new environments or more locally, into different habitat patches. These patterns are consistent with experimental movement data (Chapter 2) where *T. granifera* showed a higher upstream bias than *M. tuberculata* at low levels of competition. In addition to different movement rates, these species are distributed differently in the stream, with *M. tuberculata* occurring mainly along edges of the stream and *T. granifera* occurring throughout the stream bed, and *T. granifera* showing an increase in density in sunny reaches of the stream in which dense riparian canopy has been removed due to human activity. *M. tuberculata* shows no such response.

I also found differences in the role of primary production versus detritus-based resources for these species in a competitive environment. These differences might account for some of the difference in spatial distribution in these streams, since edge areas tend to be more shaded than middle areas due to streamside, sometimes overhanging, vegetation. Also, on a larger and more dynamic scale, the contrasts in resource use, use of space, and a consistent upstream bias in *T. granifera* movement appear to contribute to a further contrast between the two species. Anecdotally, I observed a major flooding event that changed the distribution and abundance of the two invasive species in multiple streams. After the spate, the faster moving, more abundant species found throughout the streambed, *T. granifera*, was largely disappeared from the streambed, apparently washed downstream. However, *M. tuberculata*, the slower moving, edge-dwelling species remained. With time, *T. granifera*

populations returned to their original extent. This observation suggests, along with the empirical data on resource type, that the local distribution may be structured by an interaction between several biotic and abiotic factors including resource type, competition, habitat structure, movement behaviors, and disturbance regime. Lodge (1987) presents a similar finding for freshwater snails in which spatial distribution is structured by food preference and disturbance. Examining the potential trade-offs that promote coexistence or exclusion in a multiple invader system, such as this one, is an obvious next step.

Factors contributing to snail spatial distributions within streams may also impact their movement into new environments, providing insights into invasion dynamics. This type of information may be important to conservation biologists and managers that wish to control, prevent, or predict invasion by these or similar species into uncolonized streams.

Anthropogenic impacts are changing existing landscapes worldwide in many ways, and habitat change and invasive species are currently considered major threats to biodiversity (Orians and Soule 2001). As landscapes and habitat are altered, the characteristics that lead to invasive success, and the characteristics themselves, may be impacted as well (With 2002). This dissertation has revealed several such properties: the movement patterns of both species depend on resource level and/or competitive environment, one species thrives in areas with canopy removal while the other shows no response (at least in the competitive environment), and, anecdotally, the species appear to differ in how hydrological disturbance impacts their distribution, abundance, and recolonization dynamics. It would be interesting to investigate the potential conservation implications for these results, and to understand how this landscape and/or hydrological change affects the population spread and impacts of these

species.

*A note on the spread and impacts of these species on native ecosystems*

Despite circumglobal invasion by both study species in tropical and sometimes other areas (Abbott 1973, Dundee and Paine 1977, Pointier and McCullough 1989, Pointier et al. 1992, Appleton and Nadasan 2002, Duggan 2002), the potential for carrying disease causing parasites that affect humans (Dundee and Paine 1977) and animals (Mitchell et al. 2000), and the possible alteration of native environments, remarkably, the impact of *M. tuberculata* and *T. granifera* invasions on native organisms, communities, and ecosystems has not been thoroughly explored. In the United States, *M. tuberculata* occurs in Florida, Texas, and Louisiana (Dundee and Paine 1977). An intermediate host for a heterophyid trematode, *M. tuberculata* is currently implicated in contributing to the transmission of this parasite to fish and birds, including an endangered freshwater fish, in Texas (Mitchell et al. 2000). Invading *M. tuberculata* populations were reported in competition for resources with Florida native *Neritina virginea* (Roessler et al. 1977). Also, impacts on native gastropod populations by *T. granifera* populations were noted in Cuba (Jacobson 1975) and Honduras (Clarke 1987). Further research on the environmental and ecological consequences of these two invaders is needed for possible control and management actions as they continue to spread into tropical and temperate rivers across the world.

## ACKNOWLEDGMENTS

I thank Brett Albanese and Jose Rodriguez for help in the field, and the Ramdeen family for access to Ramdeen Stream. I thank the National Science Foundation (NSF/DEB 9208102, NSF/DEB 9509585, NSF/DEB 0108365, NSF/DEB 0108439) for support.

## LITERATURE CITED

- Abbott, R. T. 1973. Spread of *Melanoides tuberculata*. The Nautilus Monograph Review **87**:29.
- Albanese, B., P. L. Angermeier, and C. Gowan. 2003. Designing Mark-recapture studies to reduce effects of distance weighting on movement distance distributions of stream fishes. Transactions of the American Fisheries Society **132**:925-939.
- Appleton, C. C., and D. S. Nadasan. 2002. First report of *Tarebia granifera* (Lamarck, 1816) (Gastropoda : Thiaridae) from Africa. Journal of Molluscan Studies **68**:399-401.
- Brown, K. M. 1991. Mollusca: Gastropoda. Pages 285-314 in Ecology and Classification of North American Freshwater Invertebrates. Academic Press, Inc.
- Clarke, A. H. 1987. Apparent competitive exclusion of *Biophalaria havanensis* and *Pachychilus largillierti* by *Melanoides tuberculata* in a large Hondurian lake. Pages 24 in First International Congress on Medical and Applied Malacology. International Society for Medical and Applied Radiology Publishers, Monterrey.
- Crowl, T. A., and G. D. Schell. 1990. Factors determining population-density and size distribution of a fresh-water snail in streams - effects of spatial scale. Oikos **59**:359-367.
- Dudgeon, D. 1986. The life-cycle, population dynamics and productivity of *Melanoides tuberculata* (Muller, 1774) (Gastropoda, Prosobranchia, Thiaridae) in Hong Kong. Journal of Zoology London **208**:37-53.

- Duggan, I. C. 2002. First record of a wild population of the tropical snail *Melanooides tuberculata* in New Zealand natural waters. *New Zealand Journal of Marine and Freshwater Research* **36**:825-829.
- Dundee, D. S., and A. Paine. 1977. Ecology of the snail, *Melanooides tuberculata* (Müller), intermediate host of the human liver fluke (*Opisthorchis sinensis*) in New Orleans, Louisiana. *The Nautilus* **91**:17-20.
- Fryer, G., P. H. Greenwood, and J. F. Peake. 1983. Punctuated equilibria, morphological stasis and the palaeontological documentation of speciation: a biological appraisal of a case history in an African lake. *Biological Journal of the Linnean Society* **20**:195-205.
- Jacobson, M. K. 1975. The freshwater prosobranch, *Tarebia granifera*, in Oriente, Cuba. *The Nautilus* **89**:106.
- Laamrani, H., K. Khallayoune, B. Delay, and J. P. Pointier. 1997. Factors affecting the distribution and abundance of two prosobranch snails in a thermal spring. *Journal of Freshwater Ecology* **12**:74-79.
- Livshits, G., and L. Fishelson. 1983. Biology and reproduction of the freshwater snail *Melanooides tuberculata* (Gastropoda, Prosobranchia) in Israel. *Israel Journal of Zoology* **32**:21-35.
- Lodge, D. M., K. M. Brown, S. P. Klosiewski, R. A. Stein, A. P. Covich, B. K. Leathers, and C. Bronmark. 1987. Distribution of freshwater snails: spatial scale and the relative importance of physiochemical and biotic factors. *American Malacological Bulletin* **5**:73-84.

- Mitchell, A. J., M. J. Salmon, D. G. Huffman, A. E. Goodwin, and T. M. Brandt. 2000. Prevalence and pathogenicity of a heterophyid trematode infecting the gills of an endangered fish, the fountain darter, in two central Texas spring-fed rivers. *Journal of Aquatic Animal Health* **12**:283-289.
- Myers, M. J., C. P. Meyer, and V. H. Resh. 2000. Neritid and thiarid gastropods from French Polynesian streams: how reproduction (sexual, parthenogenetic) and dispersal (active, passive) affect population structure. *Freshwater Biology* **44**:535-545.
- Orians, G. H., and M. E. Soule. 2001. Introduction. Pages 1-10 in G. H. Orians, editor. *Conservation biology: research priorities for the next decade*. Island Press, Washington, DC.
- Pacala, S. W., and S. A. Levin. 1997. Biologically generated spatial pattern and the coexistence of competing species. in P. Kareiva, editor. *Spatial ecology: the role of space in population dynamics and interspecific interactions*. Princeton University Press, Princeton.
- Pointier, J. P. 1989. Conchological studies of *Thiara (Melanoides) tuberculata* (Mollusca: Gastropoda: Thiaridae) in the French West Indies. *Walkerana* **3**:203-209.
- Pointier, J. P., B. Delay, J. L. Toffart, M. Lefevre, and R. Romeroalvarez. 1992. Life history traits of three morphs of *Melanoides tuberculata* (Gastropoda: Thiaridae), an invading snail in the French West Indies. *Journal of Molluscan Studies* **58**:415-423.
- Pointier, J. P., R. N. Incani, C. Balzan, P. Chrosciechowski, and S. Prypchan. 1994. Invasion of the rivers of the littoral central region of Venezuela by *Thiara granifera* and *Melanoides tuberculata* (Mollusca: Prosobranchia: Thiaridae) and the absence of *Biomphalaria glabrata*, snail host of *Schistosoma mansoni*. *Nautilus* **107**:124-128.

- Pointier, J. P., and F. McCullough. 1989. Biological control of the snail hosts of *Schistosoma mansoni* in the Caribbean area using *Thiara spp.* *Acta Tropica* **46**:147-155.
- Pointier, J. P., S. Samadi, P. Jarne, and B. Delay. 1998. Introduction and spread of *Thiara granifera* (Lamarck, 1822) in Martinique, French West Indies. *Biodiversity and Conservation* **7**:1277-1290.
- Roessler, M. A., G. L. Beardsley, and D. C. Tabb. 1977. New records of the introduced snail *Melanoides tuberculata* (Mollusca: Thiaridae) in South Florida. *Florida Scientist* **40**:87-94.
- Sakai, A. K., F. W. Allendorf, J. S. Holt, D. M. Lodge, J. Molofsky, K. A. With, S. Baughman, R. J. Cabin, J. E. Cohen, N. C. Ellstrand, D. E. McCauley, P. O'Neil, I. M. Parker, J. N. Thompson, and S. G. Weller. 2001. The population biology of invasive species. *Ann. Rev. Ecol. Syst.* **32**:305-332.
- Samadi, S., C. Balzan, B. Delay, and J. P. Pointier. 1997. Local distribution and abundance of thiarid snails in recently colonized rivers from the Caribbean area. *Malacological Review* **30**:45-52.
- Sax, D. F., J. J. Stachowicz, and S. D. Gaines, editors. 2005. *Species invasions: insights into ecology, evolution, and biogeography*. Sinauer Associates, Inc., Sunderland, MA.
- Smith, M. J. 1978. *The evolution of sex*. Cambridge University Press, Cambridge.
- Soule, M. E. 1990. The onslaught of alien species, and other challenges in the coming decades. *Conservation Biology* **4**:233-239.
- With, K. A. 2002. The landscape ecology of invasive spread. *Conservation Biology* **16**:1192-1203.

## FIGURE LEGENDS

Figure 1. Movement distributions produced by each species in Ramdeen Stream. The two species exhibit different movement behaviors in natural streams. (A) *T. granifera* has a higher rate of upstream movement than (B) *M. tuberculata*.

Figure 2. The presence or absence of riparian canopy affected the local distribution and abundance of exotic snails. Density of *T. granifera* is higher in sunny locations where riparian canopy has been removed than in shaded areas where the riparian canopy is intact. There is no significant difference between the density of *M. tuberculata* in sunny versus shady areas of the stream. In shaded areas of the stream, densities of the two species do not differ; however, in sunny areas of the stream where riparian canopy has been removed, the density of *T. granifera* far exceeds that of *M. tuberculata*. Vertical bars denote 95% confidence intervals.

Figure 3. Differences in the role of primary production versus detritus-based resources for the two study species in a competitive environment. Instantaneous growth rates of *T. granifera* and *M. tuberculata* did not differ in algae-dominated experimental treatments, but *M. tuberculata* outperformed *T. granifera* in detritus-based experimental treatments. Also, *T. granifera* showed higher growth rates consuming an algal based resource relative to consuming detritus based resources. In contrast, the performance of *M. tuberculata* did not differ across resource types. Vertical bars denote 95% confidence intervals.

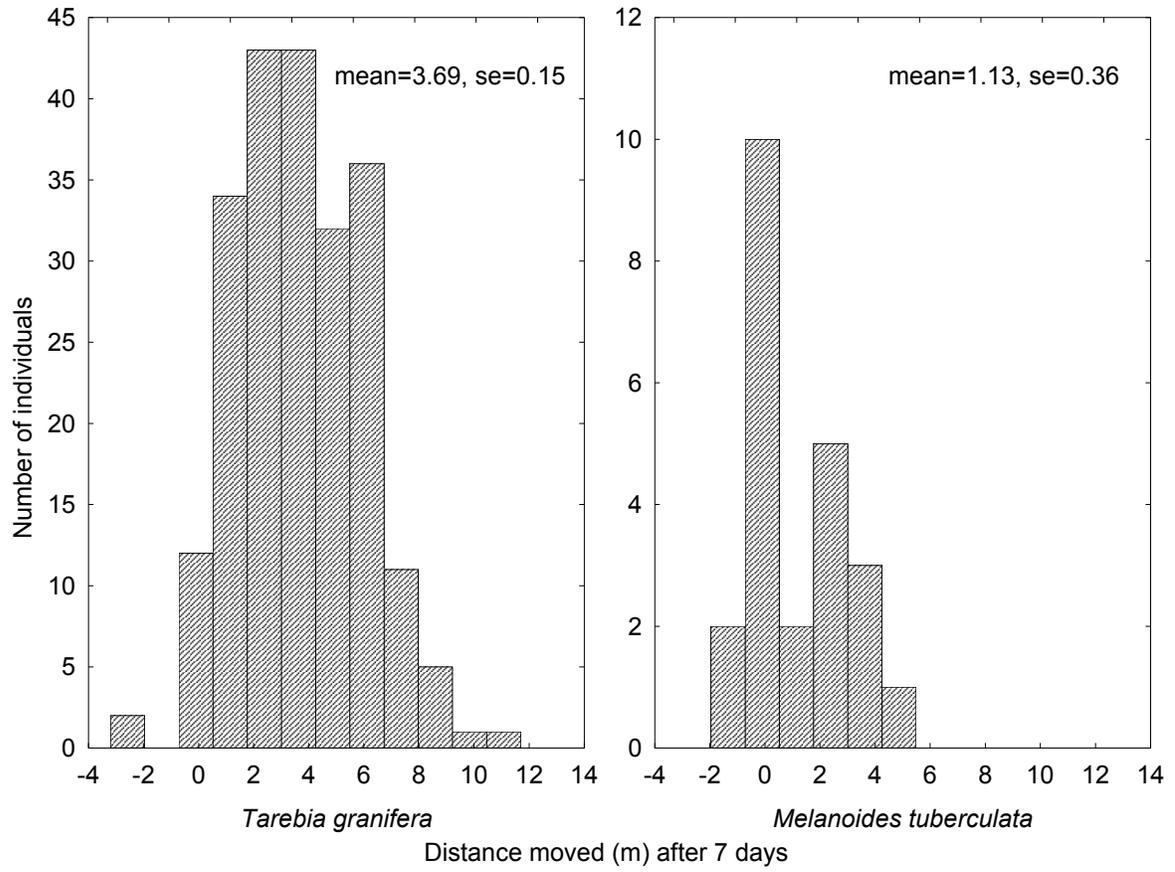


Figure 1. Movement distributions produced by each species in Ramdeen Stream

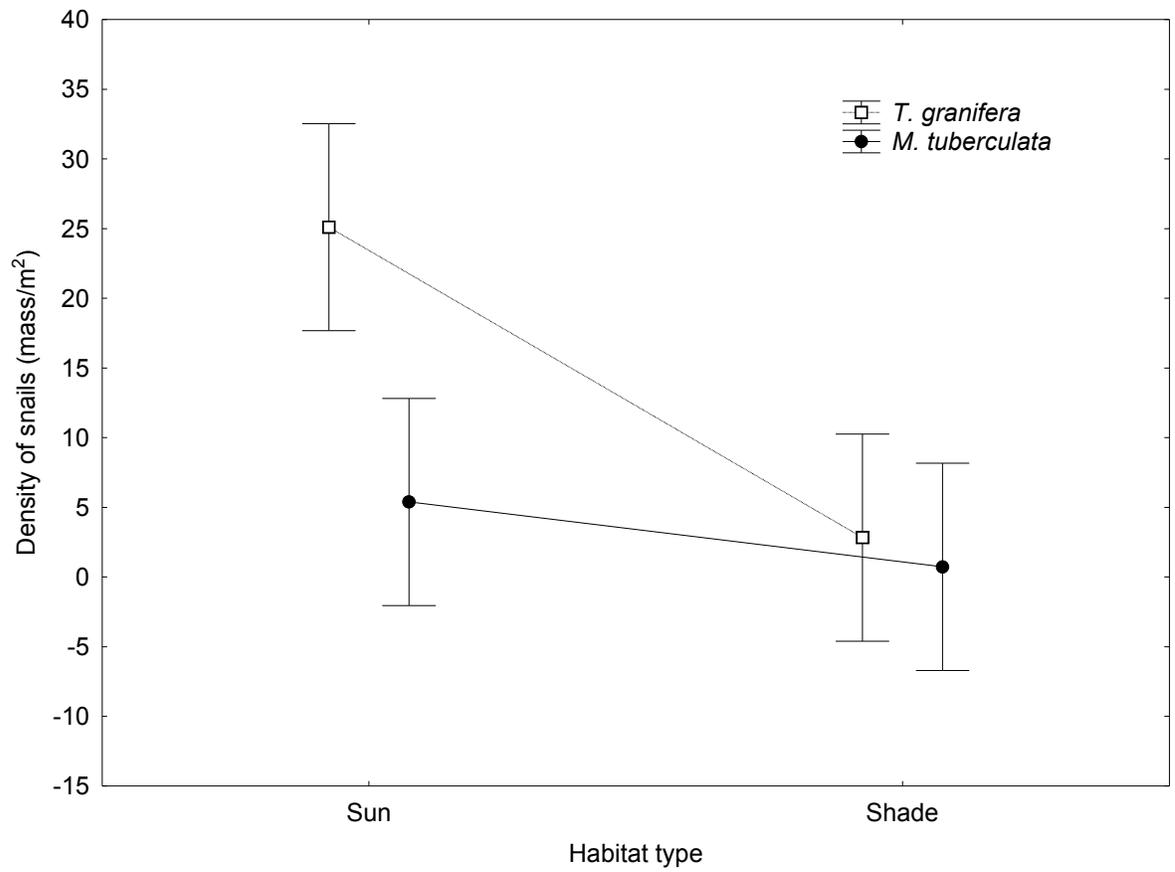


Figure 2. The presence or absence of riparian canopy affected the local distribution and abundance of exotic snails

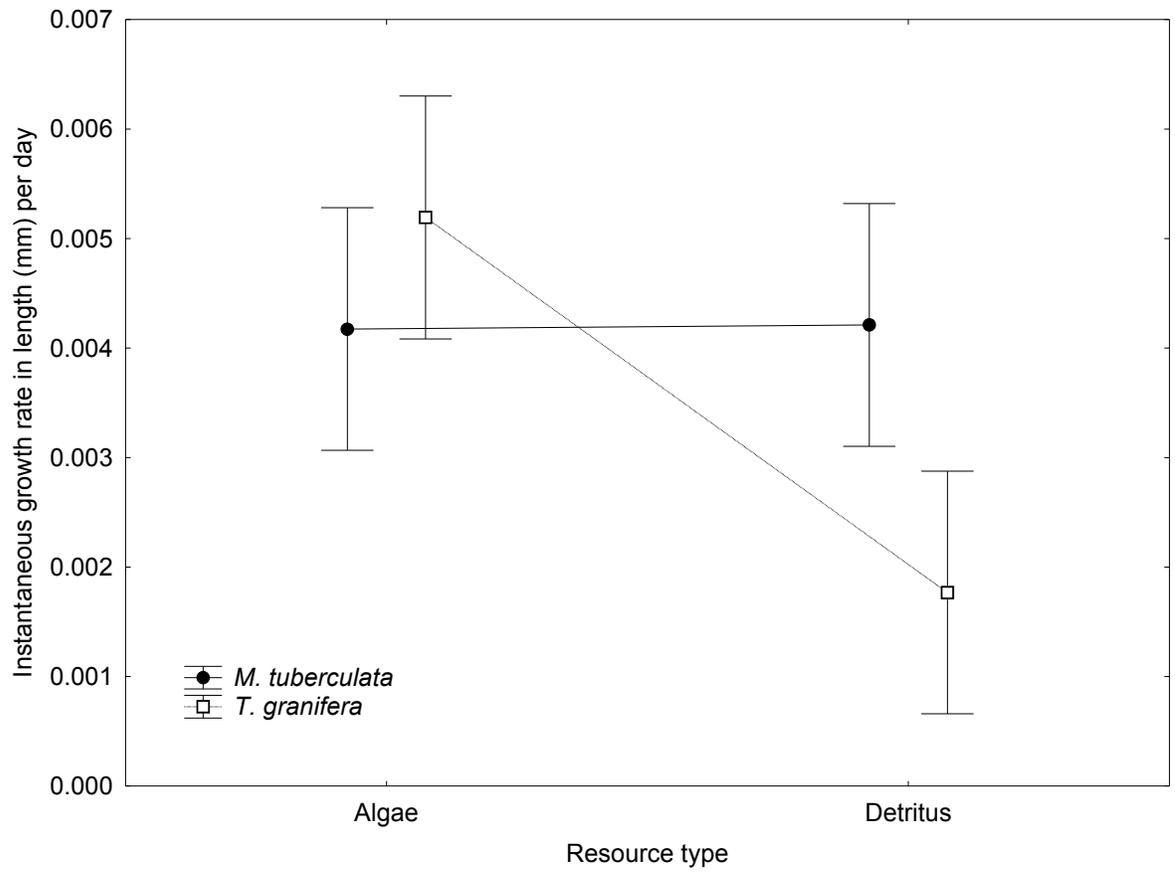


Figure 3. Differences in the role of primary production versus detritus-based resources for the two study species in a competitive environment