

HABITAT FRAGMENTATION AND RANGE MARGIN EFFECTS ON DISPERSAL AND INTERACTIONS BETWEEN COMPETITORS

A Dissertation

Submitted to the Graduate Faculty of the
Louisiana State University and
Agricultural and Mechanical College
in partial fulfillment of the
requirements for the degree of
Doctor of Philosophy

in

The Department of Biological Sciences

by

Rachel Roxann Harman

B.S., Indiana University – Purdue University Fort Wayne, 2012

M.S., Indiana University – Purdue University Fort Wayne, 2014

August 2020

ACKNOWLEDGEMENTS

First and foremost, I would like to thank my husband, Dan, who has been so supportive of my doctoral journey. We signed the marriage certificate just 5 days before moving 1,000 miles to Baton Rouge, LA, which was our “honeymoon” trip. Throughout this crazy journey, he has pushed me to be a better researcher, teacher, and person. I have received tremendous support from my family and Dan’s family as well. I would like to thank my parents, who taught me how to be a dedicated worker and the importance of a good education. I would like to thank my three siblings, with whom I have always been close, as they were always there for me if I needed to rant or chat as the case may be. During my six years in Louisiana, I was blessed with six nephews, whose laughs and shenanigans often made me smile and push harder to finish my dissertation objectives to be able to visit them on the holidays.

I have greatly enjoyed my time in Baton Rouge. The lifelong friendships, the way too tasty food, and the support of the wonderful faculty and staff made each day special. In particular, I would like to thank my adviser, Jim Cronin, who inspired me to become a better scientist and to think for myself. He supported me through sand and flour, success and failure, providing me with guidance when I needed it and letting me dive into the (literal) research marsh when I did not. I would also like to thank the other members of my committee, Kyle Harms and Bret Elderd, who were always available for discussions, laughs, and advice. I would also like to thank Barry Aronhime, who let me use my pedagogical training and express my passion for teaching as I developed curriculum for the ecology lab course.

Additionally, I would like to thank my collaborators, Jerome Goddard II and Ratnasingham Shivaji from Auburn University Montgomery and the University of North Carolina Greensboro, respectively, as it has been a pleasure working with them as we combined

detailed models with ecology. I would also like to thank Christopher Carlton for his invaluable assistance with identifying my insects and taking his time to show us how to sex *Tribolium spp.*

My coworkers and friends have always been supportive of me and there are so many of them that I would like to thank here, but I will keep the list to direct assistance of my research and not the scores of names of people that provided me with moral support, though I thank you all too. In particular, I would like to thank: Katherine Hovanes, Lorelei Patrick, Luis Santiago-Rosario, Lorissa Radunzel-Davis, Herie Lee, Joseph Johnston, Nathan Harms, Warwick Allen, Ganesh Bhattarai, Carrie Barker, Andrew Flick, Matthew Faldyn, Jordan Croy, Scott Grimmell, Jason Janeaux, and Michael Garvey for helping me count beetles, double check manuscripts, or talk through my research. You all have helped push me through this crazy experience.

During my years at LSU, I have also had the great fortune of mentoring so many undergraduates who assisted me with my research. I would like to thank Celine Rochon, Matthew Berry, Charles “Marshall” Stephenson, Madeline Guidry, Madelyn Smith, Raven Daigle, Daniel Ruppert, Taylor Boyd, Alex Hollander, Amanda Monceaux, Marshall Kellerman, Benjamin Gaither, Connor Doyl, Nicholas Uzee, Elaine Arendt, Florencia Scaglia Drusini, Mitchell Guedry, Kaylyn Riley, and Rhae Sevin for all of their hard work throughout the years.

The second chapter of my dissertation was published in the American Naturalist journal. I would like to thank them for the use of the paper for dissertation publication. Lastly, I would like to extend my thanks to the National Science Foundation (DMS-1516833, DMS-1516560, and DMS-1516519), Louisiana Environmental Education Commission, and Biograds LSU organization for their financial support of my research.

TABLE OF CONTENTS

ACKNOWLEDGEMENTS.....	ii
LIST OF TABLES.....	vi
LIST OF FIGURES.....	vii
ABSTRACT.....	ix
CHAPTER 1. INTRODUCTION.....	1
CHAPTER 2. FREQUENCY OF OCCURENCE AND POPULATION-DYNAMIC CONSEQUENCES OF DIFFERENT FORMS OF DENSITY-DEPENDENT EMIGRATION ...	7
INTRODUCTION.....	7
OBJECTIVE 1: FORMS OF DENSITY-DEPENDENT EMIGRATION.....	9
OBJECTIVE 2: PRESENCE OF DDE FORMS IN THE LITERATURE.....	11
OBJECTIVE 3: POPULATION DYNAMICS OF DDE.....	18
DISCUSSION.....	24
CONCLUSIONS.....	30
CHAPTER 3. MOVEMENT BEHAVIOR OF <i>ISCHNODEMUS CONICUS</i> (VAN DUZEE) IN FRAGMENTED SALT-MARSH HABITATS.....	32
INTRODUCTION.....	32
MATERIALS AND METHODS.....	35
RESULTS.....	47
DISCUSSION.....	59
CONCLUSIONS.....	66
CHAPTER 4. REDUCTION IN DISPERSAL IS CAUSED BY CONCURRENT SELECTION OF COMPETITIVE ABILITY IN RANGE EXPANDING POPULATIONS.....	68
INTRODUCTION.....	68
MATERIALS AND METHODS.....	72
RESULTS.....	83
DISCUSSION.....	92
CONCLUSIONS.....	100
CHAPTER 5. CONCLUSIONS.....	103
APPENDIX A. SUPPLEMENTARY MATERIAL FOR CHAPTER 2.....	110
APPENDIX B. SUPPLEMENTARY MATERIAL FOR CHAPTER 3.....	118
APPENDIX C. SUPPLEMENTARY MATERIAL FOR CHAPTER 3.....	122
APPENDIX D. COPYRIGHT INFORMATION.....	124

REFERENCES	129
VITA	152

LIST OF TABLES

Table 3.1. <i>Ischnodemus conicus</i> density-emigration model selection results using Akaike's information criterion corrected for small sample size (AICc).	49
Table 3.2. Effect of habitat type on <i>Ischnodemus conicus</i> movement behavior.	50
Table 3.3. Effect of sex and age class on <i>Ischnodemus conicus</i> movement behavior within the patch arenas	53
Table 3.4. Summary of output of the point-pattern processes for each of the ten replicate habitat landscapes	55
Table 3.5. Effect of <i>Ischnodemus conicus</i> sex and age class on movement behavior within an edge arena	57
Table 3.6. Summary of output of the point-pattern processes for each of the 5 replicate edge arenas.	58
Table 3.4. Effect of <i>Ischnodemus conicus</i> sex and age class on movement behavior within a matrix arena.....	59
Table 4.1. Summary of the methods used to select the 11 different lines with designated acronyms	78
Table 4.3. Summary table of posthoc pair-wise comparisons between the single-trait selection lines of dispersal propensity, competitive ability, and fitness	84
Table 4.7. Linear regression results for density-emigration relationships of the dispersal lines ..	90
Table A1. List of case studies used in the empirical literature review	110
Table B.1. Outputs for spatial point pattern data for distribution 5 hours after release in habitat landscapes	118
Table B.2. Outputs for spatial point pattern data for distribution 5 hours after release in habitat landscapes	120
Table C.1. Collection sites for flour beetle species used in range expansion experiments.....	122
Table C.2. Linear regression and quadratic regression results for density-emigration relationships of the dispersal lines	122

LIST OF FIGURES

Figure 2.1: Hypothetical forms of the density-emigration relationship.....	8
Figure 2.2. Mosaic representing the percent of each density-emigration form within taxonomic group.	16
Figure 2.3. Box-and-whisker plots for the number of density levels and density range for experimental and observational methods as well as for the different forms of DDE	17
Figure 2.4. Graphic representation of the primary variables incorporated into the one-patch model used to create the bifurcation-stability curves for each form of density-dependent emigration (DDE).....	18
Figure 2.5: Bifurcation-stability curve of population persistence within an intermediate hostility matrix	22
Figure 2.6: Bifurcation-stability curve of population persistence within a high hostility matrix..	23
Figure 3.1. Image of <i>Spartina alterniflora</i> landscape on the Cameron Jetty Pier, Cameron, LA, with the small patches common around the edges of larger patches. Aggregates of <i>I. conicus</i> on <i>S. alterniflora</i> stems.....	37
Figure 3.2. 140 x 140 cm <i>S. alterniflora</i> patch designed to assess movement of individual <i>I. conicus</i>	41
Figure 3.3. Edge landscape used to assess movement of individual <i>Ischnodemus conicus</i> . Colored vials placed at the patch-matrix boundary contain insects for release. The landscape was divided into a 10x12 grid, consisting of half sand matrix and half <i>S. alterniflora</i> habitat	43
Figure 3.4. Sand matrix arena used to assess movement of individual <i>Ischnodemus conicus</i>	44
Figure 3.5. Histogram of the wing:body length ratios for female and male <i>Ischnodemus conicus</i> collected from Cameron, LA	48
Figure 3.6. The density-emigration relationship of female blissid bug <i>Ischnodemus conicus</i> from experimental trials conducted in 2015 and 2016	49
Figure 3.7. Movement and final location of individual <i>Ischnodemus conicus</i> within all replicate arenas.....	51
Figure 3.8. Tests of random walk for <i>I. conicus</i> paths with two or more angles between 5 min steps.....	52

Figure 3.9. Mean (\pm SE) cumulative number of steps taken by individuals released within the habitat landscape during each hour of continuous observation	53
Figure 3.10. Mean (\pm SE) cumulative number of steps taken each hour by individuals released in the matrix.....	56
Figure 4.1. Image of the dispersal landscape used to separate high and low dispersers and measure dispersal variables	75
Figure 4.2. Dispersal of red flour beetle selection lines representing the core and front of a range	85
Figure 4.3. Dispersal of confused flour beetle selection lines representing the core and front of a range.....	86
Figure 4.4. Linear regression to test the density-emigration relationship for each selected line for both flour beetle species.....	89
Figure 4.4. The change in emigration with a competing species for selection lines representing the core and front of an expanding range.....	91
Figure 4.5. Fitness as measured by survival of offspring to the pupal stage.....	92
Figure C.1. Linear regression for each selection line and both species.....	123

ABSTRACT

Dispersal is a fundamental process that affects local and regional dynamics, including population persistence, range expansion, and interspecific interactions, particularly as disturbance through habitat fragmentation and climate change. Here, my main objective was to ascertain how fragmentation affects dispersal and the interactions of competitors within the local patch and regional landscape. In my second chapter, I assessed dispersal through a literature review and population persistence model to examine the breadth and frequency of different density-emigration forms that occur in nature, including forms that are not prevalent in the literature. I conclude that these rare forms have important population dynamic consequences and that studies of density dependence should include methods that are better able to test for these forms. In my third chapter, I quantified individual and group movement of *Ischnodemus conicus* (Van Duzee), and, by using methods proposed in my first chapter, I was able to detect the rare non-linear, u-shaped density-dependent emigration. This form was likely promoted by the edge-avoiding, clustering behavior observed within individual movement experiments. Empirical assays such as this are lacking and can be used in predictive models for population dynamics. In my fourth chapter, I took a novel approach to studying the dispersal-competition-fecundity tradeoff that is predominately studied by changing just one of these traits. I applied concurrent selection pressures of dispersal and competition onto populations to represent the interacting tradeoffs that occur in the evolving range core and range front of an expanding population using *Tribolium castaneum* (Herbst) and *T. confusum* (DuVal) populations. I additionally assessed the traditional single trait selection tradeoffs between competitive and dispersal ability and fecundity by selecting for all traits and assessing responses to each one. Overall, my research evaluates dispersal at multiple scales, from individuals within a patch to communities in a landscape and

examines previous research while suggesting improvement for the future. This work is an important contribution to landscape and dispersal ecology and can be applied to studies of invasion and conservation biology.

CHAPTER 1. INTRODUCTION

Across the globe, anthropogenic fragmentation of habitats has increased (Saunders et al., 1991) and population persistence is often threatened (Anholt 1995; Debinski and Holt, 2000; Hanski 1999) as a consequence of disturbance-mediated changes of within-patch movement (Haynes & Cronin, 2006), matrix-boundary behavior (Ricketts 2001), emigration (Hanski 1999, Poethke and Hovestadt 2002), and gene flow (Cossu et al. 2017). In these variable systems, dispersal connects populations, promoting spatial synchrony that allows populations to persist (Anholt 1995; Hanski 1999; Hanski and Gilpin 1997) and expand their range (McPeet and Holt 1992, Neubert and Caswell 2000).

The movement of individuals within a habitat determines the likelihood of encountering the edge of the patch-matrix and may be influenced by the abundance of resources (Franke and Yakubu, 2008; McClintic et al., 2014), presence of conspecifics (Bartelt et al. 2008; Stevenson et al., 2017), and interspecific competition (Senger et al. 2007; Svenning et al. 2014). In fragmented landscapes, individuals have a greater chance of encountering the edge in smaller patches, which provides more opportunities for emigration to occur (Haddad 1999). However, the more hostile matrix may create edge effects that promote individuals either aggregating at (e.g., Campbell and Hagstrum 2002; Desrochers et al. 2003; Nowicki et al. 2014) or avoiding (e.g., Cronin 2009; Gates and Gysel 1978; Jacob and Brown 2000) the edge instead of emigrating. Consequently, the movement decisions of individuals within a patch can affect the overall metapopulation persistence of the species, but this is primarily theoretical. Empirical research has not kept up with theory, and an individual's response to fragmentation is often one of the least understood

life history traits concerning the biology of a species (Evans et al., 2018; Hooten et al., 2017; Patterson et al., 2017).

The probability of an individual to emigrate from a patch may also be dependent upon the density of the population. Common density-emigration relationships including positive (+DDE; Bowler and Benton 2005; Hovestadt and Poethke 2006), negative (-DDE; Matthysen 2013; Serrano et al. 2005), or density-independent (DIE; Levins 1969; Hanski and Gilpin 1991). Theoretical studies have compared DIE, +DDE, and -DDE, and showed +DDE populations have a greater chance of establishing a new population as individuals are less likely to leave in low densities (Sæther et al. 1999) but range expansion is theoretically faster with -DDE populations as individuals emigrate more readily from unfavorable habitats that likely contain few conspecifics (Altwegg et al. 2013). DIE populations, on the other hand, emigrate at the same rate despite density, which accelerates population expansion compared to +DDE and allows for more individuals to remain in newly colonized patches compared to -DDE (Altwegg et al. 2013). However, a population's response to density is not necessarily constrained to these three forms and nonlinear forms such as u-shaped (uDDE) or hump-shaped (hDDE), can theoretically occur (Amarasekare 2004) but little is known about their dynamics nor prevalence in nature.

If the emigrating individuals reach the range front, they are theoretically exposed to different biotic selection pressures (Travis and Dytham 2002; Hughes et al 2007). As few individuals colonize new patches and intraspecific competition is low, populations likely have high growth rates and evolution of selected traits may quickly occur (Masson et al. 2018; Philips et al. 2008; Shine et al. 2011). Through spatial sorting, the best dispersers accumulate at the range front (compared to less-mobile individuals in the core) and, if dispersal traits are heritable, dispersal propensity may increase each generation and accelerate range expansion (Monty and

Mahy 2010; Phillips 2015). Additionally, founder effects, created by the lack of genetic variability of populations colonized by few individuals, increase kin-competition and thus dispersal rates as individuals emigrate to alleviate competitive pressures on relatives (Van Petegem et al. 2018). However, the propensity to disperse and competitive ability are both energetically costly and often trade-off in populations (Fronhofer and Altermatt 2015). This range expansion process assumes that competition decreases as an individual moves away from the core, that only one trait (either dispersal or competitive ability or fecundity; DCF) is evolutionarily selected and changes in the other traits are in response, and that the landscape does not include intra-specific competition. However, each of these assumptions do not fully represent range dynamics in a landscape and empirical research is needed as models can easily under- or over-predict range expansion speeds of invasive species and species escaping disturbed environments (Svenning et al. 2014).

My main objective was to ascertain how fragmentation affects dispersal and the interactions of competitors within the local patch and regional landscape by addressing the research gaps mentioned above. I accomplished this in a dynamic dissertation that researches dispersal at several scales, from individuals and populations within a patch to evolving communities in a landscape.

In my second chapter, I analyzed dispersal through a systematic literature review of the five different density-emigration forms to examine the breadth and frequency of DDE forms that occur in nature. I created biologically plausible explanations for each form and predicted that while there is a biological purpose to study the population-dynamic consequences of the -DDE, uDDE, and hDDE forms, they are not as prevalent in the literature as DIE and +DDE. Lastly, I helped develop a simple and flexible modeling framework based on reaction-diffusion to assess

how the different forms of DDE affect population dynamics for a one-dimensional, single-patch system with a matrix that has 1 of 3 hostility levels. I hypothesized that the different forms of DDE would influence the population response to fragmentation, including changes in minimum patch size and population persistence.

This review gave the foundation for my third chapter, which addresses the lack of data concerning individual movement, and connects this to the probability of an individual to emigrate from a patch. I used the blissid bug *Ischnodemus conicus* (Van Duzee) (Hemiptera: Blissidae) as my research organism. Little empirical research has studied *I. conicus* or its congeners, and nothing is known concerning its dispersal behavior. This bug is a major herbivore on *Spartina alterniflora* (Loisel) (Poacea), which is commonly planted to serve as an erosion control along the Gulf coast, so not only is understanding the species' movement interesting as an entomological system, but as the insect lives in a standard patch surrounded by a simple, yet harsh matrix, its movement can easily be generalized to other systems.

Using this system, I assessed dispersal by quantifying (1) the potential for long-distance dispersal as the proportion of macropterous (long-winged) individuals, (2) the density-emigration relationship of populations in a small, fragmented patch, and (3) the movement behaviors of individuals within a *Spartina* patch, hostile sand matrix, and at the edge between. I hypothesized that macropters would be present in the landscape. But they would be rare and long-distance dispersal events would be unlikely to occur. I also predicted that the DDE form would be negative as the species aggregates and is less likely to emigrate from high densities. Lastly, I hypothesized tortuous, short movement of individuals in the habitat and edge landscapes that would result in clumped distribution and reflect its predicted -DDE form, whereas movement within the sand matrix would have little tortuosity and larger step size that

would allow the insect to cross the hostile matrix quickly. These assays on movement can be used as the first step toward developing predictive models for population dynamics.

In my fourth chapter, I addressed the research gaps pertaining to range expansion by taking the novel approach of applying concurrent selection pressures of dispersal and competition onto populations to represent the interacting tradeoffs that occur in the evolving range core and range front of an expanding population. I compared these population responses to the customarily used single-trait selection tradeoffs between competitive and dispersal ability with the hypothesis that the additive selection pressures would reduce the extent to which each DCF (dispersal, competition, and fecundity) trait is selected (as modelled by Burton et al. 2010).

I additionally incorporated fecundity selection, which is often measured only as a reaction to other trait selection and predicted that an increase in fitness would promote dispersal. I then modelled this with the competition-colonization tradeoff. As the response to tradeoffs is often species-specific, if not population dependent, I used two species, *Tribolium castaneum* and *Tribolium confusum*, that have high niche overlap but vary in their normal responses to competition to test the differences between species. I predicted that the weaker competitor would show a greater decrease in DCF traits with competition selection pressures. Additionally, I assessed how applying different selection pressures changes an individual's reaction to a competing species with the hypothesis that high competition would promote interspecific coexistence in comparison to the other selection lines representing the core or the front of a range. Results from this experiment can be applied to dispersal events related to the invasion of exotic species and population range expansion in response to habitat disturbance.

Lastly, in the fifth chapter of this dissertation, I summarize the overall biological implication of my research to advance our understanding of population dynamics, species

invasions, and conservation biology. I conclude by briefly describing the research I plan to do in the future.

CHAPTER 2.

FREQUENCY OF OCCURENCE AND POPULATION-DYNAMIC CONSEQUENCES OF DIFFERENT FORMS OF DENSITY-DEPENDENT EMIGRATION¹

INTRODUCTION

Emigration of organisms is a key process affecting colonization (Amarasekare 1998; Clobert et al. 2009), minimum patch size (Poethke and Hovestadt 2002), local densities, population stability (Hanski 1999), and species coexistence (Cadotte et al. 2006; Levins and Culver 1971). From a regional or metapopulation perspective, the magnitude of dispersal affects spatial synchrony and is fundamental to population persistence (Anholt 1995; Hanski 1999; Hanski and Gilpin 1997; Ims and Yacoz 1997) and range expansion (Altwegg et al. 2013). As in the classic work of Levins (1969), early metapopulation models assumed density-independent emigration (DIE; e.g., Hanski and Gilpin 1991; Levins 1974; Pacala and Roughgarden 1982; Shmida and Ellner 1984). However, the more widely accepted view of emigration behavior is that species should exhibit a positive relationship between conspecific density and emigration (+DDE; Amarasekare 2004; Bowler and Benton 2005; Matthysen 2012), and many subsequent models incorporated this form of emigration (e.g., Hovestadt and Poethke 2006; Pulliam 1988; Sæther et al. 1999). Alternative forms of density-dependent emigration (DDE), including negative density-dependent emigration (-DDE) or nonlinear forms such as u-shaped density-dependent emigration (uDDE) or hump-shaped density-dependent emigration (hDDE), are

¹ A version of this chapter previously appeared as Harman, R. R., J. Goddard, R. Shivaji, and J. T. Cronin. 2020. Frequency of occurrence and population-dynamic consequences of different forms of density-dependent emigration, *American Naturalist*. The definitive version is available at <https://www.journals.uchicago.edu/doi/10.1086/708156>.

theoretically plausible (see Fig. 2.1) but have received almost no attention in the literature (but see Amarasekare 2004).

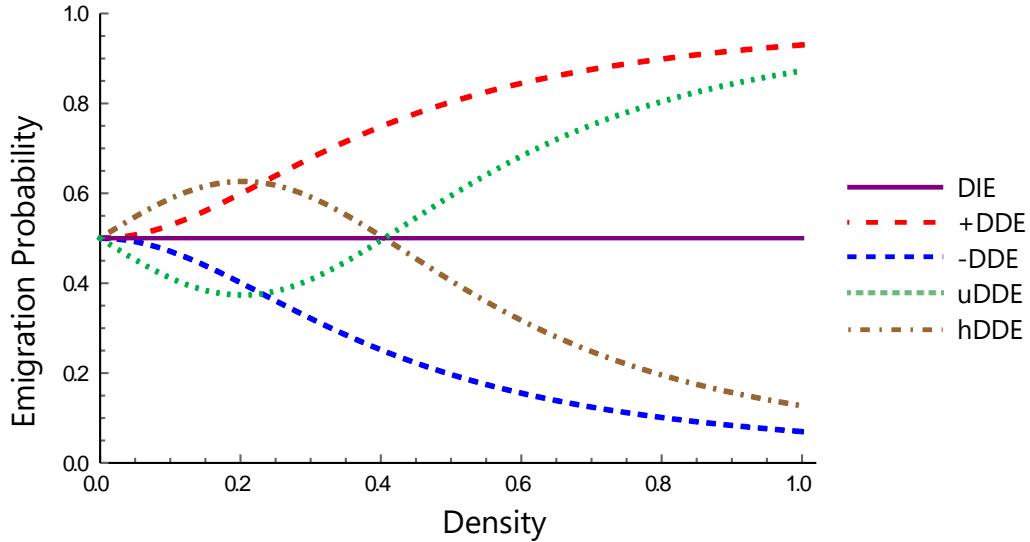


Figure 2.1: Hypothetical forms of the density-emigration relationship, including density independent emigration (DIE), positive density-dependent emigration (+DDE), negative density-dependent emigration (-DDE), u-shaped density dependent emigration (uDDE), and hump-shaped density dependent emigration (hDDE).

Although DIE and +DDE are widely reported in the literature, there has not been a systematic review that examines the breadth and frequency of DDE forms that occur in nature. Moreover, we know very little about the population-dynamic consequences of -DDE (but see Amarasekare 2004; Matthysen 2005; Rodrigues and Johnstone 2014; Sæther et al. 1999), uDDE, and hDDE forms. Our study has three objectives. First, we describe each form of DDE in Fig. 2.1, provide biologically plausible explanations for its occurrence, and, where possible, report what is known about its population-dynamic consequences. Second, we conducted an extensive review of the published literature that examined the relationship between conspecific density and emigration from a patch and assessed the range and frequency of different forms of DDE. Lastly, we develop a simple and flexible modeling framework based on reaction-diffusion to assess how

the different forms of DDE affect population dynamics for a one-dimensional, single-patch system with a matrix that has one of three hostility levels. Our intention with this model is to illustrate how each form of DDE can potentially influence the minimum patch size for population persistence, generate Allee effects, and affect population stability.

OBJECTIVE 1: FORMS OF DENSITY-DEPENDENT EMIGRATION

The evolution of +DDE (Fig. 2.1) has been attributed to the population benefits of avoiding inbreeding and intraspecific competition (Hamilton and May 1977; Handley and Perrin 2007; Travis et al. 1999). As such, non-gregarious species are expected to exhibit +DDE (Bowler and Benton 2005) as they receive little benefit from group living. Mathematical models predict that +DDE decreases the extinction probability in spatiotemporally variable environments (Amarasekare 2004). Theoretically, in non-stable environments, current patch quality does not determine future offspring value as resources are likely to change, leading to resource competition at high densities and promoting the evolution of +DDE strategies (Rodrigues and Johnstone 2014). Positive DDE may increase mean per-capita fitness (Hovestadt et al. 2010), partially because the form promotes population growth in small populations as dispersal probability is low (Amarasekare 2004).

In contrast, -DDE results in fewer individuals leaving at high densities (Fig. 2.1), suggesting some benefit for species living in a group (Bowler and Benton 2005; Kim et al. 2009; Matthysen 2012; Serrano et al. 2005). Gregarious behavior in a population can underlie an Allee effect (Allee et al. 1949; Cantrell and Cosner 2007; Donahue 2006) and is often a consequence of the benefits of group living outweighing the costs of increased intraspecific competition, such as instances where conspecific attraction increases the chance of finding a mate (see review by

Gascoigne et al. 2009), extra-pair mating opportunities (Serrano et al. 2005), defense against predators (Hammill et al. 2015), or foraging success (Kim et al. 2009). Under -DDE, the species is not expected to be resource limited at high density, but if it is, uDDE should arise (see below). With -DDE, population stability at the patch level has been shown to increase with an increase in growth rate (Sæther et al. 1999). Lastly, -DDE is likely to evolve in stable environments with constant habitat quality as individuals residing in high quality patches will constantly produce offspring with high fitness that are unlikely to leave at high densities (Rodrigues and Johnstone 2014).

Positive and negative DDE have distinct population-dynamic consequences at the metapopulation or regional scale. Positive DDE species have a greater chance of establishing a new population as they are less likely to leave a previously unoccupied patch while their densities are low (Sæther et al. 1999). Therefore, +DDE species are expected to have a larger range than -DDE species, but range expansion may be faster in -DDE than +DDE species as the former species emigrate more readily from unfavorable habitats that predominately contain low population densities (Altwegg et al. 2013). Range speed may also increase as -DDE is more likely to evolve low dispersal costs and consequently higher dispersal rates (Rodrigues and Johnstone 2014). Conversely, the +DDE relationship will be the strongest when the cost of dispersal is greatest (Travis et al. 1999). Over the entire metapopulation, -DDE species should have a higher probability of local population extinctions as individuals are more likely to leave the patch when densities are low; however, in the small range of occupied patches, extinction risk will be reduced (Sæther et al. 1999).

Very little attention has been given to nonlinear forms of density-dependent emigration, despite early recognition of its potential importance (e.g., Johst and Brandl 1997; Travis et al.

1999). For the u-shaped relationship (uDDE), the initial negative slope and high emigration rate at low density can be caused by the same factors that promote an Allee effect (Allee et al. 1949; Altwegg et al. 2013; Kim et al. 2009; Matthysen 2012). However, at high densities, the negative effects of conspecific density, such as competition, encourage emigration. This combination of unfavorable effects of density has been noted in blue footed boobies (Kim et al. 2009) and strains of ciliated protozoa *Tetrahymena thermophila* that are highly aggregative (Jacob et al. 2016).

Lastly, hump-shaped DDE (hDDE) has not been considered in any theoretical treatise. Biologically, this form could exist when the benefits of living in small and large groups are greater than intermediate-sized groups. For example, small groups may be less noticeable to predators while larger groups may be more defensible, thus intermediate-sized populations are less advantageous. With some genetic strains of ciliates, Jacob et al. (2016) found +DDE at low-to-intermediate density levels but in larger populations, emigration was reduced, potentially owing to bottlenecks in the movement through narrow corridors.

OBJECTIVE 2: PRESENCE OF DDE FORMS IN THE LITERATURE

Methods

We compiled a database of emigration studies that were found in the Web of Science (www.webofknowledge.com). The search included all records in the database up to January 2, 2019. We used the search terms “density-dependent dispersal”, “density-dependent emigration”, “density independent emigration”, “density independent dispersal”, and “dispersal” plus “density”. Review papers and relevant references from the collected articles were also searched. Articles were retained from the database if they (1) included data on emigration, (2) were empirically based (either experimental or observational), (3) used two or more conspecific

density levels, and (4) had a study organism that engaged in active dispersal. We retained studies with only two density levels but we acknowledge that those cases necessarily preclude the detection of nonlinear DDE (e.g., uDDE and hDDE). Although passive dispersal (e.g., transport by wind or water currents) can be density dependent (e.g., Kellner and Hubbell 2018; Sugiyama et al. 2018), we focused our study on species whose individuals make their own decision when to leave based on local density, patch size, boundary conditions, matrix composition, etc.

Our Web of Science search yielded 115 articles on the relationship between conspecific density and emigration. Several of these articles included data for more than one species or multiple tests for the same species (e.g., for different age classes or stages, different sexes, or in response to different environmental contexts). For articles that subjected species to different treatments and reported more than one form of DDE, we treated each type of DDE for that species as an independent replicate in our analysis. We did this because we were most interested in the range of DDE forms and averaging within a species could be misleading. Based on these criteria, we had 145 studies of DDE (Appendix A).

Among the case studies, emigration was quantified in a number of ways: as the proportion leaving the patch (76% of studies), dispersal distance (18%), genetic relatedness (3%), or proportion of alates or macropters (3%). The proportion emigrating from a patch is a direct measurement of the emigration rate, and although it is the metric most often used, these other measurements are often regarded as good proxies for emigration. Dispersal distance is often used with species that emigrate from the natal habitat (e.g., from a nest; Molina-Morales et al. 2012). The genetics of a population measures DDE by calculating the relatedness of the individuals among patches (e.g., Van Hooft et al. 2008) or the distance separating full siblings (e.g., Derosier et al. 2007). Lastly, in some insects, the proportion of long-winged individuals

(macropters) in a population can be used as an index of dispersal capability (Denno et al. 2001). The production of macropters has been positively correlated with conspecific density in a number of insect species (e.g., Poniowski and Fartmann 2011; Strong and Stiling 1983).

For each study, the relationship between emigration and density was assigned to one of five DDE forms: DIE, +DDE, -DDE, uDDE, or hDDE. Assignment was based on the author's demonstration of a statistical relationship between density and emigration (e.g., regression, ANOVA, general linear mixed model). Unless the authors had already done so, if there were >3 density levels, we reanalyzed the data to test for nonlinearities in the density-emigration relationship. In all such cases (n=40), we extracted the data from the original figures and analyzed the relationship between density and emigration using a nested set of predictor variables (constant only, constant + density, constant + density + density²). Akaike information criteria corrected for small sample size (AICc) was used to choose the best model to explain variation in emigration; and therefore, determine the most likely form of DDE. The model with the smallest AICc value was deemed best, but all competing models with an AICc value within 2 of the best model were considered to have substantial support (Burnham et al. 2011). The analyses were performed using the statistical package mcmcplots in RStudio (RStudio Team (2016). RStudio: Integrated Development for R. RStudio, Inc., Boston, MA). Seven of the cases were reclassified as either uDDE or hDDE based on this model-selection procedure. Appendices A and B identify which cases we found a different form of DDE than reported by the authors.

Quadratic regression is not a rigorous method for determining if a relationship is truly u- or humped-shaped as opposed to being monotonically concave or convex (Simonsohn 2018). For the above seven reclassified cases and four of the six cases originally classified as hDDE and uDDE (we could not obtain the raw data for two cases), we used the Robin Hood algorithm

proposed by Simonsohn (2018) that estimates two regression lines and tests whether there is a significant sign change between the slopes.

Similar to the review by Sibly et al. (2005) that explored the relationship between density and the per-capita population growth rate, we also examined whether the form of DDE varied with taxonomic group. Species were grouped according to broad taxonomic classes (insect, mammal, bird, fish, reptile, other invertebrate, and microorganism). Because of low sample size, reptiles (n=4 cases) were not included in subsequent taxonomic statistical analyses. We also assessed whether the frequency of each form of DDE differed between observational or experimental studies and whether the number of density levels or the range of densities influenced the detection of any particular form of DDE. For the density range, we took the ratio of the highest and lowest densities in the study. Finally, because of low sample sizes, all nonlinear forms of DDE, including uDDE and hDDE, were combined into the category “nonlinear” for methodological comparisons (number of densities, study method, and density ratio).

To evaluate whether the proportion of each DDE form varied significantly with taxonomic group or study methods (observational/experimental), we used separate Pearson’s chi-square tests for independence with Monte Carlo simulations of 10,000 iterations. Differences among DDE forms in the number of density levels and density ratio were assessed with generalized linear models. To account for the right-skewed data and excess of low values, the error distribution was defined as negative binomial. Chi-square statistical analyses were performed with RStudio. The generalized linear models were analyzed using SAS (Version 9.4, SAS Institute Inc., Cary, NC) Proc GLIMMIX and all other analyses were performed with JMP (JMP®, Version 14. SAS Institute Inc., Cary, NC). Figures were created using JMP.

Results

Overall, the 145 case studies of DDE spanned a wide range of taxa including insects (43%), mammals (15%), birds (16%), fish (8%), invertebrates (10%), micro-organisms (6%), and reptiles (2%). As predicted, the majority of cases exhibited +DDE (36%) or DIE (30%) forms. Interestingly, -DDE was reported in 25% of the cases. Finally, 6% and 3% of the cases were classified as uDDE and hDDE, respectively. These nonlinear forms of DDE have been reported only since 2009; however, four cases of uDDE and hDDE pre-dating 2009 were reclassified by us (see Appendix A). Following more rigorous testing using the Robin Hood method of Simonsohn (2018), we could confirm only one case of uDDE (Maag et al. 2018) and two cases of hDDE (Jacob et al. 2016; Chatelain and Mathieu 2017; Supplementary Material provided to American Naturalist for publication, Table S2).

We found no evidence that the frequencies of different forms of DDE varied among taxonomic group ($\chi_{220} = 19.81$, $p = 0.47$; Fig. 2.2). However, the frequencies of each form of DDE did depend on whether the study was observational or experimental (38% and 62% of all studies, respectively). Cases reporting DIE and +DDE were significantly more likely to be experimental than observational: 72% of the cases of DIE and 69% of the cases of +DDE occurred in experimental studies ($\chi_{21} = 19.36$, $p < 0.0001$ and $\chi_{21} = 14.44$, $p = 0.0001$ respectively). Conversely, in 58% of -DDE cases were observational studies ($\chi_{21} = 4.0$, $p = 0.046$). Finally, the thirteen nonlinear cases had methods equally shared between observational (43%) and experimental (57%) methods ($\chi_{21} = 0.98$, $p = 0.32$).

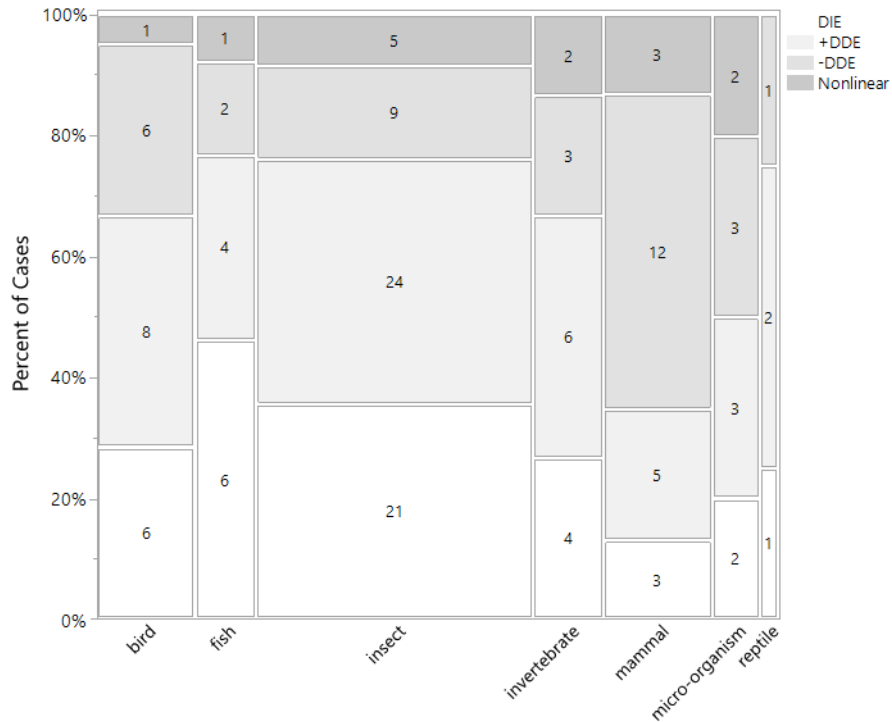


Figure 2.2. Mosaic representing the percent of each density-emigration form within taxonomic group. Numbers represent the number of cases within each category. The width of each column represents the proportion of each taxon among all cases. The density-emigration forms include density-independent (DIE), positive (+DDE), negative (-DDE), and nonlinear forms (u-shaped, h-shaped and all forms with a significant quadratic term in the model combined).

Among the 145 case studies in our review, the number of densities or density levels was often quite low. Twenty-two percent of the cases had only two densities and an additional 21% had three. Not surprisingly, observational studies averaged more than twice as many densities as the experimental studies (14.4 ± 3.1 [median = 7] versus 5.9 ± 0.7 [median = 3.5] $F_{1,129} = 29.2$, $p < 0.001$; Fig. 2.3). Additionally, the range of densities, measured as the ratio of the highest-to-lowest density, was 1.2 times greater for observational (21.4 ± 6.0 [median=6.3] compared to experimental studies (17.6 ± 4.0 [median = 6]; $F_{1,121} = 29.9$, $p < 0.001$; Fig. 2.3). The number of densities was significantly different among DDE forms ($F_{3,127} = 5.66$, $p = 0.001$; Fig. 2.3) with cases of DIE (5.2 ± 0.6 [median = 5]) utilizing a third of the densities of cases of nonlinear DDE (14.3 ± 6.8 [median = 4]) and half the densities of cases of +DDE (8.3 ± 1.4 [median = 4]) and -

DDE (11.0 ± 3.1 [median = 5]). The number of densities was also significantly higher for nonlinear DDE cases than +DDE cases ($p = 0.05$). DIE cases also utilized a narrower range of densities than the other DDE forms ($F_{3,119} = 5.77$, $p = 0.001$; Fig. 2.3). Studies with DIE had a high:low density ratio of 9.1 ± 2.6 (median = 4.0). Studies with +DDE, -DDE, and the nonlinear forms had a ratio of 25.7 ± 7.8 (median = 7.5), 17.3 ± 4.1 (median = 8.0) and 24.2 ± 8.0 (median = 16.0) respectively (Fig. 2.3).

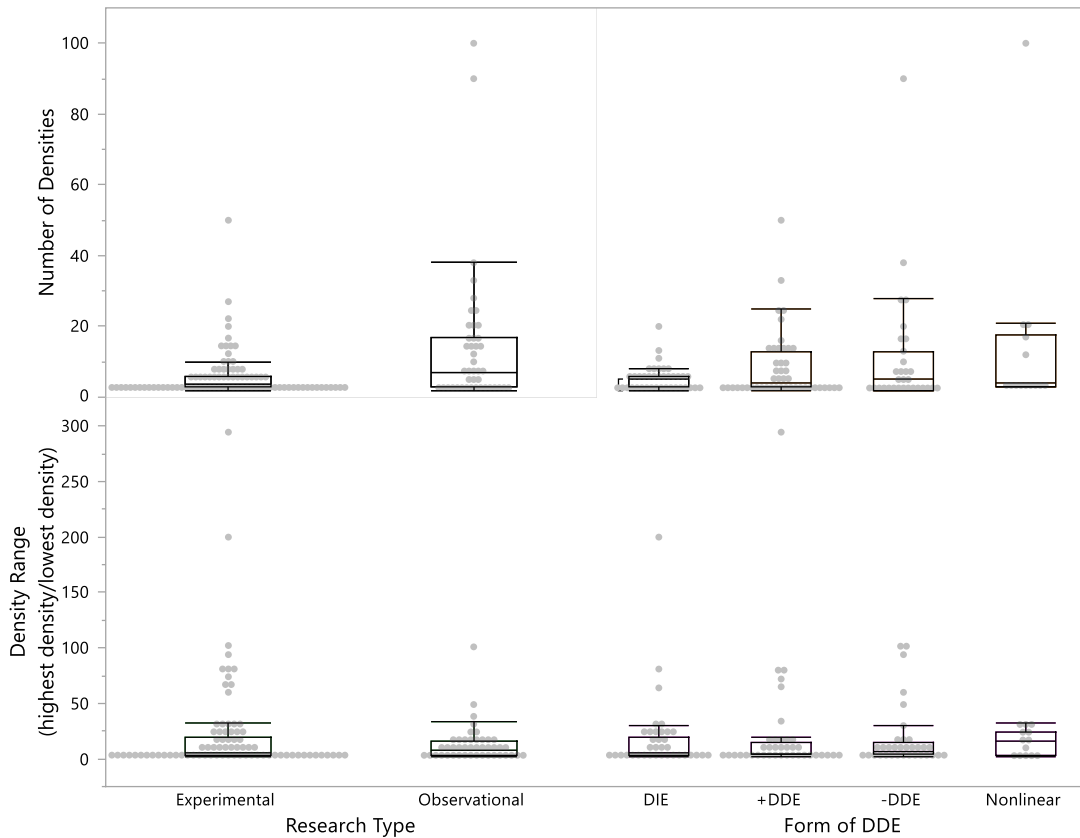


Figure 2.3. Box-and-whisker plots for the number of density levels and density range for experimental and observational methods as well as for the different forms of DDE (density independent [DIE], positive [+DDE], negative [-DDE] or all nonlinear forms combined). The box plot shows the median (horizontal bar) and the 25% and 75% quantiles (ends of the box). Whiskers are ± 1.5 (range between the 25% and 75% quantiles). Grey dots are the raw data.

OBJECTIVE 3: POPULATION DYNAMICS OF DDE

Methods

Although a wide range of DDE forms are evident in nature, little is known about the long-term population consequences for populations that exhibit each form. To illustrate the key differences in population persistence and minimum patch size between the DDE forms, we mathematically analyzed a theoretical population model based on the reaction diffusion framework. Our flexible, one-patch model allows patch size, boundary condition, and matrix hostility to vary with a defined form of DDE (Fig. 2.4). This approach is not an exhaustive analysis of the local population-dynamic consequences of different forms of DDE; however, we demonstrate, with a broadly applicable model, that the form of DDE can have important consequences for within-patch population dynamics, such as population persistence in patches that meet a minimum patch size (Schultz and Crone 2005).

One-dimensional patch (Ω) of length (ℓ) and a population density (u) with intra-patch diffusion (D), carrying capacity (K) and growth rate (r). Individuals in the population emigrate utilizing one of five DDE functions ($\alpha_i(u)$).

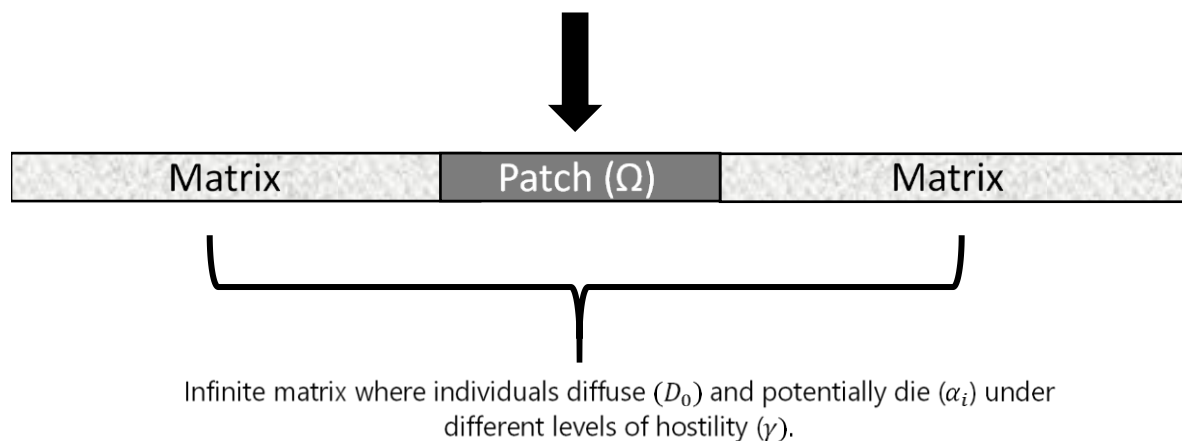


Figure 2.4. Graphic representation of the primary variables incorporated into the one-patch model used to create the bifurcation-stability curves for each form of density-dependent emigration (DDE).

Edge permeability can be dependent on the matrix surrounding the patch (Reeve et al. 2008) as matrix degradation increases mortality of dispersers (Maciel and Lutscher 2013); therefore, we utilize three matrix hostility levels to assess population persistence. First, we consider a one-dimensional patch $\Omega = (0, \ell)$ surrounded by a hostile matrix where $\ell > 0$ represents the patch size. The model is based on a derivation given in Cronin et al. (2019) and the references therein. Here, $u(t, x)$ represents the density of a theoretical population (u) inhabiting patch Ω with the variable t representing time and x representing spatial location. The model is then:

$$\begin{aligned} u_t &= Du_{xx} + ru\left(1 - \frac{u}{K}\right); t > 0, x \in \Omega \\ D\alpha_i(u)\frac{\partial u}{\partial \eta} + \frac{\sqrt{S_0 D_0}}{\kappa}[1 - \alpha_i(u)]u &= 0; t > 0, x \in \partial\Omega \end{aligned} \quad (1)$$

where the parameter D is the diffusion rate inside the patch, D_0 is the diffusion rate in the matrix surrounding the patch, S_0 is the death rate in the matrix, $\alpha_i: [0, \infty) \rightarrow [0, 1]$ encodes the DDE relationship as a function of organism density that outputs the probability that an organism remains in the patch upon reaching the boundary ($\partial\Omega$) with $i = 1, 2, 3, 4$, or 5 depending on the density-emigration relationship, and κ is a parameter encapsulating assumptions (see Cronin et al. 2019) regarding the patch/matrix interface such as movement behavior. Also, $\partial u / \partial \eta$ represents the outward normal derivative of u and the reaction term is standard logistic growth with intrinsic growth rate r and carrying capacity K of the population inside the patch, Ω . The parameters D, D_0, S_0, r, K and κ are always positive. The dynamics of (1) with constant α_i and $\kappa = 1$ are well known (see e.g., Cantrell and Cosner 2003).

Following a standard nondimensionalization, (1) becomes:

$$\begin{aligned} u_t &= \frac{D}{r\ell^2}u_{xx} + u(1 - u); t > 0, x \in \Omega_0 \\ \alpha_i(u)\frac{\partial u}{\partial \eta} + \ell\gamma[1 - \alpha_i(u)]u &= 0; t > 0, x \in \partial\Omega_0 \end{aligned} \quad (2)$$

where the patch size ℓ is now present as a parameter inside the model, $\Omega_0 = (0, 1)$, $u(t, x)$ now measures a percentage of the carrying capacity K ; t has been scaled by the intrinsic growth rate r ; and $\gamma = \sqrt{(S_0 D_0)} / (D\kappa)$ describes the hostility of the matrix where $\gamma \approx 0$ implies a low level of hostility and $\gamma \gg 1$ implies a situation where an organism faces almost immediate mortality upon entering the matrix. Lastly, through the nondimensionalization process, κ , only has an impact on the interpretation of the matrix hostility, γ , and does not qualitatively change the bifurcation-stability curves resulting from the model. Using these important parameters found in (2), we can illustrate the potential dynamical differences between the DDE forms in a clear, generalizable reaction-diffusion model.

To assess the effects of different DDE forms on the persistence of a population with dynamics that are governed by (1), five $\alpha_i(u)$ functions were selected with $\alpha_1(u)$, $\alpha_2(u)$, $\alpha_3(u)$, $\alpha_4(u)$, and $\alpha_5(u)$ representing DIE, +DDE, -DDE, uDDE, and hDDE respectively (see supplementary material for details). Each $\alpha_i(0)$ -value is designed so that any corresponding differences in the results are due only to the density-emigration relationship. We then employed an adaptation of the time-map analysis method given in Foneska et al. (2019) to study the structure of positive steady-state solutions of (2); i.e., the conditions under which population persistence is possible. An algorithm was written in Mathematica (version 11.2, Wolfram Research Inc.) to generate bifurcation curves based on this method which depicts the structure of positive steady states (i.e., population persistence) of (2) as the main parameters patch size, ℓ , and matrix hostility, γ , are varied. The time-map analysis method and resulting bifurcation curves provide a complete picture of the number and types of positive steady states for (2).

To augment these bifurcation curves, we performed a linearized stability analysis of the trivial steady state of population extinction, $u(x) \equiv 0$, and determined the stability properties of

this state, including the location of the state's change from stable to unstable, based upon the parameters in the model. Further, we employed the time-map analysis method and Mathematica (version 11.2, Wolfram Research Inc.) to computationally determine the actual profile of each steady state. A linearized stability analysis was then used on these steady-state profiles to numerically estimate the stability properties of each steady state. The final product of this analysis is a bifurcation-stability curve of the patch size ℓ versus the maximum value of the steady-state profiles with an indication of whether or not each steady state is stable, or unstable for each fixed γ (matrix hostility). Note that all stable steady states are asymptotically stable.

Results

We fixed values for the intrinsic growth rate, r , and patch diffusion rate, D , and produced bifurcation-stability curves for three scenarios: 1) low matrix hostility $\gamma \approx 0$, 2) intermediate matrix hostility, and 3) high matrix hostility $\gamma \gg 1$. The scenarios of low matrix hostility (see supplementary material) and intermediate (Fig. 2.5) hostility yielded qualitatively similar model predictions.

In all cases of matrix hostility, there is a minimum patch size, denoted as ℓ^* , for each of the forms of DDE. For any patch with size larger than ℓ^* the model predicts that any nonnegative initial density profile will tend to a positive steady state as time, $t \rightarrow \infty$ and lead to unconditional persistence. Depending on the form of DDE and patch size, the steady state may be precariously close to zero and the local population may be prone to extinction given a large enough stochastic event that negatively affects the population. For patches whose size is below the minimum patch size ℓ^* , population persistence depends on the density-emigration relationship and proximity of the actual patch size to ℓ^* . In all cases of matrix hostility, sufficiently small patches are predicted

to go extinct ($u \equiv 0$) and patch sizes greater than π are predicted to have unconditional persistence as there is enough core size to ensure that the effects of the hostile matrix are mitigated. Specifically, for a hostile matrix (Fig. 2.6), there is no change in the minimum patch size between the DDE forms.

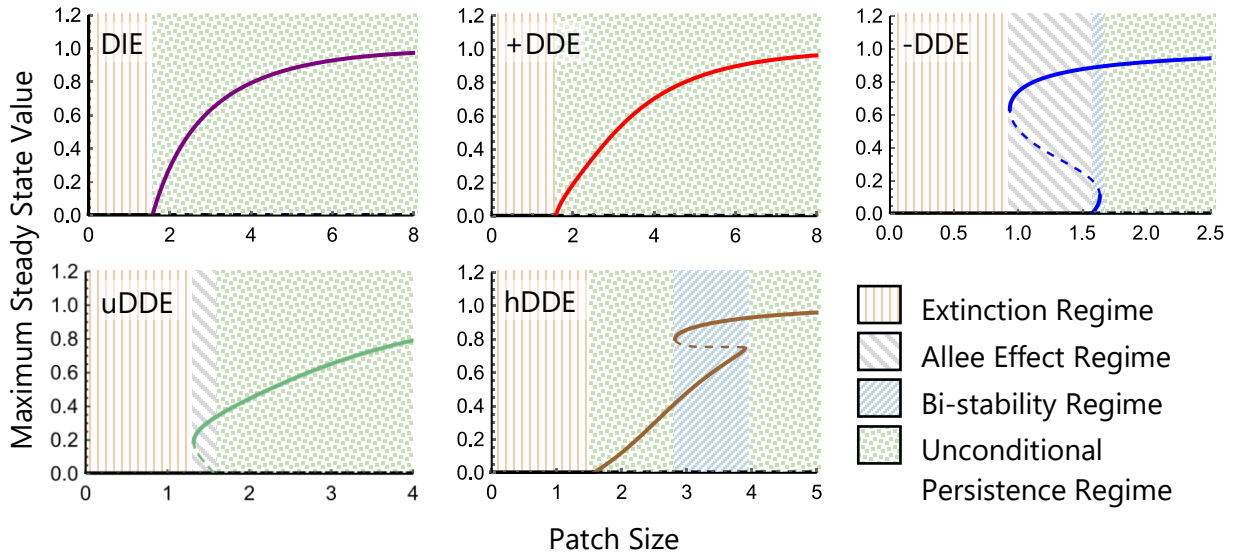


Figure 2.5: Bifurcation-stability curve of population persistence within an intermediate hostility matrix. Solid curves indicate stable steady states and dashed curves indicate unstable steady states. The density-emigration forms include density-independent (DIE), positive (+DDE), negative (-DDE), u-shaped (uDDE), and hump-shaped (hDDE). Note, the scaling of the x-axis differs among DDE forms in order to more clearly show Allee and bistability regimes.

For both a low (supplementary material) or an intermediate hostility matrix (Fig. 2.5), for DIE, +DDE, and hDDE, ℓ^* is exactly the minimum patch size for the population to persist. Below this threshold patch size, successful colonization would not be possible and the population would go extinct. For patches whose size is greater than ℓ^* , the model predicts unconditional persistence for any positive initial density profile. However, populations with patch sizes below ℓ^* but sufficiently close to ℓ^* , have conditional persistence. The model predicts an Allee effect for patches with this size range (Allee effect regime) for the -DDE or uDDE forms. An Allee effect arises in a reaction-diffusion model whenever the trivial state (zero population size) and a

positive steady state are both stable with at least one unstable state separating the basin of attraction for these stable states. For patches whose size is below the Allee effect regime, the model predicts population extinction. In patches with larger size, a mono-stability regime exists with predictions of unconditional persistence.

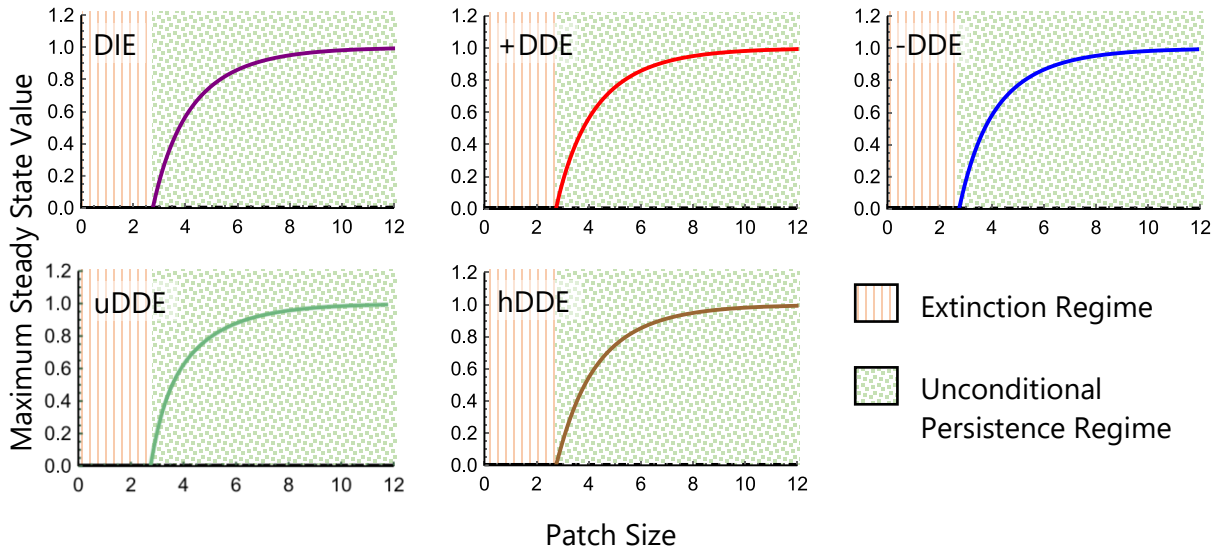


Figure 2.6: Bifurcation-stability curve of population persistence within a high hostility matrix. Solid curves indicate stable steady states. The density-emigration forms include density-independent (DIE), positive (+DDE), negative (-DDE), u-shaped (uDDE), and hump-shaped (hDDE).

When matrix hostilities are low (supplementary material) and intermediate (Fig. 2.5), populations with -DDE forms are predicted to exhibit bi-stability in patches with size larger than ℓ^* but sufficiently close to it. Likewise, a similar bi-stability region exists in the case of hDDE for patches with size slightly larger than ℓ^* . The bi-stability region predicts two positive steady states that are stable, with an unstable state partitioning the basin of attraction for these stable states.

For a high hostility matrix, the theoretical organism has a high probability of dying upon leaving the patch. Within this severe environment, model predicts a minimum patch size ℓ^* ($\ell^* \approx 2.7$; Fig. 2.6) that is the same for each of the forms of DDE and is larger than each of the

intermediate and low hostility matrix landscapes. However, for patches with size greater than ℓ^* the model predicts population persistence. In such a high hostility matrix, the model predicts very little dynamical differences between density-emigration forms.

DISCUSSION

Ecological theory has been rather limited in its view of how density influences emigration. Although our literature review confirmed that +DDE and DIE are the most common forms of density-dependent emigration (36% and 30% of the cases, respectively), -DDE accounted for 25% of the cases and nonlinear forms (uDDE and hDDE) accounted for another 9% of the cases. Importantly, our models suggest that these non-paradigmatic forms of DDE (-DDE, uDDE, and hDDE) can cause interesting and complex within-patch dynamics that are not observed when considering only traditional forms of DDE. Specifically, our models reveal the possibility of Allee effects that can cause a decrease in minimum patch size, allow populations to persist in very small patches, and cause populations to suddenly crash if the patch is further reduced in area. Forms of DDE that have negative density-dependent emigration at high densities (-DDE and hDDE) can also have two steady states within smaller patches.

We suggest that negative and nonlinear forms of DDE are more common than our literature review has revealed. Studies tend to use very few density levels, particularly experimental studies. In fact, 22% of the 145 studies used only two density levels; thus precluding the detection of nonlinear DDE. Another 21% of the studies used only three density levels, the absolute minimum number needed to detect nonlinearities in the density-emigration relationship. Necessarily, because of the replicated nature of experimental studies, the number of density levels is often small. In the case of our literature review, experimental studies used one-

half as many density levels as observational studies, with a median of only 3.5 density levels. Furthermore, our analysis of the literature revealed that studies reporting evidence for DIE had a density range, measured as the ratio of the highest-to-lowest density level, that was one-half the range used to detect the other forms of DDE. The ability to detect density dependence in any of its forms (e.g., density-dependent per-capita growth) has long been known to be limited by sample size, number of densities, or range of densities (e.g., Fowler et al. 2006; Hassell 1986). Of course, these methodological limitations have been recognized by those who study species emigration. For example, the Glanville fritillary butterfly, *Melitaea cinxia*, was reported as having both -DDE and +DDE (Kuussaari et al. 1996; Kuussaari et al. 1998). By combining results from these two studies, and, effectively expanding the density range, Enfjall and Leimar (2005) concluded that uDDE was a better fit for this species. Clearly, future observational studies and experiments should include a broader range and number of densities to better characterize this relationship.

Models have predicted that -DDE creates unstable populations in which population density is poorly regulated and thus unlikely in nature (Amarasekare 2004; Wolff 1997). Despite this theoretical disadvantage to populations, -DDE was found in one fourth of the studies. At least over a portion of the density range, -DDE is expected for species actively engaged in group living (Bowler and Benton 2005; Kim et al. 2009; Matthysen 2012). Intuitively, we would expect that as the density of a gregarious species gets too high, increased rates of emigration should follow (i.e., uDDE). Examples of a gregarious species exhibiting -DDE include the sociable weaver, *Philetairus socius* (Altwegg et al. 2014) and prairie voles, *Microtus ochrogaster* (Smith and Batzli 2006). In another interesting example, Jacob et al. (2016) established genetic lines of the ciliated protozoa *Tetrahymena thermophile* that displayed either low, medium, or high

degrees of aggregation. Those lines exhibited hDDE, -DDE and uDDE, respectively. We attempted to explore whether gregarious species were predisposed to exhibiting -DDE or uDDE. However, for many species, it was impossible to categorize them in a binary way as either solitary or gregarious and there was insufficient information from the literature to divide them by degree of gregariousness.

In addition to life history effects on DDE (see above), the form of DDE can also be phenotypically plastic and a function of pre-dispersal conditions. For example, longer exposure time to a higher number of conspecifics led to stronger -DDE in fruit flies, *Drosophila melanogaster* (Mishra et al. 2018). These high density environments could increase the stress of the individuals (Mishra et al. 2018) or provide ample opportunity for mates (see review by Kokko and Rankin 2006), decreasing emigration at high densities. Also, trophic interactions can promote gregarious behaviors, such as with the ciliate *Paramecium aurelia*, which changed from +DDE to -DDE in the absence and presence of predator cues respectively (Hammill et al. 2015). This change in emigration strategy is theoretically dependent on the predator-induced increase in costs of dispersal that outweigh the benefits of emigrating (Hammill et al. 2015). However, this change in the form of DDE is likely system dependent; the opposite result (+DDE) occurred for the backswimmer *Notonecta undulata* when predator cues were present (Baines et al. 2014).

Density-dependent emigration is an important factor that affects population persistence (Anholt 1995; Hanski 1999). In our model, both DIE and +DDE achieve a similar asymptotic stable state as patch size increases. This stability is inherent in standard population growth models and allows for local population persistence as emigration increases when densities reach carrying capacity (Dethier 1964). Populations near their carrying capacity would tend to favor the occurrence of DIE and +DDE and could explain why those two forms were found in two-

thirds of all the cases we examined. Constant population persistence, however, is not universally found in nature (e.g., Turchin and Taylor 1992). Models have incorporated nonlinear density-dependent emigration, which can increase or decrease population persistence times (Amarasekare 1998), change minimum patch size (Colombo and Anteneodo 2018), and affect the stability of predator-prey systems (Hauzy et al. 2010). To our knowledge, no other models have examined completely convex or concave uDDE and hDDE nonlinear response curves, which we show have more complex ecological consequences than nonlinearity alone.

Alternative forms of DDE change the persistence of populations within small patches with low to intermediate matrix hostility. The Allee effect regime found in populations with DDE and uDDE allows populations to persist in smaller patches than the other forms of DDE. However, population persistence and reproductive success change at minimum patch sizes (Butcher et al. 2010) particularly for area-sensitive species (Qing et al. 2016). As only a large population is able to persist in the Allee effect patches in our model, colonization by few individuals is unlikely to create a new population in these tiny patches. Divided populations from a newly fragmented large patch are the most likely inhabitants, which is why anthropogenic fragmentation is one of the leading causes of demographic Allee effects found in populations (Courchamp et al. 2008). The Allee effect is often connected with gregarious species that receive a benefit from cohorts (Kramer et al. 2018). Interspecifically, the Allee effect has been shown to induce multistability in predator-prey systems (Dhiman and Poria 2018). Although Allee effects are considered widespread, have been found in many taxa (Dennis et al. 2016), and could become more commonplace as our global climate warms (Berec 2019; Kramer et al. 2018), little empirical work has examined how Allee effects are directly caused by dispersal and habitat alteration (Kramer et al. 2009). Dispersal between populations with strong Allee effects allows

for population persistence (Wang 2016); however, populations in patches that are close to the minimum patch size are likely to crash due to stochastic events or minute decreases in the size of the patch. This has dire consequences for conservation biology as populations that appear to have high fitness may suddenly go extinct once they hit the extinction threshold in our model.

Similarly, the negative slope of $-DDE$ and $uDDE$ changes the reaction norm and produces bi-stability regimes that allows the organism to colonize and persist at a much lower density level than the other DDE forms. The different attractors create alternative stable states and can create great fluctuations in population abundance that can result in population extinction (Petraitis and Dudgeon 1999; Sutherland 1990). Most empirical work with alternate stable states has been performed with passive dispersing plants (e.g., Bertness et al. 2002) or examining entire ecosystem shifts (e.g., Van De Koppel et al. 2001; van de Leemput et al. 2016). There is some empirical evidence of population bistability in either gregarious or $-DDE$ species, such as the southern pine beetle (Martinson et al. 2013), Indo-Pacific sea urchin (Han 2016), and *Daphnia* (Nelson et al. 2001); however, emigration has not been directly connected to alternative stable states. This may be due to the lack of appropriately conducted studies, the majority of which focus on environmental changes as a treatment and do not report dispersal (for review see Schroder et al. 2005) or studies that focus on pest eradication instead of population persistence (e.g., Martinson et al. 2013).

The scale at which the study is performed can determine the density-emigration relationship measured. For example, in peregrine falcons, *Falco peregrinus*, natal dispersal distance was density independent at local scales but negatively related to density on a regional scale (Morton et al. 2018). A limited spatial scale may exclude long-distance dispersers, resulting in altered density-emigration relationships (Morton et al. 2018). Additionally, density may be

heterogeneous across a landscape, and these differences in population density may affect dispersal decisions (Bitume et al. 2013) or promote aggregation only in highly suitable habitats (e.g., damselflies; Allen and Thompson 2010) that could lead to a false positive for -DDE. Finally, density-dependent dispersal decisions (e.g., avoidance of inbreeding or competition) may differ as costs and benefits of dispersing vary with spatial scale (Bowler and Benton 2005). However, few studies have examined density dependence at various spatial scales (but see Bowler and Benton 2005; Kim et al. 2009; Morton et al. 2018).

For some species, the decision to emigrate may depend on exploratory forays into the matrix. If “foray loops” are common, as some studies with butterflies, birds and mammals suggest (e.g., Rivera et al. 1998, Roper et al. 2003, Conradt and Roper 2006), experiments that immediately remove individuals that exit the patch may overestimate emigration and predict spurious forms of DDE. Based on our literature survey, 14% of the experimental studies used this approach (Appendix A; 6 cases of DIE and 7 cases of +DDE). If the goal is to characterize the density-emigration relationship, we recommend allowing foray loops to occur or documenting that they are uncommon.

Many patch- or regional-level DDE models do not consider matrix hostility, but the choice to emigrate and thus population persistence can be dependent on the quality of the matrix (Cronin 2007; Cronin and Haynes 2004; Roland et al. 2000). In high hostility matrices, each of the DDE bifurcation-stability curves has unconditional persistence, which is partially due to the high mortality in the matrix greatly decreasing the chance that emigrating individuals will reenter the patch. Additionally, the minimum patch size is greater in patches surrounded by a more hostile matrix due to a greater edge effect. The decrease in patch area creates a decrease in the percentage of the patch that is unaffected by the edge due to the ratio of edge to patch area

(Laurance 1991), ecologically creating a smaller patch despite the area (Fagan et al. 1999). As a more hostile matrix creates a stronger edge, the core of the patch correspondingly must be larger for a population to persist. However, once a core density is reached, population persistence is stable (Cronin 2009) and there is little need for rescue from other populations.

The alternative forms of DDE create metapopulations that have more diverse interactions. In -DDE and hDDE, the innate Allee effect can decrease the rate of range expansion, creating a stable range (Amarasekare 1998; Wang 2016). As habitat is increasingly becoming more fragmented, the ability of populations to persist in smaller patches (as seen with -DDE and hDDE) may decrease the likelihood of metapopulation extinction. These small patches can then be used as stepping stones, which are crucial for long-distance range expansion (Saura et al. 2014), especially for -DDE species that are more likely to emigrate at low densities. A highly hostile matrix, however, will minimize the chances of rescue or colonization of patches, which will increase chances of extinction (Vandermeer and Carvajal 2001) and decrease range expansion speed. Lastly, change in the strength of the Allee effect can change the rate of range expansion, creating models that over- or under-predict the actual speed (Walter et al. 2017). Understanding both environmental and intrinsic density-dependent factors will better predict the movement of invasive species and metapopulation persistence in a fragmented landscape.

CONCLUSIONS

Although our literature review supports the view that density-independent and positive density-dependent emigration should be most common in nature, we found negative density-dependent emigration in one-fourth of the cases and nonlinear density dependence in another 9% of the cases. Because studies often include few density levels or focus on a relatively narrow

range of densities, nonlinear forms of DDE may have gone undetected. Methods that incorporate greater number and range of density treatments in addition to using more rigorous non-linear statistics could improve the chances of detecting these forms. Primarily, research should focus on regression-based experimental designs that incorporate densities at both very low densities and those at and above carrying capacity. Life history (e.g., gregariousness) as well as different dispersal conditions (e.g., temporal variability and environmental cues; Hammill et al. 2015; Baines et al. 2014) should be addressed or manipulated to assess plasticity in behaviors that might promote different forms of DDE. Lastly, statistics should not only incorporate quadratic analyses, but more flexible models capable of detecting a wider range of nonlinear forms, such as uDDE or hDDE (e.g., Simonsohn 2018). As our simple analytical model suggests, understanding these DDE forms can be critical for estimating population persistence, particularly in small patches. For example, rarely considered forms of DDE (-DDE, uDDE, hDDE) yield Allee effects and bi-stability regimes that are not inherent in the more well-known forms of DDE (i.e., DIE or +DDE). These new population dynamics can lead to important biological consequences such as population extinction and changes in source-sink dynamics.

CHAPTER 3.

MOVEMENT BEHAVIOR OF *ISCHNODEMUS CONICUS* (VAN DUZEE) IN FRAGMENTED SALT-MARSH HABITATS

INTRODUCTION

Habitat fragmentation transforms the landscape through selective environmental destruction that leaves multiple habitable areas that are smaller, more isolated, and divided by a less hospitable matrix (Fahrig 2003; Lindenmayer and Fischer 2006). The individuals inhabiting these subdivided habitat fragments (patches) move within and among the patches, influencing local population dynamics and metapopulation connectivity (Barton et al. 2009; Cantrell and Cosner 2007). Across the globe, fragmentation of habitats has increased through human activities (e.g, development of agriculture and urbanization; Saunders et al. 1991), which can threaten population persistence (Anholt 1995; Debinski and Holt 2000; Hanski 1999), since an increase in patch isolation or matrix hostility may influence intrapatch movement (e.g, planthoppers; Haynes and Cronin 2006) and boundary behavior (e.g., butterflies; Ricketts 2001) and limit emigration and gene flow (e.g., limpets; Cossu et al. 2017). Data concerning an individual's response to fragmentation are difficult to obtain and often the least understood aspect of the biology of a species (Evans et al. 2018; Hooten et al. 2017; Patterson et al. 2017).

The movement of individuals within a patch determines the likelihood of encountering the edge. In homogeneous conditions, a correlated random walk model and diffusive patterns of movement often adequately describe an individual's movement behavior (Hanski 1998; Johnson 2005). Intrapatch movement (e.g., speed, step lengths, and turning angles) may be biased by factors such as the abundance of resources (Franke and Yakubu 2008; McClintic et al. 2014; Wiens et al. 1995), presence of conspecifics (e.g., by use of aggregation pheromones; Bartelt et

al. 2008; Stevenson et al. 2017), interspecific competition (Senger et al. 2007), and presence of predators (Hammond et al. 2012; Sun et al. 2016).

If intrapatch movement is random, the likelihood of individuals encountering the patch edge is higher in smaller patches, which provides more opportunities for emigration to occur (Haddad 1999; Hanski 1998). However, if there is an abrupt change in environmental quality at the patch border, the hostile matrix may create edge effects that limit emigration (Fagan et al. 1999; Leopold 1933; Ries and Sisk 2010), as individuals can aggregate at (e.g., flying squirrels; Desrochers et al. 2003) or avoid the edge instead (e.g., birds, voles, parasitoids, and amphipods; Cronin 2009; Gates and Gysel 1978; Jacob and Brown 2000; Margules et al. 1994). Dispersal is often context-dependent, for example with changes in movement tortuosity in different landscapes (e.g., planthoppers and damselflies; Haynes and Cronin 2006; Jonsen and Taylor 2000; Pither and Taylor 1998) or with an emigration response to density (e.g., ciliates and fritillary butterfly; Jacob et al. 2015; Kuussaari et al. 1996; Kuussaari et al. 1998). Strong natural selection of dispersal ability may create dispersal dimorphisms, such as wing length, that can limit the long-distance dispersal capability of the individual (e.g., planthoppers, crickets, and aphids; Holder and Wilson 1992; Langellotto and Denno 2001).

Individual movement behavior provides information on the spatial structure of the population (e.g., clumped and over-dispersed patterns) that may indicate species behaviors, such as beneficial aggregating or intraspecific competition (Hooten et al. 2017; Patterson et al. 2008; Wiegand and Moloney 2014). Additionally, individual movement decisions can influence the form of the density-emigration relationship (e.g., density-independent, positive, negative, u-shaped, hump-shaped) and alter population and metapopulation persistence (Amarasekare 2004b; Harman et al. 2020). For example, species that form aggregations often show negative density-

dependent emigration (DDE) (e.g., damselflies, fruit flies, and fleas; Allen and Thompson 2010; Mishra et al. 2018; Tripet et al. 2002), as individuals are less likely to leave high densities due to a benefit of group living. Species with positive DDE, on the other hand, are prone to leave crowded densities and establish themselves in habitats with few to no conspecifics (Amarasekare 2004b).

To assess individual behavior and movement as a reaction to fragmentation, we studied *Ischnodemus falicus* (Say) (Hemiptera: Blissidae), a gregarious blissid bug that is a common pest on marsh cordgrass (*Spartina spp.*) (Wheeler 1996) in fragmented environments. Little empirical research has studied *I. falicus* (but see Johnson and Knapp 1996) or its congeners, and nothing is known concerning its dispersal behavior. Here, we assessed the potential for long-distance dispersal by quantifying the proportion of macropterous (long-winged) individuals. Macroptery is a common measurement of dispersal propensity (e.g., Denno et al. 2001; Poniatowski and Fartmann 2011; Strong and Stiling 1983) as brachypterous (short-winged) individuals often lack the ability to fly long distances. Additionally, we assessed the density-emigration relationship, predicting a negative DDE form as the species aggregates.

Lastly, movement behavior and spatial distribution of individual insects within a *Spartina* patch, hostile sand matrix, and at the edge between was quantified from paths created by continuously watched individuals in gridded landscapes. We hypothesized tortuous movement with few steps within the habitat and edge landscapes that would result in clumped distribution. In contrast, movement within the sand matrix was predicted to have little tortuosity and larger step size that would allow the insect to cross the hostile matrix quickly. These assays on movement can be used as the first step toward developing predictive models for population dynamics.

MATERIALS AND METHODS

Study system

Smooth cordgrass, *Spartina alterniflora* (Loisel) (Poaceae) is a dominant low marsh, perennial species native to the Atlantic and Gulf coasts that thrives in high salinity environments (see review by Subudhi and Baisakh 2011). Genetically identical, circular patches of cordgrass are often created as the plant primarily propagates vegetatively (Daehler and Strong 1994). In this harsh and fragmented habitat, the blissid bug, *Ischnodemus conicus*, feeds on the leaf sheaths and the xylem or phloem of smooth cordgrass (Harrington 1972). *I. conicus* was originally described from Texas (Van Duzee 1909) and its range includes the states along the Gulf of Mexico and Atlantic, with Virginia as the most northern state (Slater and Baranowski 1990). Little biology of the species is known, but its only reported host plant is *S. alterniflora* and it is primarily located on the coast (Harrington 1972).

The range of *I. conicus* greatly overlaps *I. badius* (Van Duzee) and, although information concerning this species is also very limited, the two species may share the same host and compete (Rey 1981). Harrington (1972), however, recorded *I. badius* on *S. patens* (Aiton) Muhl. alone, which may indicate that the report by Rey (1981) included misidentified *I. conicus* (Slater and Baranowski 1990).

Using the Florida Lygaeidae key (Slater and Baranowski 1990), we identified our bugs as *I. conicus* based on the color and morphology of the pronotum and interocular distances, which are longer for *I. conicus* than *I. badius* individuals. Additionally, our insect included macropterous individuals whereas *I. badius* has been reported as primarily micropterous (Slater and Baranowski 1990). *I. falicus* (Say), was also considered due to its similarity in appearance, but was eliminated based on host plant, distribution, and pubescence character. Voucher

specimens were submitted to the Louisiana State Arthropod Museum (reference identification LSAM0272350 - LSAM0272362 and LSAM0272363 – LSAM0272364).

Many species within the *Ischnodemus* genus exhibit long and short wing (macropterous and brachypterous respectively) morphs including *I. sabuleti* (Fallén) and *I. slossonae* (Van Duzee), while other species additionally have micropterous forms, such as *I. badius* (Van Duzee) (Slater and Baranowski 1990). *I. falcius* has been noted as social (Johnson and Knapp 1996) and produces a distinct odor (Wheeler 1996 and personal observation) that may be indicative of a communication or aggregation pheromone, there is no support that any species in the genus benefits from group living.

I. conicus is an ideal insect to study movement as it has a large body size that can easily be marked, its sex is distinguished by size (females are 30% longer than mature males) and immature juveniles can be identified by both small size and red coloration. The insect has slow movement both within and between cordgrass patches and the path is traceable. The landscape in which *I. conicus* resides is dynamic, with habitat lost through coastal erosion, rising oceans, and anthropogenic landscape modification (Boesch et al. 1994); whereas, in another location, restoration dredging projects create new landmasses, often using *S. alterniflora* as the primary provider of soil erosion resistance (Subudhi and Baisakh 2011; Zedler 2000). The dispersal of *I. conicus* individuals may determine the persistence of and ability to expand its range into the newly formed habitats. Additionally, data concerning movement can provide generalizable information of metapopulation conservation in disturbed habitats.

Field surveys and experiments

Research was conducted within a saltmarsh adjacent to the Cameron Jetty Pier in Cameron, Louisiana, USA. The site included numerous patches of *S. alterniflora* on the sandy beach that were above the average high tide mark (Fig. 3.1). Occasionally, storm activity would result in water levels several centimeters above the ground. Here, the highest adult *I. conicus* population densities occurred in September through December with few individuals found during the rest of the year. In October and November 2017 surveys, populations had clumped distribution, with an average of 2.7 (variance = 19.7; Fig. 3.1) insects per stem (approximately 1260 insects per square meter) and aggregates as high as 30 insects on a single *S. alterniflora* stem. Additionally, we found very few *I. conicus* individuals at our study site within the adjacent *S. patens* patches at any time of the year.



Figure 3.1. Image of *Spartina alterniflora* landscape on the Cameron Jetty Pier, Cameron, LA, with the small patches common around the edges of larger patches (left). Aggregates of *I. conicus* on *S. alterniflora* stems (right).

Field survey: I. conicus emigration

To determine the proportion macropters in the Cameron Jetty *I. conicus* population, we collected 150 males and 180 females between the collection dates of September 12 and October

3, 2015. On each date, the insects were collected by sweep netting ten 2 m x 2 m sections of *S. alterniflora* patches. They were transported to the lab on ice and subsequently frozen. The right forewing of each insect was measured from the edge of the pronotum to the tip of the membrane while attached to the insect as well as the full body length using an ocular micrometer inserted into the eyepiece of a dissecting microscope (20-times magnification). The ratio of wing length to body length was calculated for each individual and a histogram created using Microsoft Excel 2016.

Field experiment: Density-emigration relationship

Between June and October 2015, an experiment was performed at the Cameron Jetty Pier to assess the relationship between *I. conicus* density and the proportion emigrating from a 30 cm diameter (33 ± 7 stems; mean \pm SE) patch that was surrounded by a bare-sand matrix at least 50 cm wide. Patches of this size were common and often supported *I. conicus* individuals. Thus they were found or created by cutting stems below the sand to reduce the diameter of the patch to the desired size. Based on a previous experiment (R. R. Harman unpublished data), these 30-cm diameter patches are not so small as to preclude natural boundary behavior by *I. conicus*. In comparison to an equivalent area of host plants within a much larger *Spartina* stand, the proportional loss of marked and released *I. conicus* was 1.4 times lower in the discrete patch ($T_{19} = 4.09$, $p < 0.001$).

Using sweep nets, adult female *I. conicus* were collected from large *S. alterniflora* patches along the Cameron Jetty's marsh. As brachypterous individuals dominated the samples (see Results), all tests were performed with only brachypters. Densities ranging from 3-180 were used. The highest density used in the experiment was twice the density of *I. conicus* per stem

observed within the landscape during peak activity (5.5 compared to 2.7 insects per stem). Using a wide range of densities has been shown to increase the ability to detect different forms of density-dependent emigration, including non-linear relationships (e.g., u-shaped and hump-shaped; Enfjall and Leimar 2005; Fowler et al. 2006; Harman et al. 2020).

After collecting the insects, we placed them into vials and chilled them on ice for 15 minutes. We then transferred the insects to a vial lightly coated with Dayglo fluorescent powder (Dayglo Corporation, Cleveland, Ohio, USA) and gently tumbled the individuals to mark them. This marker has been used in other dispersal studies with insect movement (e.g., Cronin 2003; Dickens and Brant 2014; Fryer and Meek 1989; Turchin and Thoeny 1993) with no significant harm to the insect nor changes in dispersal behavior. Male *I. conicus* and juveniles were not used because the movement of gravid females primarily determines population spread (Cronin 2003; Dickens and Brant 2014; Haynes and Cronin 2003). To mediate environmental effects on dispersal, trials were limited to days that were sunny to partially overcast. Replicate releases that occurred during pre-storm conditions with elevated wind speeds were removed from the dataset. All releases occurred between 10 a.m. and 3 p.m.

The 30 cm patches were cleared of insects via sweep netting before the vials with *I. conicus* were placed upside down into the center of the patch for 30 minutes. After the insects settled, the vial was gently removed. Marked insects remaining in the patch were counted 180 minutes after release by carefully searching each stem. Dead insects that had not left the release point after three hours were subtracted from the initial density (mean dead \pm SE = 19% \pm 4). Proportion emigrated was calculated as the (number remaining in the patch) / (initial density – number died). We performed a total of 34 mark-release trials.

The density-emigration experiment was repeated with 6 additional releases in September 2016, using the same methods and density range as in the previous year. To determine the relationship between density and the proportion emigrating, and whether it was linear or quadratic, we used Akaike information criteria corrected for small sample size (AICc) to choose the most informative model. The full model included year of study, density and density². Year was treated as a fixed factor and not a repeated measure because different generations occur each year and individuals were collected from a wide area, making the bugs used between the two time periods largely independent of one another. The model with the smallest AICc value was selected as best fit, but all competing models with a delta AICc value ≤ 2 were considered to have substantial support (Burnham et al. 2011). If the quadratic form was selected by the model, it was further checked for a full change in slope, as expected from a humped- or u-shaped relationship. We used the Robin Hood method (Simonsohn 2018) to estimate if the curve included both a significant negative and positive line.

Greenhouse experiment: Individual movement in landscapes

Patch arenas

An individual's decision to move within a habitat can determine its chances of finding the edge and thus emigrating from the habitat. However, measuring the diffusion rate of marked insects within the large, dense *Spartina* patches at Cameron was challenging as the insects were difficult to locate after release (1.5% recovery) and the high densities needed to obtain sufficient data from replicated mass mark-recapture experiments was not feasible. Thus, we created simplified landscape arenas based on the methods in Haynes and Cronin (2006). All experiments were performed within a greenhouse at Louisiana State University (Baton Rouge, Louisiana,

USA) to limit weather-related interference. To minimize variation in nutritional quality of *S. alterniflora*, small shoots were collected from one main source patch at the Cameron Jetty Pier in November 2016. We potted 3 to 5 rhizomes in sand in 14 x 14 cm “habitat” pots and fertilized with half a tablespoon of 14:14:14 (N:P:K) Osmocote slow release pellets (The Scotts Company, Marysville, OH) every six months. This stem density was 41% of that observed in the field (204 stems/m² and 490 stems/m² respectively) so movement could be more easily monitored within the experimental patch.

We created patch arenas of 140 x 140 cm by placing the pots together in a 10 x 10 square with the sand filled to the rim. Pitfalls between pots covered with insect netting and leveled off sand. To form a grid to trace the movement of individual insects, we subdivided each pot into quarters using flagging tape, resulting in a 20 x 20 grid of 400 7 x 7 cm cells (Fig. 3.2).



Figure 3.2. 140 x 140 cm *S. alterniflora* patch designed to assess movement of individual *I. conicus*. The landscape was divided into 7 x 7cm cells in a 20 x 20 grid.

In February and March 2017, *I. conicus* were collected from Cameron Jetty Pier, chilled on ice during transport to LSU, and then transferred to potted *S. alterniflora* until needed for experiments. Insects were kept for a maximum of 7 days and were only used once before

discarding them. Adult brachypterous females and males, as well as juveniles, were used in the microlandscape experiments to quantify the movement behavior of the main life stages of this bug. For each trial, 2-3 individuals from each age and sex class (total 6-8 individuals) were randomly selected from our reservoir of bugs. They were chilled on ice for 15 minutes and then gently tumbled in vials lined with Dayglow powder. The individuals within each age and sex class were marked with different colored pigments for easy identification.

Marked insects were allowed to settle for 20 minutes inside vials at the release point within the center of the arena. After the vials were gently lifted and the insects were released, individual movement within the grid and timing of movement was recorded continuously for 5 hours. Additionally, at 20-minute intervals, the location of stationary individuals was checked by carefully searching the stems at the last known location of the insect. This more active search provoked no apparent reaction from the bugs and was necessary as *I. conicus* often crawls between the stem and the leaf sheath to forage and are out of view. Only 9 of the 67 individuals used in the experiment were lost during the observation period and these individuals were subsequently excluded from any analysis. The pots in which the insects came into contact were replaced before the next experiment. Pots of *S. alterniflora* were reused after a minimum of a week had passed and the plants had recovered from any visible signs of herbivory. Ten replicate patch arenas were used, and the behaviors of 58 individuals were recorded.

Habitat-matrix edge arenas

To assess boundary behavior of *I. conicus* individuals, a similar landscape to the patch arena was used to make the edge arenas. The *S. alterniflora* habitat pots were used in addition to “matrix” pots (14 x 14 cm) that were filled with sand. Due to the limited dispersal observed in

the previous habitat landscapes, we were able to use a smaller 10 x 12 pot arena for the edge landscapes (Fig. 3.3). The edge was 5 pots wide, and both the patch and the matrix extended 3 pots deep.



Figure 3.3. Edge landscape used to assess movement of individual *Ischnodemus conicus*. Colored vials placed at the patch-matrix boundary contain insects for release. The landscape was divided into a 10x12 grid, consisting of half sand matrix and half *S. alterniflora* habitat.

Repeating the methods used in the habitat landscapes, insects were chilled, marked, and settled in inverted vials in the center of the landscape. The release was always within the cordgrass patch, but at the edge (Fig. 3.3). The timing and location of movement was continuously recorded for 5 hours. To limit biased movement due to the greenhouse environment, the arenas were disassembled and rotated by 90° between replicate trials. Five replicate arenas were used for a total of 32 recorded movement paths (not including 5 lost individuals).

Matrix landscapes

Movement within the matrix was analyzed in arenas created by leveling sand on an 86 x 86 cm plywood board. A 12 x 12 grid with 7 x 7 cm cells was created using flagging tape and

overlain on the sand (Fig. 3.4). As before, 6 to 8 individuals were chilled, marked, and allowed to settle in the inverted vials. After the vials were removed, the position within the grid and time of movement of each individual was recorded continuously for 3 hours. By the third hour, all of insects had left the arena. To eliminate potential odor cues left by the insects, the sand was removed between replicates and replaced. Ten replicate landscapes were used with 62 released individuals (7 bugs were excluded from the analysis because they disappeared from the system too quickly for any movement data to be recorded and an additional 3 were excluded as they died during the experiment).



Figure 3.4. Sand matrix arena used to assess movement of individual *Ischnodemus conicus*. The landscape was divided into a 12 x 12 grid with 7 x 7 cm cells.

Data and statistical analysis of movement

The overall rate of movement of an individual is determined by the movement velocity, tendency to move, and path tortuosity (Bowler and Benton 2005; Russell et al. 2003). Similar to the methods in Haynes and Cronin (2006), for individuals within each landscape, the movement velocity was measured as the mean step length (cm) per 5min interval. Biased population drift was assessed as the mean difference in X and Y coordinate (Turchin and Thoeny 1993) in displacement (cm) from the release point to insect location 5 hours later (habitat and edge

landscapes) or 15 minutes later (matrix landscape). If the 95% confidence interval overlapped the release area (within 3cm of 0), population drift did not occur.

The angle between each step was calculated for paths that had 2 or more step lengths. The angle at time t was plotted against the angle at $t + 1$ for each path. A significant correlation between the two angles and a high R^2 would indicate a correlated random walk, whereas a lack of a correlation or low R^2 value would reflect complete random movement. Path tortuosity was additionally assessed by calculating the fractal dimension (Fractal D) for each individual within the matrix; however, the movement paths of individuals in both the habitat and edge landscapes had too few of steps (mean \pm SE: 2.7 ± 0.5 and 4.4 ± 1.6 respectively) to properly assess the Fractal D of each path. Fractal D estimates range from 1 to 2 with outputs near 1 representing highly linear movement and near 2 suggesting random Brownian movement (Mandelbrot 1967). Although the fractal method has been criticized (Turchin 1996), it has often been validated as a proper estimate of movement behavior (Doerr and Doerr 2004; Rogers et al. 2013). The Fractal D for each path was calculated with Fractal 4.0 software (<http://www.nsac.ns.ca/envsci/staff/vnams/Fractal.htm>) using the fractal mean method, which corrects for estimation errors when the last divider step does not fall on the edge of the path (Mandelbrot 1967).

We additionally assessed the spatial pattern within each replicate using second order spatial point-pattern processes commonly used to assess insect dispersion in a landscape (e.g., Alspach and Bus 1999; Hahn et al. 2017; Wehnert and Wagner 2019). Point-pattern processes compare the spatial relationship on pairs of points to determine if the individuals are hyperdispersed, clumped, or random in space when compared to a completely spatially random (CSR) model (Wiegand and Moloney 2014). We used the pair-correlation function ($g(r)$), which

compares the arrangement of data points within multiple spatial scales using growing circles of radius (r). The function can assess the scale at which a change in spatial pattern occurred (if any) as well as the difference in intensity of the point density when compared to CSR, which can be estimated using the shape of the estimation (Perry and Enright 2006; Wiegand and Moloney 2004). Larger point densities that decline to a CSR of 1 indicate a clustered pattern while patterns that increase from CRS indicate hyperdispersion at r . As CSR equals one, the point density is a multiple of the random expected diffusion (e.g., a value of 20 indicates a neighborhood density that is 20 times higher than expected with a random pattern).

The spatial arrangement of individuals at five hours after release was used for analysis using the statistical package spatstat in RStudio. Null expectations of CSR were constructed with 95% confidence envelopes generated by the Monte Carlo simulation with 1000 iterations for each replicated release. The scale of the radius was automatically set to 1, the 7 cm width of the cell. Graphic outputs were created by the spatstat package were used to compare the calculated values to the null expectations. Analysis of spatial displacement between juveniles, males, and females was also calculated within each replicate using pairwise $g(r)$ comparisons. Lastly, density heat maps were created to display the difference in dispersion among replicates as well as among juveniles, males, and females within replicate.

In addition, initial movement in the edge microlandscape was recorded by dividing the movement into three equal probability occurrences, assuming random movement, of along the edge (330-30° and 150-210°), into the patch (30-150°), or into the matrix (210-330°) relative to the border (Haynes and Cronin 2006). This was assessed using chi-square goodness-of-fit tests with 1000 Monte Carlo simulations for each microlandscape using RStudio (with the expectation that each direction would have 1/3 chance to be selected). Movement metrics were tested for

normalcy using Goodness of Fit tests in RStudio. Failure of this test resulted in analysis using Kruskal-Wallis tests as the data could not be normalized by transformation due to being heavily skewed with 0s. Data figures were created using JMP and movement data was represented by a figure drawn in Microsoft PowerPoint 2016.

RESULTS

Field survey: I. conicus emigration

Both adult male and female *I. conicus* are wing dimorphic. The majority of the population, 90% females and 96.7% males, consists of the short-winged phenotype with a wing-body length ratio that ranged from 0.16 to 0.31 (Fig. 3.2). Macropterous individuals had a distinctly greater wing:body length ratios, ranging from 0.4 to 0.57 (Fig. 3.2). Only 10% of females and 3.3% of males were macropters (N = 180 and 150, respectively; Fig. 2). In all of our time in the field and conducting experiments in the greenhouse, we have never observed any individuals in flight.

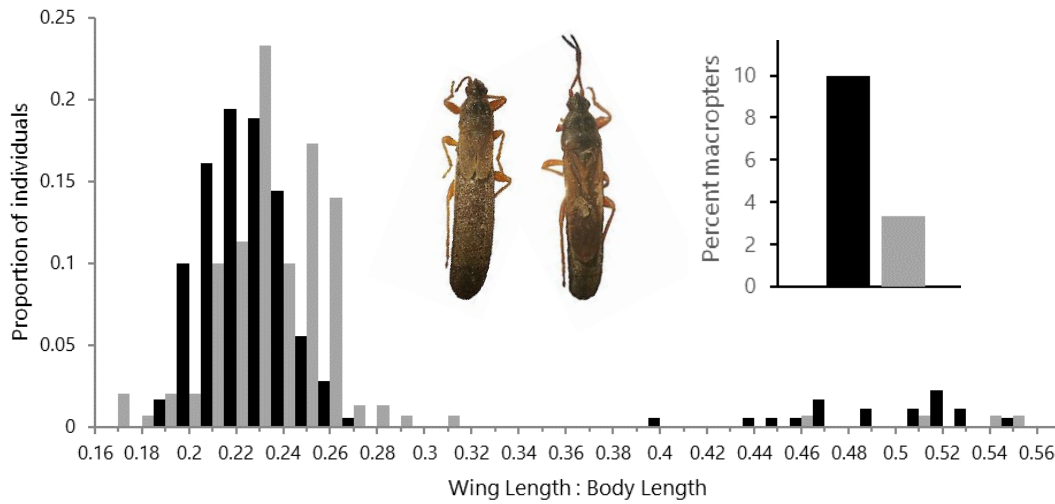


Figure 3.5. Histogram of the wing:body length ratios for female (N = 180; black bars) and male (N = 150; grey bars) *Ischnodemus conicus* collected from Cameron, LA. Images are of a brachypterous (left) and macropterous (right) female, and the inset bar graph depicts the percent males and females that were macropterous.

Field experiment: Density-emigration relationship

The density-emigration relationship was concave-nonlinear with a quadratic fit to the data ($F_{2,37} = 6.97$, $p = 0.003$, $R^2 = 0.27$; Fig. 3.6). The full model ($x + x^2 + \text{year}$; AICc weight = 0.85) was selected by the AICc analysis. All other models were not supported by the model selection (Table 3.3). At low and high densities, the emigration in 2016 appears greater than in 2015. The Robin Hood method showed no evidence that the curve had a significant negative followed by a significant positive slope that would indicate a u-shaped relationship (left side: $p = 0.001$, right side $p = 0.217$, break at a density of 71.51).

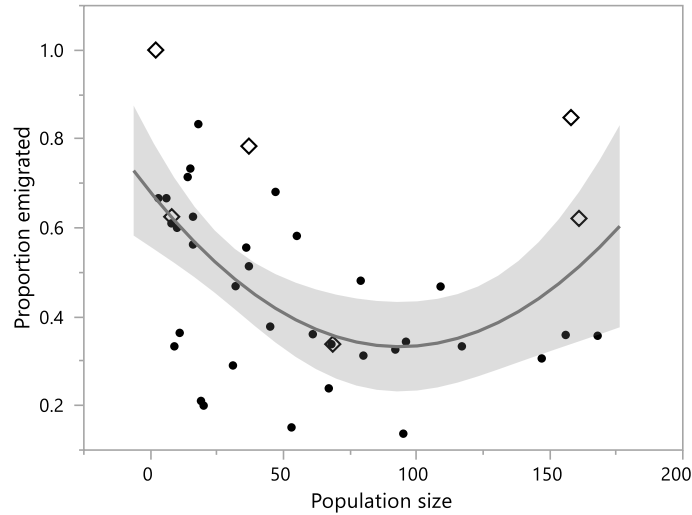


Figure 3.6. The density-emigration relationship of female blissid bug *Ischnodemus conicus* from experimental trials conducted in 2015 (circles) and 2016 (diamonds). The best fit model of a quadratic curve with 95% confidence bands is shown.

Table 3.1. *Ischnodemus conicus* density-emigration model selection results using Akaike's information criterion corrected for small sample size (AICc).

Model	AICc	Δ AICc	AICc weight
$x + x^2 + \text{year}$	-23.29	0	0.85
$x + \text{year}$	-19.08	4.2	0.10
$x + x^2$	-16.56	6.73	0.03
year	-15.18	8.11	0.01
x	-9.52	13.76	0
0	64.12	87.41	0

Greenhouse experiments: Individual movement

Movement within the patch

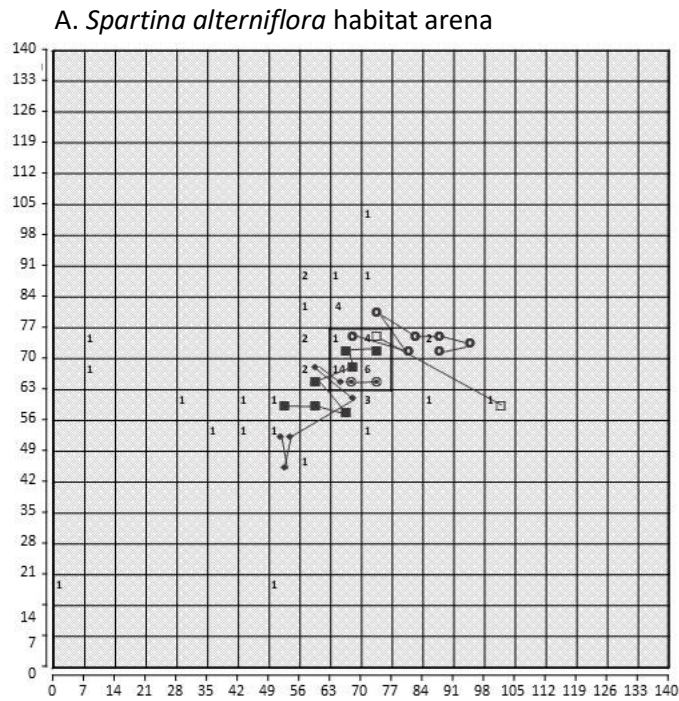
The 58 *I. conicus* insects released within the patch arena displaced a mean distance of just 2 cells (15.08 cm) within 5 hours (Fig. 3.7). The 46 insects that did move changed direction (95.02°) between short steps (0.57 cm) and made slow progress (0.10 steps per 5 m; Table 3.2). The path did not differ from a random walk due to the lack of correlation when path angle at

time t was regressed against the next angle at time $t + 1$ ($F_{1,23} = 0.86$, $p = 0.36$, $y = 0.07x + 74.07$; Fig. 3.8). The majority of movement occurred within the first three hours (55.6, 23.3, and 11.9% of the steps taken during hours 1, 2, and 3, respectively) with little movement in the fourth or fifth hour (6%, and 3% of total steps, respectively, Fig. 3.9). The displacement of individuals was unbiased in direction as the population did not drift from the release area (0-3 cm, XY) with the mean ($\pm 95\%$ CI) locations of X and Y equaled to -5.9 cm (± 5) and -1.2 cm (± 3.5) away from the exact center, respectively.

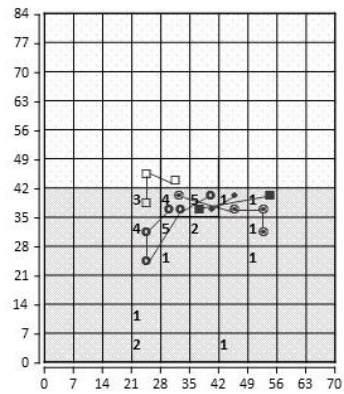
When comparing among the classes of females, males, and juveniles, the overall displacement was 2.6 times greater for females than juveniles. Two-thirds of the 12 insects that did not move from the release cell were juveniles (displacement = 0 cm for 1 female, 3 males, and 8 juveniles). However, the paths of individuals that did move were not significantly different in speed, step size, nor turning angle among the three classes (Table 3.3).

Table 3.2. Effect of habitat type on *Ischnodemus conicus* movement behavior. The Kruskal-Wallis analysis (H_{df}) was performed for each comparison of the movement paths within the *Spartina alterniflora* patch (P), edge of the patch (E), and sand matrix (M) arenas. Comparison tests are summarized in the “effect” column.

Dependent variable	Patch	Edge	Matrix	Statistic	Effect
Displacement (cm)	15.08 \pm 2.49	12.02 \pm 1.84	49.65 \pm 0.96	$H_2=77.0$, $p<0.0001$	M > P,E
Speed (steps per 5m)	0.10 \pm 0.04	0.10 \pm 0.04	3.08 \pm 0.47	$H_2=83.62$, $p<0.0001$	M > P,E
Step size (cm)	0.57 \pm 0.14	0.53 \pm 0.10	116.18 \pm 17.81	$H_2=83.57$, $p<0.0001$	M > P,E
Turning angle	95.02 \pm 10.57	100.81 \pm 11.98	75.75 \pm 7.94	$H_2=3.53$, $p=0.17$	M=P=E
Fractal D	N/A	N/A	1.27 \pm 0.04		



B. Edge arena



C. Matrix arena

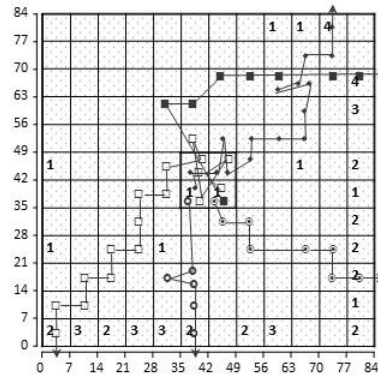


Figure 3.7. Movement and final location of individual *Ischnodemus conicus* within all replicate arenas. Numbers within the quadrant represent the number of individuals residing there at 5 hours. Five representative paths were selected to show the varying ranges of displacement with step locations (markers). For each path, the starting point was within the 14 x 14 cm center (dark outline).

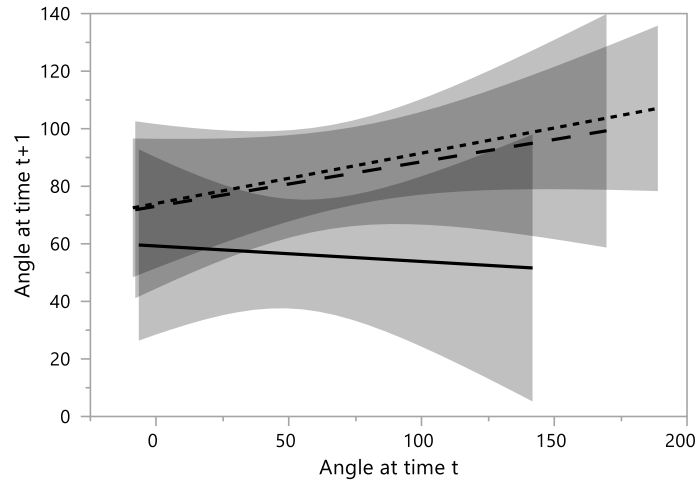


Figure 3.8. Tests of random walk for *I. conicus* paths with two or more angles between 5 min steps. Linear regression with 95% confidence bands is shown for insects released in the patch (N = 25; dashed line), edge (N = 20; solid line), and matrix (N=69; dotted line). There is no correlation for any line, suggesting the paths fit a random walk model.

As expected with the limited displacement of individuals, the *I. conicus* populations released into each patch arena replicate were clumped in distribution at spatial small scales (Table 3.4; Appendix 1). Interestingly, in the 7 arenas with at least 2 insects of each class, displacement patterns differed between sex and age. In each arena, females were hyperdispersed from other females, but were generally clumped with males and juveniles (Table 3.4). Males showed a similar trend, but in 6 of the 7 arenas and maintained hyper-dispersion for shorter distances than females. Lastly, juveniles were clumped at small spatial scales in 6 of the 7 arenas. This indicates that the movement, although similar in speed, step size and turning angle, occurred in different directions with females actively separating from each other, juveniles moving in tandem, and males moving somewhere in between. Although this displacement is calculated with only 2 to 3 individuals in each class, the pattern is replicated in each arena.

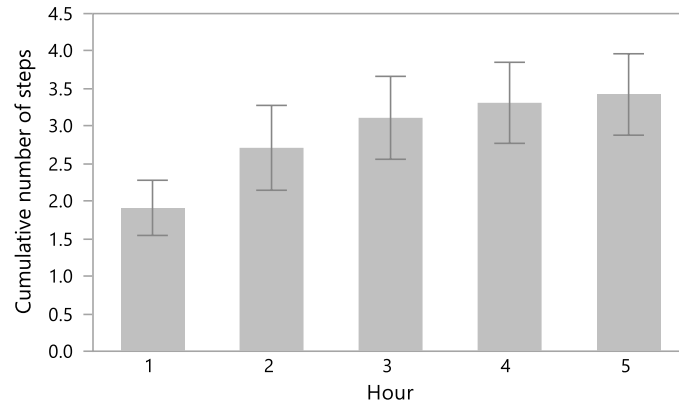


Figure 3.9. Mean (\pm SE) cumulative number of steps taken by individuals released within the habitat landscape during each hour of continuous observation.

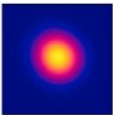
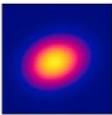
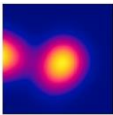
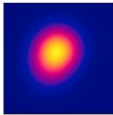
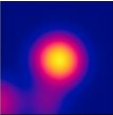
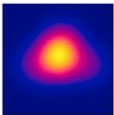
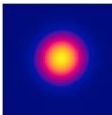
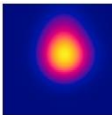
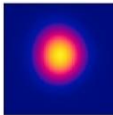
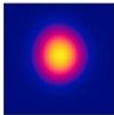
Table 3.3. Effect of sex and age class on *Ischnodemus conicus* movement behavior within the patch arenas. The Kruskal-Wallis analysis (H_{df}) was performed for each test of movement variables. Comparison tests between females (F), males (M), and juveniles (J) are summarized in the “effect” column.

Dependent variable	Female	Male	Juvenile	Statistic	Effect
Displacement (cm)	22.12 \pm 5.21	14.72 \pm 4.07	8.36 \pm 2.95	$H_2=8.59$, $p=0.01$	F > J
Speed (steps per 5m)	0.08 \pm 0.02	0.13 \pm 0.08	0.03 \pm 0.01	$H_2=1.44$, $p=0.49$	F=M=J
Step size (cm)	0.55 \pm 0.11	0.84 \pm 0.35	0.28 \pm 0.05	$H_2=2.95$, $p=0.23$	F=M=J
Turning angle	92.63 \pm 15.39	91.86 \pm 17.62	105.81 \pm 18.34	$H_2=0.48$, $p=0.79$	F=M=J

Movement at the patch-matrix edge

The movement of *I. conicus* insects released in the edge arenas was not significantly different from those released in the patch arenas (Table 3.2). The 32 released insects displaced a mean distance of 2 cells (12.02 cm) and the 28 individuals that left their release cell moved slowly (0.10 steps per 5 min; mean step size = 0.57 cm) and often turned between each step (mean turning angle = 95.02 degrees; Table 3.2) with a lack of correlations between consecutively taken angles, suggesting a random walk ($F_{1,18} = 0.06$, $p = 0.81$, $y = -0.05x + 59.23$; Fig. 3.8). The variables of overall displacement as well as the step size, speed, and turning angle of movers did not differ between females, males or juveniles (Table 3.5). Similar to the patch arena, the majority of movement in the edge arena occurred in the first few hours after release (58, 30, and 11% of the total steps occurred in the 1st, 2nd, and 3rd hours, respectively) with only 1% of steps within hour 4 and no movement in the 5th hour (Fig. 3.10).

Table 3.4. Summary of output of the point-pattern processes for each of the ten replicate habitat landscapes. Spatial pattern (clumped, random, and hyperdispersed) were estimated at different scales (radius = r) the pair-correlation function ($g(r)$) (see Appendix 1 for graphic output).

		Replicate release in habitat landscape									
Density heat map 5 hours after release											
Number <i>I. conicus</i> in analysis		4	6	6	5	8	7	3	7	6	6
Population	$r=0$	Clumped	Clumped	Clumped	Clumped	Clumped	Clumped	Clumped	Clumped	Clumped	Clumped
	$r=1$	Clumped	Clumped	Clumped	Clumped	Clumped	Random	Clumped	Random	Clumped	Clumped
	$r=2$	Random	Clumped	Random	Random	Random	Random	Random	Random	Clumped	Clumped
Female : Female	$r=0$		Hyperdisp	Hyperdisp		Hyperdisp	Hyperdisp		Hyperdisp	Hyperdisp	Hyperdisp
	$r=1$	N/A	Hyperdisp	Hyperdisp	N/A	Hyperdisp	Hyperdisp	N/A	Hyperdisp	Hyperdisp	Hyperdisp
	$r=2$		Hyperdisp	Hyperdisp		Clumped	Hyperdisp		Hyperdisp	Hyperdisp	Clumped
Male : Male	$r=0$		Hyperdisp	Hyperdisp		Hyperdisp	Clumped		Hyperdisp	Hyperdisp	Hyperdisp
	$r=1$	N/A	Clumped	Hyperdisp	N/A	Clumped	Clumped	N/A	Random	Hyperdisp	Clumped
	$r=2$		Clumped	Hyperdisp		Clumped	Clumped		Clumped	Hyperdisp	Clumped
Juvenile : Juvenile	$r=0$		Hyperdisp	Hyperdisp		Clumped	Clumped		Clumped	Clumped	Clumped
	$r=1$	N/A	Clumped	Hyperdisp	N/A	Random	Random	N/A	Random	Random	Random
	$r=2$		Clumped	Clumped		Random	Random		Random	Random	Random
Female : Male	$r=0$		Clumped	Clumped		Clumped	Hyperdisp		Clumped	Hyperdisp	Clumped
	$r=1$	N/A	Random	Random	N/A	Random	Hyperdisp	N/A	Random	Clumped	Random
	$r=2$		Random	Random		Random	Hyperdisp		Random	Clumped	Random
Female : Juvenile	$r=0$		Hyperdisp	Clumped		Clumped	Hyperdisp		Clumped	Clumped	Clumped
	$r=1$	N/A	Clumped	Random	N/A	Clumped	Hyperdisp	N/A	Random	Random	Random
	$r=2$		Clumped	Random		Random	Hyperdisp		Random	Random	Random
Male : Juvenile	$r=0$		Clumped	Clumped		Clumped	Clumped		Clumped	Hyperdisp	Clumped
	$r=1$	N/A	Random	Random	N/A	Random	Random	N/A	Random	Clumped	Random
	$r=2$		Random	Random		Random	Random		Random	Clumped	Random

Although path variables were similar in the patch and edge arenas, the direction of movement was influenced by the addition of a hostile sand matrix. The initial direction was biased along the edge of the patch (65%) rather than moving into the patch (32%) or into the matrix (3%; $\chi^2 = 14.72$, $p < 0.001$). Within the 5 hr observation window, only 5 insects entered into the matrix at any point, never moved beyond 7 cm into the sand, and quickly returned to the patch (mean \pm SE = 5.8min \pm 1.66). The movement of individuals did generate drift into the habitat side of the arena with a mean X and Y (\pm 95% CI) of 2.2cm (\pm 3.1) and -7.7cm (\pm 3.71); however, the highest population densities were found along the edge (14 insects in the 10 cells along the edge compared to the 18 insects in the 50 cells of the patch).

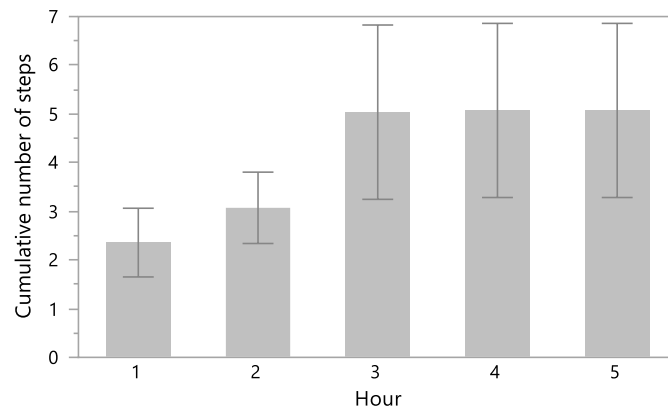


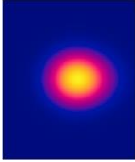
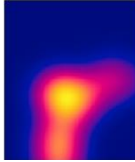
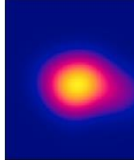
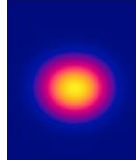
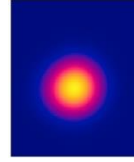
Figure 3.10. Mean (\pm SE) cumulative number of steps taken each hour by individuals released in the matrix.

Table 3.5. Effect of *Ischnodemus conicus* sex and age class on movement behavior within an edge arena. Measurements reported as mean \pm SE for each class. The Kruskal-Wallis analysis (H_{df}) was performed for each test and results from the multiple comparison between female (F), male (M), and juvenile (J) are summed in the “effect” column.

Dependent variable	Female	Male	Juvenile	Statistic	Effect
Displacement (cm)	16.38 \pm 3.46	10.74 \pm 2.99	8.08 \pm 2.52	$H_2=4.65$, $p=0.10$	F=M=J
Speed (steps per 5m)	0.11 \pm 0.03	0.15 \pm 0.09	0.06 \pm 0.02	$H_2=1.63$, $p=0.44$	F=M=J
Step size (cm)	0.51 \pm 0.10	0.71 \pm 0.28	0.40 \pm 0.11	$H_2=0.88$, $p=0.65$	F=M=J
Turning angle	119.67 \pm 18.35	77.32 \pm 20.88	101.92 \pm 29.47	$H_2=2.01$, $p=0.37$	F=M=J

In each of the five replicate edge landscapes, the individuals were clumped at a radius of 0 (Table 3.6; Appendix 2); however, the scale at which the populations stayed clumped was generally smaller in the edge arenas (60% and 0% of arenas were clumped at $r = 1$ and 2, respectively) than the patch arenas (90% and 30% of arenas clumped at $r = 2$ and $r = 3$, respectively; Table 3.3). Similar to the patch arena, there were replicable differences in dispersion patterns when comparing within class. Females and males were more likely to be hyperdispersed from their own sex (80% of arenas at $r = 0$) with females maintaining hyperdispersion at greater scales (Table 3.5). Juveniles were often clumped with each other at $r = 0$ (60% of arenas), similar to the patch arena (71% of arenas). Similar to the patch arenas, populations released at the edge of the habitat included females moving in opposing directions to each other, juveniles moving more in tandem, and males moving at angles to one another, all with similar speed, step size, and angular paths.

Table 3.6. Summary of output of the point-pattern processes for each of the 5 replicate edge arenas. Spatial pattern (clumped, random, and hyperdispersed) were estimated at different scales (radius = r) the pair-correlation function ($g(r)$). Displacement was further compared between males, females, and juveniles within each replicate arena using the point-pattern process. (see Appendix 2 for graphic output).

		Replicate release in habitat landscape				
Density heat map 5 hours after release						
Number <i>I. conicus</i> in analysis		6	7	6	7	6
$g(r)$	$r=0$	Clumped	Clumped	Clumped	Clumped	Clumped
Approximate difference to expected density	$r=1$	Clumped	Clumped	Clumped	Clumped	Clumped
	$r=2$	Random	Random	Random	Random	Random
	$r=0$	Clumped	Hyperdisp	Hyperdisp	Hyperdisp	Hyperdisp
Female : Female	$r=1$	Clumped	Hyperdisp	Hyperdisp	Clumped	Hyperdisp
	$r=2$	Random	Hyperdisp	Clumped	Hyperdisp	Hyperdisp
	$r=0$	Hyperdisp	Hyperdisp	Hyperdisp	Clumped	Hyperdisp
Male : Male	$r=1$	Clumped	Clumped	Clumped	Random	Hyperdisp
	$r=2$	Clumped	Clumped	Clumped	Random	Hyperdisp
	$r=0$	Clumped	Hyperdisp	Clumped	Hyperdisp	Clumped
Juvenile : Juvenile	$r=1$	Random	Hyperdisp	Random	Clumped	Random
	$r=2$	Random	Clumped	Random	Clumped	Random
	$r=0$	Clumped	Hyperdisp	Clumped	Clumped	Clumped
Female : Male	$r=1$	Random	Clumped	Random	Clumped	Random
	$r=2$	Random	Clumped	Random	Random	Random
	$r=0$	Clumped	Clumped	Hyperdisp	Clumped	Clumped
Female : Juvenile	$r=1$	Random	Random	Clumped	Clumped	Random
	$r=2$	Random	Random	Clumped	Random	Random
	$r=0$	Clumped	Clumped	Hyperdisp	Clumped	Clumped
Male : Juvenile	$r=1$	Random	Random	Clumped	Random	Random
	$r=2$	Random	Random	Clumped	Random	Random

Movement within the matrix

The *I. conicus* released in the matrix arena displaced at least 4-times further (49.65 cm) with a 30-times greater speed (3.08 steps per 5 min) and steps 218-times longer (116.18 cm) than the insects released in the habitat and edge arenas (Table 3.2). Individual movement within sex and age class did not differ in displacement, speed, step size, nor turning angle (Table 3.4) and all insects left the arena within 3 hr (mean = 70 min). The movement paths of the *I. conicus* in all

arenas were similar in mean angle and also lacked a correlation between consecutive angles ($F_{1,67} = 2.23$, $p = 0.13$, $y = 0.17x + 74.07$; Fig. 3.8), suggesting a random walk; however, the fractal analyses of each path suggested more linear paths than a random walk (fractal $D = 1.27 \pm 0.04$). Lastly, there was no population drift of movement with a mean X and Y ($\pm 95\%$ CI) of 3.89 cm (± 3.84) and 1.94 cm (± 2.82), respectively, 15 minutes after release.

Table 3.4. Effect of *Ischnodemus conicus* sex and age class on movement behavior within a matrix arena. Measurements reported as mean \pm SE for each class. ANOVA (F_{df}) analysis was performed for normal data whereas Kruskal-Wallis analysis (H_{df}) was performed as a nonparametric analysis. Results from the multiple comparison tests between the classes Female (F), male (M), and juvenile (J) are summed in the “effect” column

Dependent variable	Female	Male	Juvenile	Statistic	Effect
Displacement (cm)	49.39 \pm 1.54	50.20 \pm 1.65	49.15 \pm 1.94	$F_2=0.10$, $p=0.90$	F=M=J
Speed (steps per 5m)	3.14 \pm 0.76	3.82 \pm 0.84	1.56 \pm 0.55	$H_2=3.45$, $p=0.18$	F=M=J
Step size (cm)	16.00 \pm 3.67	22.02 \pm 4.83	7.95 \pm 3.00	$H_2=3.44$, $p=0.18$	F=M=J
Turning angle	82.18 \pm 12.63	58.40 \pm 13.68	95.86 \pm 12.06	$F_2=1.77$, $p=0.80$	F=M=J
Fractal D	1.3 \pm 0.07	1.23 \pm 0.06	1.27 \pm 0.09	$H_2=0.78$, $p=0.68$	F=M=J

DISCUSSION

The gregarious nature of *I. conicus* appeared to strongly influence the lack of movement within the habitat and the density-emigration relationship; however, once emigrated, the movement paths of the individuals were linear and, compared to the speed within habitat areas, fast (Table 3.1). The lack of movement within the habitat and edge landscapes was surprising as we expected the individuals to move randomly until finding a proper host plant.

Movement within the habitat

Random movement within a patch increases the chances of an individual encountering the edge of the habitat; however, *I. conicus* individuals appeared to find a suitable, close food source and remain there throughout the continuous observation window of 5 hours and displaced little more in 24 hours. The lack of movement may be due to the individuals maintaining an aggregation at the release area. Like other chinch bugs in the family *Ischnodemus sp.* can be highly gregarious, primarily as juveniles and as adults when copulating (Johnson and Knapp 1996; Wheeler 1996), an observation that we also made in the field. Aggregating species theoretically receive some benefit from group living (e.g., Gascoigne et al. 2009; Hammill et al. 2015; Serrano et al. 2005) that outweighs the costs of limited resources, but this benefit is unknown for *I. conicus* and, as far as we know, has not been studied for the genus as a whole. Other hemipteran species profit from an increased defense against predators (e.g., treehoppers and aphids; Cocroft 1999; Siddiqui et al. 2019), assistance in rearing offspring (see review by Mas and Kolliker 2008) and a greater mating success (e.g., water striders; Han and Brooks 2014). If there is cooperative interaction within *I. conicus* populations, the clustering created by short-distance dispersal may increase local population size (Harada et al. 1995) and stability.

If clustering is not induced by cooperative-based behavior, populations with low dispersal rates are expected to have lower reproduction, delayed maturity, and higher mortality rate due to overcrowding and resource limitation (Harada et al. 1995; Stamps et al. 1987). In this scenario, the lack of movement may be due to the close availability of *S. alterniflora* stems, which are used as food and refuge. If resources are readily available, there is little need to move and search. In the field, recapturing marked individuals proved difficult in larger patches, as we needed to peel back the *S. alterniflora* leaves to locate hidden insects beneath the leaf sheath. This behavior

is similar in *S. pectinata* habitats, where *I. falicus* both lays its eggs and aggregates within the leaf sheaths (Harrington 1972; Johnson and Knapp 1996; Wheeler 1996). Once hidden within the leaf sheath, the insect is unlikely to move, even when exposed by searching methods.

Movement at the patch-matrix edge

The limited movement in the edge landscapes was similar to that in the habitat (Table 3.1), which may be related to the gregarious nature of the species or an equal resource availability for the insects at the edge compared to the interior of the patch. For congeners, several individuals have been reported to be sustained by one grass stem (Johnson and Knapp 1996), thus the need to move further into the patch to find more abundant resources may be minor. Alternatively, the abrupt change to the harsh sand matrix created a boundary that promoted movement parallel to the edge. This barrier can also be reflective, with individuals moving back into the habitat instead of emigrating out, as seen with ladybird beetles (Kareiva and Perry 1989) or aphids (Kareiva 1987); however, even though there was some population drift into the habitat, the highest densities were at the edge of their landscape (Fig. 3.10). Dense populations at the edge have been attributed to greater resource availability (e.g., game and bird species Gates and Gysel 1978) or refuge space (e.g., small mammals Bartholomew 1970) at the merging of the two habitat types. However, with a harsh matrix deprived of a food source and a random arrangement of plants of a standardized quality in the habitat, aggregation at the edge due to an increase in resources is not likely.

Edge-biased distributions are common in insect species (see review by Nguyen and Nansen 2018) and a higher hostility matrix bordering a patch can reduce the permeability of dispersal at the edge, particularly if the change in habitat is abrupt (Fagan et al. 1999; Ries and

Debinski 2001), as in our landscapes. Aggregation at the patch edge has been noted in several insect taxa including butterflies, flour beetles, planthoppers, and aphids (Athanassiou et al. 2005; Campbell and Hagstrum 2002; Haynes and Cronin 2003; Nowicki et al. 2014). The interspecific interactions between edge-aggregating species can further alter a species' movement patterns (Fagan et al. 1999), for instance, with parasitoid and predator movement (e.g., Altamirano et al. 2016; Reeve and Cronin 2010). The sand matrix found around *S. alterniflora* stands at our site could be considered high in hostility as there is no refuge nor food there.

Emigration out of a habitat

In addition to the matrix hostility at the habitat edge, an individual may consider its knowledge about the landscape to make adaptive or appropriate dispersal decisions. Theoretically, the benefits of dispersing must outweigh the risks for emigration to occur (Bowler and Benton 2005). Like other gregarious species in Blissidae, *I. conicus* may use chemical cues to sense its environment to weigh the risks (e.g., southern chinch bug, *Blissus insularis* (Barber) (Adesso et al. 2012)). Similar to Adesso et. al (2012) with the chinch bug and Wheeler (1996) with *I. conicus*, we noticed a distinct, pungent odor, which would suggest a released volatile compound. If used for aggregation, these odor cues can maintain nonsocial gregarious populations (Courchamp et al. 2008). The presence of conspecifics often indicates a high quality patch (Gilbert and Singer 1973), especially for a gregarious species. Without these cues, such as with our edge landscapes located in the middle of a greenhouse, there would be no perceived benefit of emigrating into a hostile matrix, unlike with our field patches.

As aggregating species receive some benefit from group living, theoretically, the population should emigrate with a negative relationship to density (Bowler and Benton 2005;

Matthysen 2005), but if resources are limited due to high densities, emigration should be promoted in very high densities (Jacob et al. 2016; Kim et al. 2009). Initially, we hypothesized that the density-emigration relationship would be negative, but the shape was quadratic, displaying a uDDE form. Although this curve did not fit the requirements of Simonsohn (2018), many papers measuring density-dependence utilize only quadratic regressions and AIC model selection to stipulate a full curve of the data (e.g., Altwegg et al. 2014; Jacob et al. 2016; Kim et al. 2009)..

In a review of the frequency of occurrence of different forms of DDE, Harman et al. (2020) found only 9 other cases of u-shaped DDE, representing only 6% of the studies, concluding that u-shaped DDE may be more readily found if methods included a wider range of released densities. As determined by the Robin Hood method (Simonsohn 2018), the upward trend in our u-shaped curve started at a density of 79 insects per 30 cm diameter patch (Fig. 3.6). This is an average density of 2.4 insects per stem, which is slightly below the 2.7 insects per stem found in the field during high population events. By increasing the release density to twice that of the highest densities, we were able to see the u-shaped form. Although we pushed the densities, this high treatment is not irrelevant as it was not uncommon to find stems harboring groups as high as 30 insects in the landscape, particularly during the copulation season. Additionally, populations that persist in a shrinking patch will automatically become denser as the area declines. As the beaches along the Gulf of Mexico shrink with rising ocean levels, and the *S. alterniflora* habitats are reduced in number and area, these high densities could become more prevalent unless the population maintains carrying capacity by increasing emigration into the matrix.

Movement within the matrix

When released within the matrix, the insects had low residency time and moved unbiasedly in direction directly off of the landscape. Although the movement tortuosity of *I. conicus* in the matrix could not be compared to the short path lengths of insects released in the habitat and edge landscapes, the fractal D of *I. conicus* (1.28) is similar to that of other species searching for resources. For example, in an experiment by Haynes and Cronin (2006), planthoppers (*Prokelesia crocea*) displayed more linear movement in harsh, mudflats (mean fractal $D \approx 1.1$) and in an undesirable, exotic food source (mean fractal $D \approx 1.2$) than in their primary food (mean fractal $D \approx 1.5$). The absence of a resource chemical cue with wheat bulb fly (*Delia coarctata*) resulted in a more linear path (fractal $D = 1.11$) than when presented with the cue (fractal $D = 1.22$) at low concentrations (Rogers et al. 2013). Lastly, in treecreepers (Passeriformes: Climacteridae), individual birds that had a larger search area had less tortuous paths and more direct movement towards potential resources (Fractal D range $\approx 1.0 - 1.5$), primarily with males in an attempt to avoid competition. The differences in the fractal dimension of paths may reflect the behaviors of the individuals and relate to how one perceives its environment, with less tortuous movement potentially indicating movement between resources (Wiens et al. 1995).

Dispersers typically suffer costs in the matrix, such as higher risks of predation, failure to find a new resource, reduction in fecundity, or death (see review by Bonte et al. 2012). They may use fast, linear movement in an attempt to quickly transfer through the harsh environment (Farina 2000). These costs can occur either within the matrix itself or are a lingering effect of prior investment into dispersing (Bowler and Benton 2005). Movement within high hostility landscapes often increases these costs and the death of most dispersers may create dimorphism of

dispersal traits (Roff 1994), such as wing length in insects (e.g., planthoppers and crickets Denno 1994; Langellotto and Denno 2001). With *I. conicus*, long-winged females were 3-fold more numerous than macropterous males in Cameron. Long-distance dispersal of females may be evolutionarily selected as gravid females can establish new populations without needing a male (Haynes and Cronin 2003). However, brachypterous morphs often have higher reproduction and are preferred over winged morphotypes in stable environments (Addesso et al. 2012; Denno et al. 1991). The cost of long distance dispersal may be high in the isolated Cameron populations, promoting a higher proportion of brachypters, which may be why we observed only short-distance walking movements contrary to reports of *I. conicus* as a flying house pest in Texas (Merchant 2011).

Metapopulation connectivity

Overall, the movement behavior of *I. conicus* suggests that large populations will be able to persist in stable habitats; however, in landscapes that are becoming more fragmented, gene flow between populations and colonization of uninhabited marsh areas may be restricted. *I. conicus* has shown limited long-distance dispersal, as the population is primarily composed of brachypterous individuals that form aggregates in a habitat. The Allee effect that is innate in aggregating species creates stable ranges (Amarasekare 2004a; Wang 2016) as individuals are less likely to emigrate from competition in high densities as well as establish in uninhabited patch. Additionally, similar to other species in its family, *I. conicus* may create dense populations by using an aggregating pheromone, a lure that cannot be sensed with the far distances separating isolated habitats and is missing altogether in empty habitats.

Even though populations of gregarious species can thrive in high densities in small patches, any reduction in the patch size could result in sudden population extinction (Harman et al. 2020) with little chance of dispersing individuals rescuing the population, particularly in a highly hostile matrix (Vandermeer and Carvajal 2001). Although more stable but less preferred habitats can be used as refuges (Elkin and Possingham 2008) or stepping stones for dispersal, the habitats need to be spatially clustered to maintain metapopulation connectivity for organisms with limited dispersal ability (Doak et al. 1992). Additionally, when the cost of movement is high, emigrants are more prone to first identify their destination patch and then move directly towards it, resulting in the majority of individuals entering the same, often closest, patch and minimizing the inter-patch connectivity of a landscape (Barton et al. 2009).

For highly disturbed (e.g., wave action and storms) and constantly eroding coastal environments, rescue and colonization events may determine the persistence of a population. At the current rate of coastal erosion, areas along the coast where *S. alterniflora* thrives are predicted to be submerged by 2025, limiting the current habitats for *I. conicus*. Through dredging projects that build new land to replace areas removed by industrialization, such as building refineries, *S. alterniflora* habitats are created along the Gulf coast. However, colonization of uninhabited marsh areas, such as those created by dredging, is theoretically difficult for this aggregating, short-distance dispersing species.

CONCLUSIONS

Our assays of individual movement, spatial arrangement, and density-dependent emigration, suggest that *Ischnodemus conicus* populations have a trifecta of intrinsic (gregarious behavior and morphology) and extrinsic (landscape) variables that promote large population

persistence in stable environments yet hinder dispersal between populations and range expansion. The gregarious nature of these insects, as shown by the clustered dispersion and u-shaped density-emigration form, limits competition and local population extinction of high densities. This lack of movement is enforced by the individual's morphology, as long-distance dispersal is restricted by the brachypterous population majority and the potential use of aggregating pheromones. The harsh boundary and hostile nature of the mud matrix further impedes emigration from the habitat, as the edge is not very permeable to individuals, who instead move along the boundary and aggregate. Those that do emigrate are likely to move linearly into the closest occupied patch and this population may go extinct unless the densities are high enough to bypass the Allee effect.

All three variables of this system limit population connectivity and the potential for range expansion because individuals are less likely to leave their original patch and enter into a new habitat or one with few conspecifics. In habitats changed by disturbance, fragmentation, or habitat loss, population persistence is often assisted by metapopulation connectivity through dispersal; thus, the attributes that promote large populations of *I. conicus* in stable environments may now threaten its existence.

Further research is needed to determine if the pheromone excreted by the species serves to lure conspecifics or if it has other functions, such as sex identification, communication, or predator deterrent. Lastly, further empirical work concerning how individual movement behavior influences population and metapopulation spatial distribution and connectivity is needed.

CHAPTER 4.

REDUCTION IN DISPERSAL IS CAUSED BY CONCURRENT SELECTION OF COMPETITIVE ABILITY IN RANGE EXPANDING POPULATIONS

INTRODUCTION

In disturbed environments, such as those influenced by climate change, habitat fragmentation, or exotic species introductions, an individual's fitness depends on its ability to compete locally or to disperse to a more suitable habitat (Fahrig 2003; Ferriere and Legendre 2013; Pither and Taylor 1998). In rapidly changing environments, dispersal is theoretically favored, as movement allows offspring to be distributed across different environmental conditions in a bet-hedging strategy (Armsworth and Roughgarden 2005; McPeck and Holt 1992). Dispersal influences spatial population dynamics, such as population persistence (Bowne and Bowers 2004; Cronin and Haynes 2004; Kendall et al. 2000) and the speed of range expansion (Fronhofer and Altermatt 2015; Neubert and Caswell 2000; Phillips 2015). Understanding species' range dynamics is highly relevant to conservation (Caplat et al. 2016; Huntley et al. 2010) and invasion biology (Lustenhouwer et al. 2019; Svenning et al. 2014); however, the spatio-temporal context of range expansion is poorly understood (Masson et al. 2018; Melbourne and Hastings 2009), as eco-evolutionary dynamics often differ between the habitat's core and front of an expanding range (Fronhofer and Altermatt 2015; Suarez and Tsutsui 2008; Urban et al. 2007).

The population characteristics of dispersal, density-dependence (e.g., competition), and growth rate (e.g., fecundity) are intrinsic to population dynamics (Burton et al. 2010) and changes to any one of these three characteristics (termed "DCF" for dispersal, competition, and fecundity) are likely to influence the other two (Bonte et al. 2012; Fronhofer and Altermatt

2015). Trade-offs may be evolutionarily acquired and plastic to changes in environment conditions (e.g., Jacob et al. 2020; Liang et al. 2018; Mishra et al. 2018).

The range core, the initial location of an expanding population, is expected to have high densities (e.g., Hudina et al. 2015; Szucs et al. 2017; Weiss-Lehman et al. 2017; but see Fronhofer and Altermatt 2015; Dallas et al. 2017). This competitive environment theoretically selects individuals with low fecundity and other K-selected traits (e.g., Burton et al. 2010; Lachmuth et al. 2011) as parents invest more energy into fewer offspring in an attempt to increase fitness. Consequently, population growth rates decrease to limit additional competition (e.g., Davis 2005; Martin and Martin 2001) and individuals may emigrate to escape the competitive pressure (Hamilton and May 1977; Travis and Dytham 1999).

Emigrating individuals are likely predisposed to dispersal through a combination of phenotypic traits, often referred to as dispersal syndromes (Buoro and Carlson 2014; Clobert et al. 2009; Cote et al. 2017). These syndromes may include a plastic response to environmental conditions (Holt 1987; Lowe and McPeck 2014), such as density (Amarasekare 2004b; Bowler and Benton 2005) and landscape hostility (Haynes and Cronin 2006; Ricketts 2001). On the other hand, syndromes may include morphological or behavioral phenotypes that give the individual an advantage when dispersing (Matthysen 2012; Mishra et al. 2018) or ability to detect or avoid competition (Ravigne et al. 2006; Willi and Fischer 2005). Changes in emigration from the core may affect the probability of population extinction (Amarasekare 2004b; Harman et al. 2020) and colonizing at the range front (Bowler and Benton 2005).

Individuals that disperse to the range front are likely exposed to different biotic selection pressures (Travis et al. 2005; Travis and Dytham 2002; Hughes et al. 2007) that lead to the evolutionary divergence of the DCF traits (e.g., Fronhofer and Altermatt 2015; Ochocki and

Miller 2017; Weiss-Lehman et al. 2017). Through spatial sorting, the best dispersers accumulate at the range front (compared to less-mobile individuals in the core) and, if dispersal syndromes are heritable, dispersal propensity may increase with each generation and accelerate range expansion (Phillips 2015; Monty and Mahy 2010). Founder effects may increase the rate of trait evolution (Masson et al. 2018; Shine et al. 2011; Philips et al. 2008). With low competition, populations may have increased growth rates (Hanski et al. 2004; Phillips 2015) with individuals characterized by r-selected traits (Burton et al. 2010). However, the lack of genetic variability increases kin competition (Van Petegem et al. 2018) and inbreeding (Banks and Lindenmayer 2014; Gros et al. 2008) within the growing range front population.

However, as the propensity to disperse and competitive ability are both energetically costly and often trade off evolutionarily in populations (Fronhofer and Altermatt 2015), any additional inter- or intra-specific competition at the range front may slow down the speed of range expansion and dampen population growth (Alzate et al. 2017; Svenning et al. 2014; Urban et al. 2012). Within the range front, establishing individuals often compete with native species, which may slow the range expansion speed as dispersing individuals trade off dispersal prowess with higher interspecific competitive ability (Svenning et al. 2014) or facilitate emigration and thus further range expansion as individuals avoid competition altogether (Cantrell et al. 2007). Interspecific competition may halt expansion altogether through competitive exclusion (Nguyen-Ngoc et al. 2012) or alternative stable states created by priority effects of the first established species (Belyea and Lancaster 1999; De Meester et al. 2016). Conversely, the static core population may compete with a newly established competitive species that is expanding its own range (e.g., Engelen and Santos 2009). Interspecific interactions within range ecology have been given much theoretical attention, particularly with invasive species movement (Dunstan and Bax

2007; Fisher 1937; Fraser et al. 2015; Hastings et al. 2005); however, empirical studies to support the models are lacking (Burton et al. 2010; Kubisch et al. 2014).

Populations in expanding ranges have been classically studied by placing selection pressure on either dispersal or competitive abilities and measuring the response of each DCF trait (e.g., Arnold et al. 2017; Weiss-Lehman et al. 2017; but see Alzate et al. 2017). However, evolutionary selection of multiple traits may influence survivorship, inter- and intra-specific competitive behavior, and colonization rate (Burton et al. 2010). Here, we provide the first comprehensive experiment that tests for multi-trait selection of two competing species. First, we tested the evolutionary response of selection pressure applied to multiple traits, specifically to both competitive and dispersal ability concurrently. We predicted that the additive selection pressures would reduce the extent to which each DCF trait is selected in populations representing the range front and core (as modelled by Burton et al. 2010). Second, we directly tested the DCF response of selecting for fecundity, which is often measured as a trade-off, but primarily as a response to competition and dispersal selection. We predicted that selection for high fecundity would increase the individual's ability to disperse at the cost of its ability to compete. Third, we the evolution of DCF traits may differ between species, we placed similar selection pressures on 2 species that are known competitors with the expectation that the weaker competitor would show a greater decrease in DCF traits with competition selection pressures. Lastly, we test if the different selection pressures would change interactions with a competing species and predict that high competition would promote temporary interspecific coexistence with high dispersers compared to selection for higher dispersal alone.

To address these hypotheses, we bred separate selection lines for 6 generations that selected for each DCF trait as well as each combination of high- and low-selected intraspecific

competitive and dispersal abilities, creating 10 selection lines (5 lines representing the range core and front populations) and one control. We used the model research species red flour beetles (RFB, *Tribolium castaneum* (Herbst) (Coleoptera, Tenebrionidae)) and confused flour beetles (CFB, *T. confusum* (DuVal)) that are commonly used to investigate competition and dispersal in a controlled environment (e.g., Arnold et al. 2017; Campbell and Hagstrum 2002; Weiss-Lehman et al. 2017).

MATERIALS AND METHODS

Study system

Since the 1940s, flour beetles in the genus *Tribolium* have been used in experiments due to their availability, manipulability, and short generation time. Both RFB and CFB are global grain pests found wherever grain is stored, such as in granaries, mills, and warehouses; however, CFB are less common in sub-tropical and tropical areas than RFB (USDA 2015 and personal observation). Both CFB and RFB complete their entire life cycle in the milled flour that is their food source, so it is relatively simple to conduct laboratory experiments with the beetles in a simulated “natural habitat”. The generation time (egg to adult) for CFB is approximately 34 days whereas RFB is slightly shorter at 30 days, which allows for multi-generational experiments in a timely manner. A flour beetle lifespan is 1-3 years and depends mostly on optimal temperature and humidity (USDA 2015). Female fecundity is dependent on density with female RFB fecundity commonly ranging from 12-16 eggs per day and CFB females laying 7-12 eggs per day (Birch et al. 1951).

RFB and CFB not only compete over resources, but they also predate upon each other (Alabi et al. 2008; Dawson 1967). RFB are generally noted as the superior competitor (Park

1948); however, competition exclusion experiments result in neither species excluding the other and community persistence is common (e.g., Birch et al. 1951; Goodnight and Craig 1996; Park 1948) despite the high niche overlap of the two species (Edmunds et al. 2003).

Unlike CFB, RFB adults are capable of flight, but they primarily move by walking (Romero et al. 2009). As their food source is temporary and populations can quickly grow, flour beetle dispersal between resource patches is common (Campbell and Hagstrum 2002; Ziegler 1976). Dispersal ability of the flour beetle has been tied to an individual's morphology (Arnold et al. 2017) and sex (Stevenson et al. 2017), population density (Agashe and Bolnick 2010), and environmental quality (Van Allen and Rudolf 2016). Dispersal ability is genetically dominant with one to a few loci determining the trait (Korona 1991; Ritte and Lavie 1977) and the ability rapidly evolves across expanding ranges (Weiss-Lehman et al. 2017).

Creation of genetic lines

To ensure genetic diversity, flour beetles were collected from several granaries in Louisiana (October 12-20, 2017), Indiana (December 22-27, 2017) and Kentucky (December 28-30, 2017) (for a full list of locations, see Appendix A) as well as purchased from the Carolina Biological Supply Company (Burlington, NC). Flour beetle species (*T. castaneum* and *T. confusum*) were separated, and beetles from different locations were mixed into populations. Populations of both species were maintained at ≤ 10 beetles per gram (half the maximum equilibrium capacity of beetles noted in Park (1948)) in containers containing 200 g of a standard medium (95% whole wheat flour and 5% nutritional yeast). All experiments were conducted in growth chambers at standard environment of 30° C, 70% \pm 5 RH, and 24/7 darkness at Louisiana State University, Baton Rouge, Louisiana, USA. Thirty populations of each flour beetle species

were maintained throughout the experiment by mixing individuals from the different populations every 2 generations spanning 2 months. These founding populations became the control for all experiments.

Dispersal, competition, and fecundity (DCF) traits were selected for using CFB and RFB from the control populations nine generations after beetles were collected from the field. On September 4, 2018, pupae were removed from the control populations. Solitary individuals placed into 10 g cups with 2 g flour and left to mature into virgin adults for 2 wk. These beetles were designated as “generation 0”, and individuals were randomly placed into 3 groups for trait selection, one for each DCF trait.

Dispersal lines

To separate high and low dispersers of each flour beetle species, rectangular prism dispersal arenas (Fig. 4.1) with a path run length of 120 cm were created. The landscape consisted of 10 g flour patches (5 cm long x 5 cm wide x 2 cm deep) alternating with 5 x 5 x 2 cm matrix of whole wheat berries (15 g). Neither CFB nor RFB can consume whole wheat berries and beetles preferred not to inhabit the matrix (only 10-30% were found in the whole wheat berries; Harman unpublished data). The purpose of the matrix was to slow the speed of dispersal and allow the beetles to colonize distinct patches. To select for dispersal propensity, 100 beetles (10:1 ratio of beetles to flour) were anesthetized with CO₂, gently stirred into the patch of flour at one end of the arena, and placed in the growth chamber for 24 hours, giving them sufficient time to disperse according to Weiss-Lehman et. al (2017). Four replicate landscapes with 100 released insects in each were placed in the same environment chamber. After the dispersal period, each of the patches and matrix habitats were separated, and the flour

beetles in each patch and matrix were counted. The low dispersal selection line (D_L) was bred from the 40 beetles with the shortest dispersal distances (the lower 10%) whereas the high dispersal selection line (D_H) was bred from the 40 individuals with the highest dispersal distance (the upper 10%). Five random insects from either the upper or lower 10% were placed in 10 g flour ($N = 8$) for 1 week and removed. The eggs laid during this time became the first generation, and 25 days later, after maturing into pupae, this generation was separated into individual 10 g cups consisting of 2 g flour, keeping the males and females separate. Two to 3 wk after the pupae emerged as adults, the virgin beetles were placed in the arenas using the same methods as used for generation 0. From the D_H line, the highest 10% of dispersers in the arenas were collected and bred for the second generation. Likewise, D_L lines were bred from individuals with the lowest 10% dispersal distance each generation. As before, four replicate releases of 100 beetles were used. Six generations were bred with these selection parameters; however, at the 4th generation, the 120 cm landscape was lengthened to 180 cm due to a higher proportion of individuals moving the full length of the arena.



Figure 4.1. Image of the dispersal landscape used to separate high and low dispersers and measure dispersal variables. The arena consisted of three adjacent 60 x 5 x 5 cm rectangular prisms that connected to each other and allowed a beetle to move a maximum distance of 180 cm. The white squares are habitable patches of flour whereas the brown squares are less habitable areas of whole wheat berries.

Competitive lines

For both CFB and RFB, selection for competitive ability was concurrently done for six generations after separating from the control. High competitive ability was favored by rearing juveniles in environments with high density (>20 larvae per gram of mix) whereas low competitive ability was selected for by rearing juveniles in low density environments (<5 larvae per gram of mix). High competition selected lines (C_H) were created by placing 10 adult insects in 10 g of flour for 1 wk and, assuming 5 females laid ten eggs each day, the final egg density was approximately 350 eggs in each 10 g container. Low competition selection lines (C_L) included 5 adult beetles in 10 g of mix that were removed a week later. To further limit competition, the egg-laden flour was subdivided into 5 2 g portions and mixed with 8 g of fresh flour with an approximate final egg density of 35 eggs per 10 g of flour (assuming an average of 2.5 females laying 10 eggs each day) and a 10-fold difference in larval densities between the high and low competition lines. Ten replicate high competition populations and 20 replicate low competition populations were made using 100 parental beetles each generation. For low competition-selected lines, 250 offspring that survived and matured into pupae in the cups with the lowest juvenile densities (approximately 10 cups) were separated into individual cups with 2 g of flour and used to breed the next generation. From the high competition line, 250 pupae were randomly selected from the highest juvenile density populations (5 of the cups) and also placed individually into cups. After 2-3 wk, the newly emerged adults were bred together using the same protocols for each line.

Dispersal-competitive lines

To assess if competitive ability selection affected a disperser's dispersal propensity, 400 of the generation 0 offspring that survived the high competition densities were placed in the dispersal arenas and the individuals that moved the furthest (top 10%) and shortest (bottom 10%) were the first generations of $D_H C_H$ and $D_L C_H$ respectively. Similarly, 400 beetles of the low competition generation 0 offspring were selected for and against dispersal propensity, creating the $D_H C_L$ and $D_L C_L$ lines. The selection of these four lines fit the protocol parameters for both competitive ability and dispersal propensity each generation of both RFB and CFB.

Fecundity lines

Lastly, selection for high and low fecundity (F_H and F_L respectively) was accomplished by placing one virgin pair into 10 g of flour for one week with 30 replicates. The offspring from the 2-3 most fecund females were bred for the H_F line in each generation whereas the offspring from the least fecund females (approximately 10 females) were bred for the F_L line.

Altogether, 10 selection lines were bred and one control line was maintained (Table 1). These lines represented the different selection pressures of the range core and range front. In the core, selection would theoretically favor low dispersal ability (D_L), high competitive ability (C_H), and low fecundity (F_L); however, the core also selects for these traits concurrently ($D_L C_H$) and may contain low densities with low levels of competition ($D_L C_L$). The range front, on the other hand, is colonized by dispersers (D_H) that are likely to become more fecund (F_H) as selection for competitive ability is low (C_L). Selection pressure to compete and disperse coincidentally adds pressures on the population in both the expected low densities of the front ($D_H C_L$) as well as high

densities ($D_H C_H$) that may be created over generational time or found when two populations meet.

Table 4.1. Summary of the methods used to select the 11 different lines with designated acronyms.

Trait	Selection for trait	Selection against trait
	High dispersal (D_H)	Low dispersal (D_L)
Dispersal propensity (D)	Individuals with the highest 10% dispersal distance selected. (Range front)	Individuals with the lowest 10% dispersal distance selected. (Range core)
	High competition (C_H)	Low competition (C_L)
Intraspecific competitive ability (C)	Individuals that survive to pupal stage in high density environments of >20 larvae per gram of mix. (Range core)	Individuals surviving to pupal stage in low density environments of <5 larvae per gram of mix. (Range front)
	Low fecundity (F_L)	High fecundity (F_H)
Fecundity (F)	Individuals selected from breeding pairs producing the most offspring. (Range front)	Individuals selected from breeding pairs producing the fewest offspring. (Range core)
	Low dispersal, high competition ($D_L C_H$)	Low dispersal, low competition ($D_L C_L$)
Dispersal propensity x Intraspecific competitive ability (DC)	High dispersal, high competition ($D_H C_H$) Lines selected for high competition are additionally selected for high or low dispersal propensity. (Range core and front respectively)	High dispersal, low competition ($D_H C_L$) Lines selected for high competition are additionally selected for high or low dispersal propensity. (Range core and front respectively)
	Control (T)	
Control (T)	Thirty populations maintained and interbred every other generation to limit selection	

Measuring dispersal propensity

For the dispersal selection lines, dispersal propensity was measured during the selection process for high and low dispersers ($N = 400$ insects per selection). The location within 5 cm intervals was recorded for each individual beetle. At generation 0, and the final generation 6, RFB and CFB from the C_H , C_L , F_H , F_L , and T lines were also released at a density of 10 insects per gram mix in the dispersal arenas to record dispersal distance for a total of 200 insects released in 4 replicate dispersal arenas for each selection line. Replicates with less than a 90%

recovery rate were discarded and replaced with a fifth replicate using different insects within the selection line.

The dispersal experiment provided four key measurements of dispersal propensity: net displacement, maximum distance, proportion emigrated, and diffusion. Net displacement was calculated as the sum of all distances divided by the number of relocated insects. The maximum distance was measured as the furthest distance of an individual in each arena. Proportion emigrated was calculated as the number of individuals that left the first patch (length = 5 cm) divided by the number of recovered beetles. Lastly, diffusion was calculated as 1 divided by the slope of the linear regression with x as distance² and y as the natural log of the number of recaptures at each distance (Kareiva 1982).

Density-mediated emigration

The effect of selection line on the propensity to disperse was also determined by the proportion of beetles emigrating from populations of different density using the beetles from the 6th generation lines. A smaller 5 cm wide x 15 cm long rectangular prism arena was created with one end closed and the other open to allow for emigrants to fall into a petri dish, simulating an open landscape (or absorbing boundary). A 5 x 5 x 1 cm (5 g of flour) patch was located at one end of the arena followed by 10 x 5 x 1 cm of whole wheat grain (15 g) that represented the matrix. The insects could move back and forth within the arena, but dispersal past the distal edge of the matrix resulted in permanent emigration from the system.

Three weeks prior to the experiment, beetles within each selection line and the control were placed into 10 populations consisting of 100 beetles per 10 g flour to standardize competition and resource availability across selection lines. To assess the density-emigration

relationship, RFB and CFB males and females were randomly collected from selection line populations and released at densities of 1, 2, 5, 10, and 20 beetles per gram of mix with the highest density capped at the equilibrium density noted for red flour beetles (Park 1948). The insects were anesthetized with CO₂, gently mixed into the patch area, and placed in the growth chamber for 1 hour. Beetles were deemed as emigrants if they were in either the matrix or petri dish. Proportion emigrated was calculated by dividing the number that had emigrated by the total number released in the arena. Four replicates for each treatment and species were conducted for a total of 88 emigration trials during generation 6. An additional 4 replicates were added from the generation 0 control density-emigration data to ascertain if the control line was affected by inadvertent evolutionary change.

Fecundity

Fecundity was defined as the number of offspring produced by a breeding pair of beetles that survived until adulthood (Davis and Landolt 2012). One virgin male and female beetle was placed in 10 g flour for 7 d and transferred to the growth chamber. On the 8th day, the beetles were removed, placed in fresh 10 g flour, and moved to the growth chamber for 24 hr. This was repeated 10x for each selection line and control of each species for a total of 440 fitness replicates. The eggs laid during the 24 hr period remained in the growth chamber for 35 d and the individuals reached the adult stage. The number of adults within each replicate was counted. Replicates containing no offspring were removed from the data as the lack of offspring could indicate a misidentification of parent sex.

Interspecific competition

The competition coefficient was estimated through an interspecific competition assessment using the same methods as the density-emigration experiment but with a release of 25 selection line RFB or CFB beetles and 25 control line beetles of the opposite species (e.g., 25 D_LC_H RFB released with 25 T CFB). The proportion emigrated of the focal selection line beetles was calculated and compared to the releases of 25 and 50 beetles (5 and 10 beetles per gram flour). From this set of comparisons, interspecific competition was considered to be occurring if emigration of the focal selection line beetles was significantly greater in the two-species community than in release densities of 50 beetles. If the two treatments were not significantly different, the focal selection line beetles reacted to the other species similarly to their own conspecifics. It is possible that the focal selection line beetles would not react to the other species at all, which would be indicated by a significant difference between the two-species community and 50-beetle density and a lack of difference between to the 25 beetle density.

Statistical analysis

We tested for differences in net displacement, mean distance, proportion emigrated, diffusion, and fecundity between each selection line. For each response variable, a separate linear model was run with species, selection line, and species × selection line interaction as fixed effects. Net displacement and diffusion were analyzed using a general linear model (GLM) with a gamma distribution. Maximum distance, proportion emigrated, and fecundity were analyzed using a GLM with a Weibull distribution. Akaike information criteria corrected for small sample size (AICc) was used to select the best distribution model for the GLM analysis (Burnham et al. 2011). As each response variable included a significant interaction between species and selection

line, the GLM was performed to test effects of selection lines within each species. Separate Tukey-Kramer HSD post-hoc analyses were performed to test for differences in each response variable between selection lines. All analyses were performed in JMP Version 15 (SAS Institute).

To investigate if the selection lines differed in their emigration responses to density, we tested the interaction between selection line and proportion emigrated using GLM with a normal distribution. Released population density was used as a continuous factor, with species as a fixed categorical factor. Initially, the GLM included an interaction term of release density \times species, but this was dropped from the model as RFB and CFB differed in response to density (see Results), and the model was used to assess selection lines differences within species using JMP. Post-hoc analysis of the data was performed using Tukey-Kramer HSD. Additionally, for each selection line, we analyzed the relationship between density and emigration using a nested set of predictor variables (constant only, constant + density, constant + density + density²). AICc was used to select the best model to determine if the relationship was linear or quadratic. The model with the smallest AICc value was deemed best (Burnham et al. 2011).

Lastly, to test differences in emigration between RFB and CFB single species populations of 25 and 50 insects and the two-species community, a GLM with a normal distribution was used. The model was run with a full factorial of selection line, species, and release treatment. The full interaction term of line \times species \times treatment did not significantly add to the model ($p > 0.05$) and was dropped. GLM analysis was done again within selection line by species with Tukey HSD post-hoc analysis. All analyses were performed in JMP Version 15 (SAS Institute).

RESULTS

Selection of DCF traits

We found strong evidence that the selection for dispersal ability had a significant effect on the individual's propensity to disperse for both RFB and CFB populations. In post-hoc Tukey HSD pairwise comparisons, when compared to D_L , RFB of the D_H line displaced 1.3x further, were 6.3 times more likely to emigrate, and had 115% greater diffusion; however, the maximum distance was not different (Table 4.3, Fig. 4.2). The CFB in the D_H line averaged 1.19 times further net displacement and 1.08 times further maximum distance when compared to D_L and the lines were not different in diffusion nor the proportion emigrated (Table 4.3, Fig. 4.3). When assessing the density-emigration relationship, beetles of D_H and D_L lines did not significantly change in their proportion emigrating for both RFB and CFB lines, but D_H was twice as likely to emigrate across densities as D_L for RFB and 2.3 times more likely in CFB lines (Table 4.3, Fig. 4.4). Lastly, fitness was not different between the dispersal lines for RFB but D_H CFB had 1.3 times more offspring that survived until the pupal stage than D_L beetles (Table 4.3, Fig. 4.5).

We did not find evidence that selection for competition alone (C_H and C_L) affected any dispersal variable (Table 4.3, Fig. 4.2 and 4.3). When assessing the density-emigration relationship, overall emigration did not significantly differ between the competition lines for either species, but beetles of the C_L line emigrated at an increasing rate with density (+DDE). Fitness was not different between competition lines for either species (Table 4.3, Fig. 4.5).

CFB in the F_L line had 7% shorter maximum displacement and 2.3 times greater emigration than beetles in the F_H line whereas RFB fitness selection lines did not differ in any dispersal variable. Although overall emigration did not differ between lines for either species, the

RFB in the F_H line emigrated positively with density (Fig. 4.4). High fitness treatments produced 1.68 times more offspring that survived till the pupal stage (Table 4.3, Fig. 4.5).

Table 4.3. Summary table of posthoc pair-wise comparisons between the single-trait selection lines of dispersal propensity, competitive ability, and fitness. (D = dispersal, C = competition, F = fecundity, L = selection for low ability, H = selection for high ability).

Selection Lines	Species	Net displacement	Maximum displacement	Emigration	Diffusion	Density-emigration	Fecundity
D _H - D _L	RFB	t ₃₃ =5.91, p<0.0001	t ₃₃ =0.08, p=0.10	t ₃₃ =7.49, p<0.0001	t ₃₃ =4.66, p=0.002	p<0.0001	t ₈₅ =0.62, p=1.0
C _H - C _L	RFB	t ₃₃ =1.39, p=0.94	t ₃₃ =0.15, p=1.0	t ₃₃ =1.39, p=0.94	t ₃₃ =0.98, p=1.0	p=0.13	t ₈₅ =2.41, p=0.38
F _H - F _L	RFB	t ₃₃ =2.20, p=0.52	t ₃₃ =1.06, p=0.99	t ₃₃ =2.45, p=0.37	t ₃₃ =0.37, p=1.0	p=1.0	t ₈₅ =2.89, p=0.14
D _H - D _L	CFB	t ₃₃ =4.09, p=0.01	t ₃₃ =3.85, p=0.02	t ₃₃ =2.38, p=0.41	t ₃₃ =3.04, p=0.13	p=0.0006	t ₇₀ =4.41, p=0.002
C _H - C _L	CFB	t ₃₃ =3.07, p=0.12	t ₃₃ =2.65, p=0.26	t ₃₃ =3.07, p=0.12	t ₃₃ =1.82, p=0.76	p=0.99	t ₇₀ =1.83, p=0.76
F _H - F _L	CFB	t ₃₃ =1.17, p=0.98	t ₃₃ =3.92, p=0.02	t ₃₃ =6.45, p<0.0001	t ₃₃ =2.54, p=0.32	p=0.63	t ₇₀ =7.10, p<0.0001

Dispersal in the range core and front

RFB from selection lines that represented the core had a lesser propensity to disperse than those in the range front as the core beetles displaced an average of 14% (t₃₈ = 4.35, p < 0.0001) and maximum of 3% (t₃₈ = 3.41, p = 0.002) shorter distances. Additionally, 60% fewer core beetles emigrated from the first patch (t₃₈ = 4.31, p < 0.0001) and diffusion rate was decreased by 8% (t₃₈ = 4.05, p = 0.0002; Fig. 4.2). CFB from the range and core selection lines were also different in their propensity to disperse, but to a lesser degree than RFB. Compared to the CFB from the range front, the core beetles' net displacement was 17% shorter (t₃₈ = 6.06, p < 0.0001) with a 3% shorter maximum distance (t₃₈ = 2.16, p = 0.04). CFB in the core were also 55% less likely to emigrate (t₃₈ = 4.86, p < 0.0001), 5% less diffuse (t₃₈ = 2.44, p = 0.02) than the beetles from range front lines (Fig. 4.3).

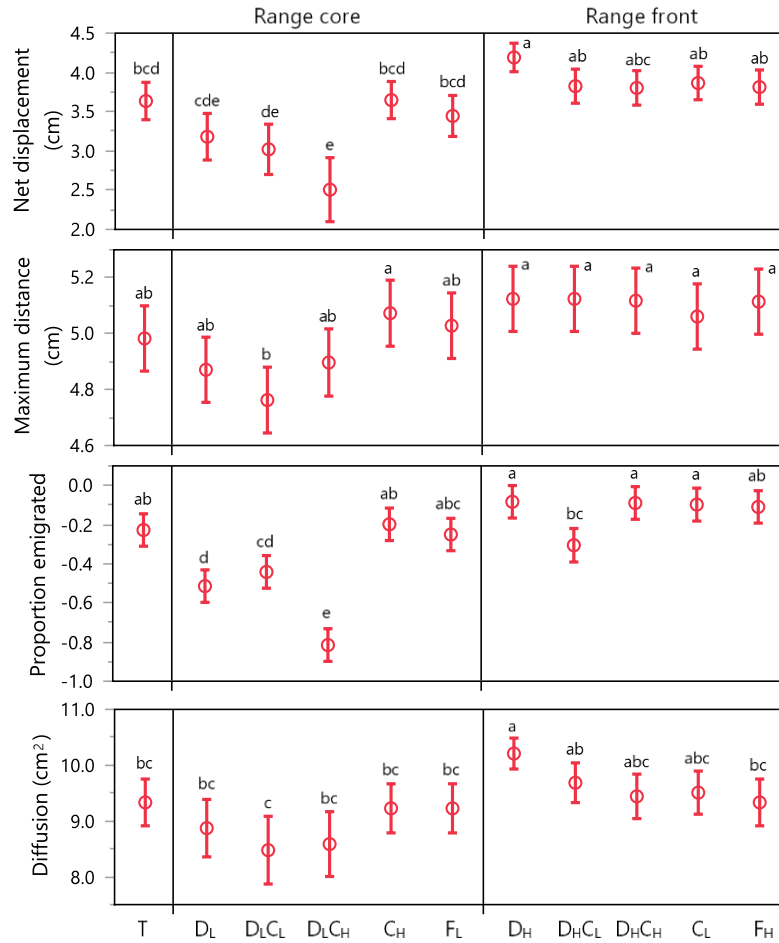


Figure 4.2. Dispersal of red flour beetle selection lines representing the core and front of a range. Least square means ($\pm 95\%$ CI) shown. Symbols with different letters are significantly different from one another ($p < 0.05$). (T = control, D = dispersal, C = competition, F = fecundity, L = selection for low ability, H = selection for high ability).

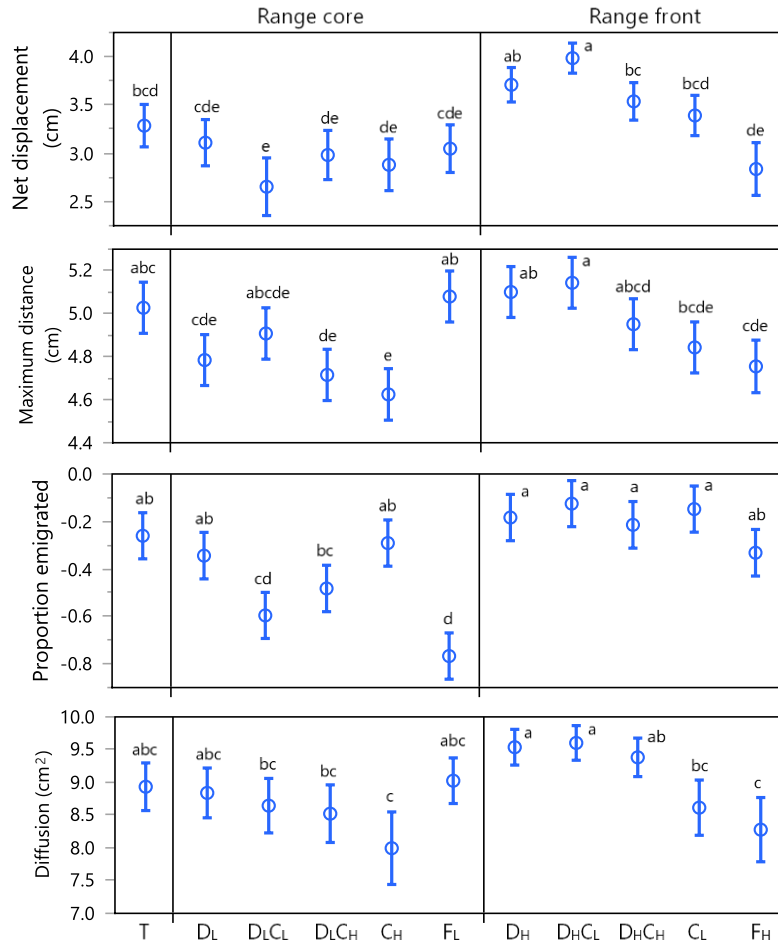


Figure 4.3. Dispersal of confused flour beetle selection lines representing the core and front of a range. Least square means ($\pm 95\%$ CI) shown. Symbols with different letters are significantly different from one another ($p < 0.05$). (T = control, D = dispersal, C = competition, F = fecundity, L = selection for low ability, H = selection for high ability).

Of the five RFB selection lines representing the core, the D_LC_H line had the lowest propensity to disperse. Beetles of the D_LC_H line had an average 30% shorter net displacement than the control ($t_{33} = 4.87$, $p = 0.001$) and the C_H and F_L selected beetles whereas the other low dispersal lines did not significantly differ from the other core lines. All low dispersal lines had a significantly lower proportion of emigrants than the control (Fig. 4.2). D_L ($t_{33} = 4.89$, $p = 0.0009$) and D_LC_L beetles ($t_{33} = 3.71$, $p = 0.03$) average only 47% of the emigration as the control beetles, but the proportion of D_LC_H beetles emigrated was 50% of that (D_L compared to D_LC_H; $t_{33} = 5.23$,

$p = 0.0004$). The core lines did not differ in RFB diffusion nor maximum distance, except for $D_L C_L$ and C_H ($t_{33} = 3.83$, $p = 0.02$).

CFB core lines selected for low dispersal only differed between the proportion of D_L and $D_L C_L$ beetle emigrants with low competition limiting emigration by 44% ($t_{33} = 43.72$, $p = 0.03$). When compared to the control, high competition C_H and $D_L C_H$ lines had 8% ($t_{33} = 4.89$, $p = 0.001$) and 6% ($t_{33} = 3.8$, $p = 0.02$) shorter maximum distances respectively. Low competition, $D_L C_L$, on the other hand, had a 57% lower proportion emigrated ($t_{33} = 4.98$, $p = 0.001$) and 19% shorter net displacement ($t_{33} = 3.48$, $p = 0.05$) than the control. Lastly, CFB F_L had a lower proportion of emigrants compared to all other lines, with only 34% of the control ($t_{33} = 7.51$, $p < 0.0001$; Fig. 4.3).

The RFB lines representing the range front did not show strong evidence that a change in competition would change the beetle's propensity to disperse (Fig. 4.2). Primarily, the beetles of the $D_H C_L$ line had a 25% less of the proportion of emigrants than the other high dispersal lines (compared to D_H : $t_{33} = 2.45$, $p = 0.02$). The dispersal propensity of the CFB range front lines was more affected by competition (Fig. 4.3). $D_H C_L$ beetles displaced 1.13 times ($t_{33} = 3.66$, $p = 0.03$) further than $D_H C_H$ selected beetles. Although $D_H C_H$ was not significantly different from the D_H and $D_H C_L$ selected lines for the other dispersal traits, this high competition line was generally not significantly different from the other range front or range core lines for maximum distance and diffusion whereas the D_H and $D_H C_L$ were (Fig. 4.3).

Influence of selection on density mediated emigration

Overall, RFB had a 1.64 times greater emigration than CFB ($t < 0.001$, Tukey adjusted $DF = 432$, $p < 0.0001$). When each species was modelled separately, there was an effect of selection line on emigration for both RFB ($F_{11,228} = 11.5$, $p < 0.0001$) and CFB ($F_{11,228} = 6.8$, $p < 0.0001$). Changes in density-emigration relationships for each DCF line are likely due to trait selection as the control lines for both species did not differ in the lack of a density-emigration relationship (DIE) nor the proportion emigrating between the generation 0 and generation 6 ($p = 1.0$ for both species). All density-emigration relationships were tested for non-linearity, but linear regressions were selected as best fitting the data for each selection line of both species (Appendix C).

Emigration did not significantly change with increasing density for all selection lines representing the core (DIE; Fig. 4.3, Table 4.7). The RFB in the D_L , $D_L C_H$, and C_H lines emigrated 40-44% less than those in the control lines ($F_{11,228} = 11.5$, $p < 0.0001$). Emigration of CFB in the core lines did not significantly differ from the controls.

The beetles representing the range front either emigrated at an increased rate with density (+DDE; RFB lines F_H and C_L ; CFB lines of C_L , $D_H C_L$, and $D_H C_H$) or a change in emigration with density was rejected (DIE; Fig. 4.3, Table 4.6). RFB emigration was greater in the D_H and $D_H C_L$ lines than the other lines representing the range front, with twice the number of emigrants as beetles in the $D_H C_H$ line ($p < 0.0001$ for both lines). Only $D_H C_L$ was significantly greater (1.3 times, $p = 0.05$) than the control lines. The beetles of the D_H and $D_H C_L$ also averaged 2.3 times greater number of emigrants than the D_L , $D_L C_H$, and C_H core lines. The CFB bred in the D_H and $D_H C_L$ also had the highest emigration rates, with 1.7 times the number of emigrants in the $D_H C_L$ than $D_H C_H$ although D_H and $D_H C_H$ lines were not significantly different. Additionally, similar to

the RFB, the D_H and D_{HCL} beetles averaged 2.3 times greater number of emigrants than the D_L , D_{LC_H} , and C_H core lines. Only the F_H beetles' emigration was significantly different (45% of the emigrants) from the controls ($F_{11,228} = 6.83, p < 0.0001$).

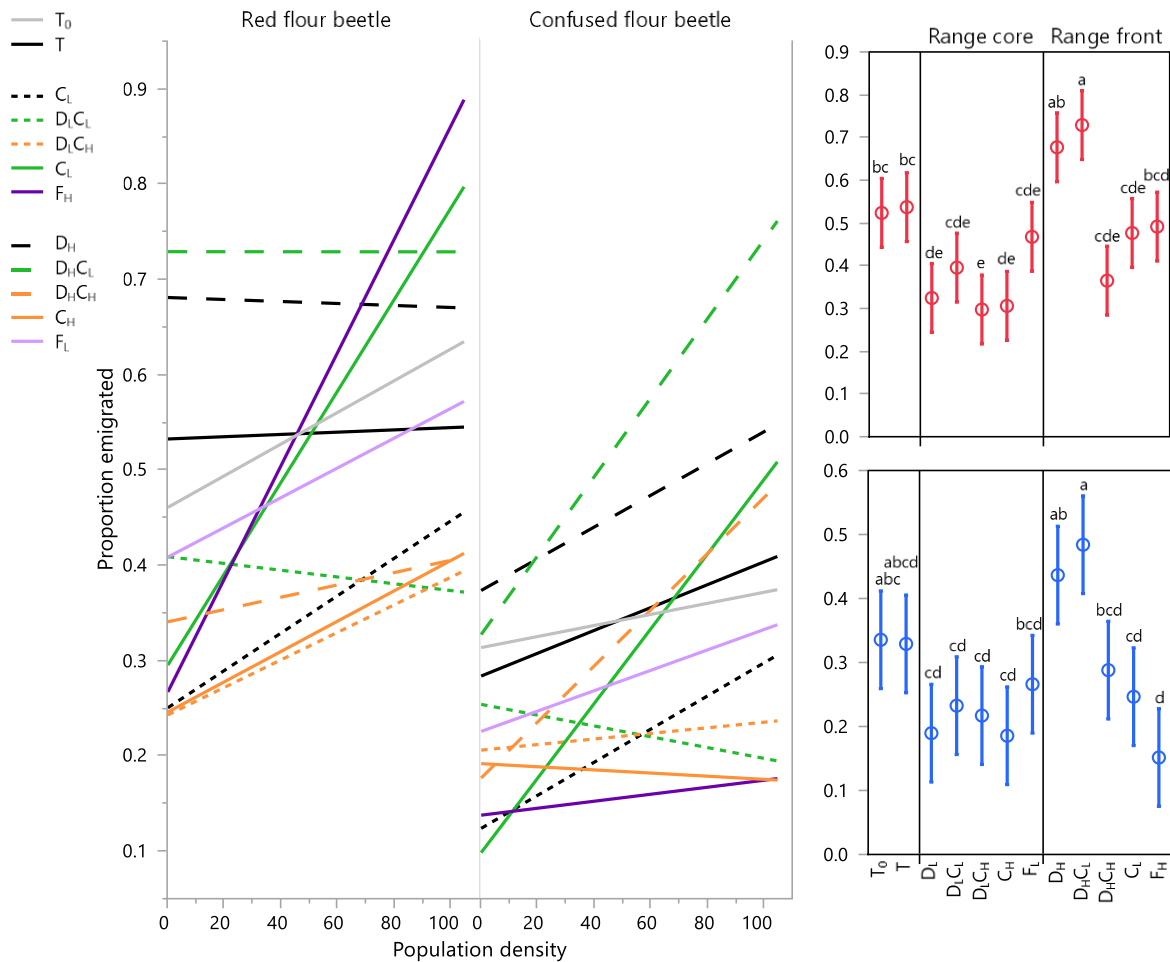


Figure 4.4. Linear regression to test the density-emigration relationship for each selected line for both flour beetle species (left). Different colors represent lines selected for high competition (orange), low competition (green), and fecundity (purples). Dashed and dotted lines indicate high and low dispersal selection, respectively. Least square means ($\pm 95\%$ CI) for overall emigration for each selection line of the red flour beetle (top, red) and the confused flour beetle (bottom, blue) are displayed (right). Symbols with different letters are significantly different from one another ($p < 0.05$). (T = control, D = dispersal, C = competition, F = fecundity, L = selection for low ability, H = selection for high ability, 0 = first generation)

Table 4.7. Linear regression results for density-emigration relationships of the dispersal lines (T = control, D = dispersal, C = competition, F = fecundity, L = selection for low ability, H = selection for high ability). DIE under density-emigration relationship represents density-independent.

		Red flour beetle					Confused flour beetle					
		Line	F	DF	R ²	p	Density-emigration	F	DF	R ²	p	Density-emigration relationship
Range core	T	0.01	1, 18	0.001	0.925	DIE	0.12	1, 18	0.006	0.73	DIE	
	D _L	2.6	1, 18	0.1	0.12	DIE	4.0	1, 18	0.18	0.06	DIE	
	D _L C _L	0.2	1, 18	0.01	0.68	DIE	0.3	1, 18	0.01	0.61	DIE	
	D _L C _H	4.1	1, 18	0.19	0.06	DIE	0.2	1, 18	0.01	0.7	DIE	
	C _H	3.3	1, 18	0.15	0.09	DIE	0.06	1, 18	0.003	0.81	DIE	
	F _L	1.7	1, 18	0.08	0.22	DIE	1.2	1, 18	0.06	0.29	DIE	
Range front	D _H	0.01	1, 18	0.001	0.91	DIE	1.9	1, 18	0.09	0.19	DIE	
	D _H C _L	0	1, 18	0	0.999	DIE	17.0	1, 18	0.49	0.001	Positive	
	D _H C _H	0.7	1, 18	0.04	0.43	DIE	5.7	1, 18	0.24	0.03	Positive	
	C _L	12.0	1, 18	0.37	0.003	Positive	14.6	1, 18	0.45	0.001	Positive	
	F _H	23.9	1, 18	0.57	0.001	Positive	0.1	1, 18	0.01	0.72	DIE	

Interspecific-mediated competition

Within the full GLM, RFB had 1.5 times the number of emigrants as CFB ($F_{45,218} = 6.8$, $p < 0.0001$) but RFB emigration was not affected by the addition of CFB control line competitors ($p = 0.96$). The addition of RFB to the CFB population increased CFB emigration by 150% ($p = 0.0002$). There was a significant effect of selection line \times species ($W_{10} = 2.1$, $p = 0.02$) and selection line \times treatment density ($W_{20} = 2.9$, $p < 0.0001$). With post-hoc comparisons assessing emigration within selection line for each species, the addition of a competing species to the release patch increased emigration rate by 3 times and 2.3 times for the C_H lines of CFB ($F_{2,9} = 7.41$, $p = 0.02$) and RFB ($F_{2,9} = 26.92$, $p = 0.0002$), respectively, when compared to single-species releases (Fig. 4.5). The CFB F_H line also had 2.2 times greater emigration when placed with the competing species than when released in densities of 50 ($F_{2,9} = 5.4$, $p = 0.03$). The proportion emigrating was not significantly affected by the addition of the other species for all other selection lines.

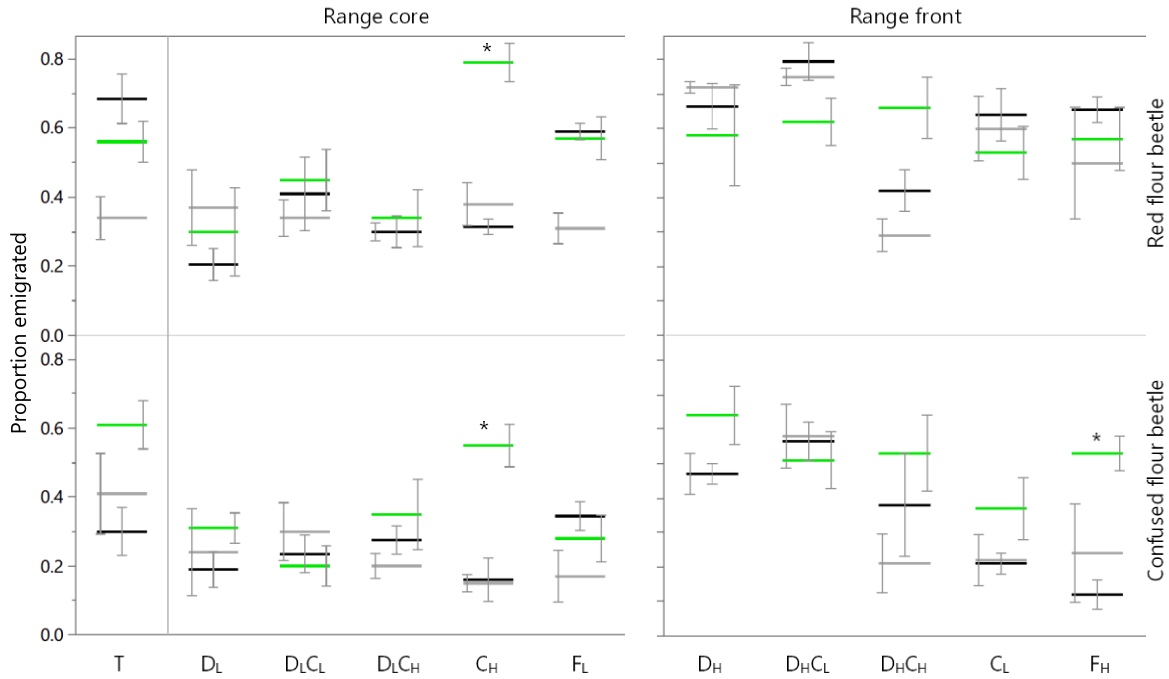


Figure 4.4. The change in emigration with a competing species for selection lines representing the core and front of an expanding range. Mean (\pm SE) proportion emigrated for each selection line when placed in population densities of 25 (light grey) and 50 (black) beetles or 2-species community consisting of 25 individuals of each species (green) is shown. Comparisons in which emigration was significantly different ($p < 0.05$) between interspecific competition treatments and release densities of 50 are indicated with (*). (T = control, D = dispersal, C = competition, F = fecundity, L = selection for low ability, H = selection for high ability).

Influence of selection on fitness

Beetle fecundity was significantly impacted by the selection process and different between the two species ($W_{10} = 28.05$, $p = 0.002$). Regardless of selection line, RFB had 108% higher fitness than CFB ($t_{155} = -3.17$, $p = 0.001$). Additionally, in post-hoc tests within each species, the CFB selection lines H_F , C_L , D_H , and $D_H C_L$, all of which represent the range front, had significantly higher fitness than the range core lines F_L , $D_L C_H$, and D_L ($W = 135.6$, Tukey-Kramer adjusted $DF = 70$; $p < 0.0001$). RFB selection lines also differed ($W = 31.25$, Tukey-Kramer adjusted $DF = 85$, $p = 0.0005$) revealed 138% higher fitness in the F_H line compared to

the control ($p = 0.006$) and $D_H C_H$ ($p = 0.03$; Fig. 4.4). There were no other detected differences for RFB lines.

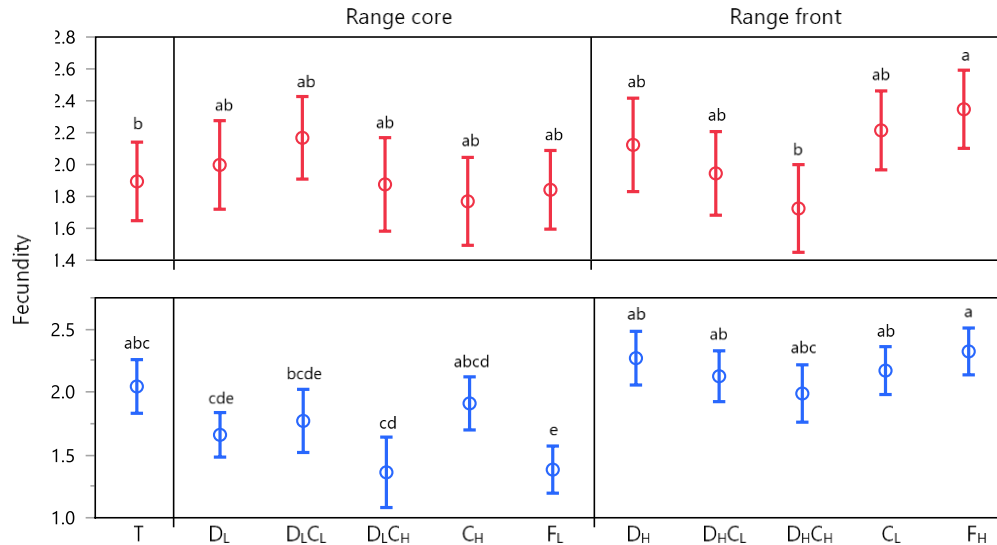


Figure 4.5. Fitness as measured by survival of offspring to the pupal stage. Least square means ($\pm 95\%$ CI) for fitness for each selection line of red flour beetle (top, red) and confused flour beetle (bottom, blue) are shown. Symbols with different letters are significantly different from one another ($p < 0.05$). (T = control, D = dispersal, C = competition, F = fecundity, L = selection for low ability, H = selection for high ability).

DISCUSSION

Heritability of DCF traits: D_L vs D_H , C_L vs C_H , F_L vs F_H

The selection lines for dispersal ability created divergent dispersal behaviors within six generations, a time line that reflects similar range experiments with RFB (Szucs et al. 2017; Weiss-Lehman et al. 2017). Dispersal is commonly a heritable trait (e.g., Donohue et al. 2005; Phillips et al. 2006; Roff 2007) that may be morphological (e.g, Arnold et al. 2017; Roff 1986; Simmons and Thomas 2004; Wheelwright 1993), behavioral, or a suite of dispersal syndromes (Clobert et al. 2009; Hudina et al. 2014; Sih et al. 2012).

Selecting for low fecundity significantly decreased the number of offspring that survived until pupation by 40% between CFB F_H and F_L lines. Fecundity is a heritable trait for some species (e.g., Long et al. 2009; Quezada-Garcia and Bauce 2014; Sgro and Hoffmann 1998). Alternatively, changes in fecundity can be caused by another heritable trait relating to fitness, such as body size (e.g., Davis and Landolt 2012; Eium and Fleming 2000) and age (e.g., Bock et al. 2019; Lansing 1942), or be determined by the health of the mother (e.g., Benton et al. 2008; Bock et al. 2019). Although environmental effects are possible, the 10 g of flour contained only one day's worth of eggs (an expected average of 12-16 for RFB and 7-12 eggs for CFB) and competition should have been minimally different between the lines. Despite these possible extrinsic variables in the system, the survival component of our definition of fecundity reflects realized population recruitment to future generations (Shaw et al. 2008).

For the competition-selected lines, we standardized the environments only in the pupal and adult stages across all lines by isolating individuals to provide adults with equal resources and ensure use of virgins in the experiments. Thus, differences in DCF traits between high and low competitors, which matured in environments with 10-fold difference in mother density, are confounded by both genetics as well as environmental differences in resource availability, cannibalism rate, and crowded conditions. Carry-over effects of environmental conditions during development could have changed the phenotypes of the adults that matured in these different competition conditions (Hamel et al. 2009; Mousseau and Fox 1998). In an experiment by Van Allen and Rudolf (2013), CFB populations raised in poor quality versus high quality environments displayed carry-over effects including slower development time (by ten days), a 3% difference in body weight, but similar survivorship. These effects persisted over generational time, even when offspring transitioned from a low quality to a high quality environment (Van

Allen and Rudolf 2013). Although their different environments were created using a preferred versus a nutrient-lacking food source, the influence of resource limitation due to overcrowding during the larval stage is similar. Extrinsic variables are likely a large contributing factor of differences within DCF traits seen within our competition-selected lines, including a low ability to emigrate and disperse, even at high densities. However, as the purpose of these experiments was to determine if selection pressure affects DCF traits in populations and not to determine the heritability of these traits, the impact of environmental variation does not limit our interpretation of the data but instead reflects population dynamics.

Selection of traits in the range core: D_L , $D_L C_H$, $D_L C_L$, C_H , F_L

The selection of traits in the core and the range front were different when comparing the range front and core. Within comparisons of the core lines, there are a few key population responses that may influence range expansion: (1) The two species of beetle, although similar in niche, differ in response to selection pressure with dispersal limited in RFB high competition lines and CFB low competition lines. (2) Low fecundity can reduce emigration from a core but promote range expansion and high competition ($D_L C_H$) selection can reduce fecundity. (3) High competition in the core C_H and $D_L C_H$ lines can further limit emigration and displacement, but the addition of a competitor promotes emigration.

Different species react differently to selection pressures within an expanding range. For RFB, high competition within the core populations is likely to slow down range expansion speeds as fewer individuals emigrate, despite density, and disperse shorter distances. This decrease may be due to the RFB overall having a higher dispersal propensity, which has been noted in other studies (e.g., Hawkin et al. 2013). This dispersal-competition tradeoff has long

been proposed (Simmons and Thomas 2004; Strona 2015) and is evident in various organisms (e.g., De Meester et al. 2015; Livingston et al. 2012) and often changes in fecundity are a response of this interaction.

Although fecundity is expected to increase within the range front populations, this increase is primarily a response to low competition in the environment (e.g., Masson et al. 2018) and not necessarily the dispersal ability itself (Svenning et al. 2014). Dispersal and fecundity have been described as having a negative tradeoff due to the energetic investment in dispersal-related traits (e.g., Stirling et al. 2001; Thompson et al. 2011; Weigang and Kisdi 2015) and the costs of dispersing through a hostile environment (Bowler and Benton 2005; Ronce 2007). Low fecundity may promote dispersal distance as, in the system, energy is not used for competition (<5 beetles per g flour), but the beetles are placed in a more competitive environment (10 beetles per g flour). This increase in emigration at higher densities was also noted in our low competition lines.

Highly dense populations can adversely affect the fecundity of adults by increasing mortality of the offspring through competition (e.g., Huang et al. 2015) or cannibalistic behaviors. Alternatively, low fecundity can be the result of per-capita provisioning of offspring (Beckerman et al. 2006), in which females produce fewer offspring but of greater quality, i.e., express *K*-selected traits (e.g., Henerly and Westoby 2001; Muller-Landau et al. 2008). This fecundity tradeoff may not directly affect the parents, particularly in populations with discrete generations, but it may increase the offspring's ability to tolerate variable environmental conditions, compete with conspecifics, and coexist or exclude a competing species (Muller-Landau 2010).

The introduction of the competing species to each of the lines only significantly displaced individuals belonging to the C_H lines of both species, suggesting that high competition selected lines were not selected to be superior competitors, but individuals were of poor quality, potentially due to resource limitations (Van Allen and Bhavsar 2014). However, as the low fecundity in high competition selected lines suggest offspring provisioning, and thus an increase in competitive ability may be reached if the population persists over generations. However, interspecific competition between species that are more and less competitive can lead to local exclusion of the inferior competitor (Cantrell et al. 2007; Luck and Podoler 1985). The dispersal of the inferior competitor species can promote regional coexistence (e.g., Chesson and Warner 1981; Livingston et al. 2012) as individuals can move to another vacant patch and become a ‘fugitive species’ (Mouquet et al. 2005). Consequently, range expansion may accelerate for the inferior competitor (Holt 2005), which, as our data suggests, may have stable ranges or slow-moving ranges.

Within invasion biology, a resident species that is a superior competitor can prevent an invading species from expanding its range ; however, even inferior competitors can slow down the invasion (Hastings et al. 2005; Svenning et al. 2014) through founder effects in which the resident species first colonized the area and filled available niche space (e.g., Jezkova 2020; Okubo et al. 1989; van der Knaap et al. 2005; Waters et al. 2013). If the invading species has +DDE, which was the case in half of our range front lines, the rate of spread of the invader is even further reduced (French and Travis 2001). Species that are +DDE are less likely to emigrate at low densities and colonizers often remain in the patch until high enough densities are reached (Amarasekare 2004a; Matthysen 2012). As interspecific competition can decrease population growth rates (e.g., Martin and Martin 2001) the lag time between dispersal events will be larger.

If the degree to which resident is inferior changes between populations, as is suggested by our data, the competitive interaction is likely to change across the range, which can greatly influence the speed of invasive range expansion (Svenning et al. 2014). Models for expanding ranges of invasive species as well as those expanding their native ranges need to include both intra- and inter- specific interaction to better predict dispersal outcomes.

Selection of traits in the range front: D_H , D_{HCL} , D_{HCH} , C_L , F_H

The selection of different DCF traits in the range suggest that different range pressures affect dispersal in three different ways: (1) high competition in the D_{HCH} can reduce dispersal propensity enough to not be significantly different from the beetles in the core, particularly within high densities. (2) Selection for low competition did not change displacement, however, beetles had +DDE (3) F_H RFB had high emigration rates at high densities, resulting in a +DDE response, and with a competing species.

As expected, lines selected for high dispersal had an overall greater propensity to disperse than their low dispersing counterparts (Table 4.4). This increase is likely due to spatial sorting promoting the occurrence of few high dispersers at the range front, which in turn, increases the range expansion speed over generational time (Fronhofer and Altermatt 2015; Travis et al. 2009). In the D_{HCH} line, the beetles selected for high dispersal and are spatially sorted from the low dispersers using the same methods as the other dispersal selection lines, but the additional high competition limits dispersal in two primary ways. The first is that additional parents used to breed each replicate for the D_{HCH} line (10 beetles with 6 replicate populations versus 5 beetles with 8 replicate populations) than the other two dispersal lines. A larger number of colonizers would increase genetic variation within the range populations and reduced the evolutionary

potential for high dispersal (Van Petegem et al. 2018) by limiting genetic drift inherent in founder effects. Secondly, the additional competitors in the natal habitat could negatively impact the health and dispersal ability of the $D_H C_H$ beetles, as noted with the $D_H C_L$ beetles, and, as a consequence, displacement and emigration may be reduced.

In spatiotemporal variable environments, +DDE is predicted to decrease the probability of local extinction (Amarasekare 2004b) as the mean per capita fitness is increased (Hovestadt et al. 2010) through promoted population growth in low densities and avoidance of intraspecific competition at high densities (Hamilton and May 1977; Handley and Perrin 2007). Density-independence, however, promotes emigration at the same rate despite conspecific competition or beneficial aggregation.

Interestingly, several lines representing the range front populations had +DDE (Table 4.7, Fig. 4.3), a form that theoretically reduces range expansion speeds as individuals in newly colonized habitats are unlikely to move forward in the range until population densities increase, creating a time lag between dispersal events (Altwegg et al. 2013). Many organisms settle in a range according to the ideal-free distribution model as individuals choose to settle in areas that maximize their fitness (Fretwell and Lucas 1970), which, for non-gregarious species, is away from competition (Altwegg et al. 2013; Matthysen 2005). Three of the five +DDE forms were low competition selected and the beetles may be emigrating from novel levels of high competition relative to their natal environment. As both C_L lines and neither D_H lines are +DDE, competition is likely driving the relationship. These populations are theoretically at a greater risk in disturbed environments as +DDE can additionally slow species' spatial response to climate change, particularly for populations with slow growing populations (Best et al. 2007; Urban et al. 2012) as the lag time is increased between dispersal events. CFB populations are more likely to

be impacted by disturbance as the species produces fewer offspring and has a slower population growth rate. Additionally, three of the four +DDE forms within competition-selected lines were CFB.

In spatiotemporal variable environments, +DDE is predicted to decrease the probability of local extinction (Amarasekare 2004b) as the mean per capita fitness is increased (Hovestadt et al. 2010) through promoted population growth in low densities and avoidance of intraspecific competition at high densities (Hamilton and May 1977; Handley and Perrin 2007). However, at the range front, selection should favor moderate rates of dispersal at densities well below the equilibrium density (Travis et al. 2009), as seen in our high dispersal selection lines, except D_{HCH} . This suggests that high dispersal selects for behavior that hastens range expansion whereas low competition in natal habitat promotes local population persistence.

Unexpectedly, RFB F_H lines also emigrated positively with density with the highest rates of emigration at the greatest densities of all lines (Fig. 4.3). F_H individuals mature in densities similar to those in the control line, which was DIE and did not change across generational time, thus the difference in the density-emigration form is unlikely to escape from conspecific competition. One main difference between the F_H lines and the other lines, however, is the probability of high kin-competition as only the offspring of the 2-3 highest fecund females were used each generation (compared to 20 females for dispersal selection and generally 12 for low fecundity selection). These offspring were randomized for experiments, but the chances of competing directly with close relatives was high. In populations with high levels of kin-competition, emigration is often increased (Van Petegem et al. 2018) as individuals leave to reduce local resource competition (Bach et al. 2006; Ronce et al. 2000) and spread their genes in surrounding populations or colonize empty habitats (Hamilton 1964). This strategy maximizes

inclusive fitness of the population (Hamilton and May 1977) and promotes range expansion speeds through the increase in emigration (Van Petegem et al. 2018). Although this was not the original intent of the H_F line, the high levels of genetic-relatedness is representative of a range front population and has been found in many range-expanding species (Hastings et al 2005; Lee 2002; Dingle 1978).

Dispersal and competition theoretically trade-off with one another as dispersal is often costly with long stretches of inhabitable matrix, interspecific competitors, environmental hazards, and predators (Fronhofer and Altermatt 2015) and the decrease in competitive ability has been attributed to traversing these harsh environments (Bowler and Benton 2005; Ronce 2007). These landscape variables, however, were not included in our standardized-short matrix landscapes, thus the risks of dispersing were weaker for our experiment, but our results clearly show that even intraspecific- and kin-competition can greatly reduce the ability for individuals to disperse at the range front.

CONCLUSIONS

Here, we took the novel approach of applying concurrent selection pressures of dispersal and competition onto populations to represent the interacting tradeoffs that occur either in the range core or range front of an expanding population. We compared these population responses to the customarily used single-trait selection tradeoffs between competitive and dispersal abilities and incorporated fecundity selection, which is often measured only as a reaction to other trait selection. As the response to tradeoffs is often system-dependent, we used two species that have high niche overlap but vary in their normal responses to competition to test the differences

between species. Lastly, we assessed how applying different selection pressures changes an individual's reaction to a competing species.

This research addresses many questions that have not been fully addressed using an empirical system. Chiefly, our results suggest that the propensity to disperse — and thus range expansion speed — is influenced by intraspecific competition in both the range front and core. High competition generally limits emigration and displacement, whereas very low competition may increase the dispersal distance but may reduce the propensity to emigrate at low densities. In this way, selection for competition within dispersing populations may slow down expansion speed. This change is slight but enough that DCF traits among the core, front, and control changed. This is expected by competition models (e.g., Svenning et al. 2014) but has yet to be shown through direct selection in an empirical experiment.

We additionally tested the tradeoffs between the propensity to disperse, competitive ability, and fecundity by placing selection pressure on each trait. This has been done in separate experiments but not coincidentally using the same parental populations. Competition on its own did not change the propensity to disperse over generational time. Although fecundity is often linked with competitive and dispersal abilities, selection for or against fecundity did not change dispersal propensity, but kin competition may have affected emigration.

Additional research investigating the effects of multiple selected traits is needed. The pairwise interactions customarily used in range expansion research can provide much information on metapopulation dynamics, but populations are influenced by multiple variables that may have opposing tradeoffs. This may have great impact on the range expansion speed of

dynamic populations, and models forecasting the movement of invasive species or populations escaping from disturbance need to include empirical data from multiple experiments such as this one.

CHAPTER 5. CONCLUSIONS

In my dissertation, I examined how habitat fragmentation and range margins effect dispersal and interactions between intra- and inter-specific competitors. My research includes different spatio-temporal scales ranging from short-term individual movement within patch to the evolution of multiple traits in landscapes. Additionally, my work details the history of dispersal research through a systematic literature review and looks to the future by using novel study organisms, incorporating original experimental design, and suggesting methods that would further research. This dissertation has advanced our understanding of population dynamics, species invasions, and conservation biology.

Chapter 2: Historical perspectives on emigration and where research should go next

In my second chapter, I addressed the limited ecological view that the density-emigration relationship is either density-independent (Hanski and Gilpin 1991; Levins 1974; Pacala and Roughgarden 1982) or positive (Amarasekare 2004; Bowler and Benton 2005; Matthysen 2012) as many models do not consider the possibility of negative density-dependent emigration (DDE) or nonlinear forms such as u-shaped or hump-shaped.

I hypothesized that empirical studies of DDE would also follow this trend with the majority of relationships being +DDE or DIE. This hypothesis was not rejected as most of the 145 studies included systems that had + DDE (36%) and DIE (30%). Unexpectedly, the alternative forms of -DDE (25%) and the nonlinear forms of uDDE and hDDE (cumulative 9%) were included in more studies than originally anticipated. The number of nonlinear forms was greatly increased by reanalyzing the data for nonlinear relationships, which added 4 cases.

However, as many studies use methods that preclude the detection of nonlinear DDE, it is likely that they are more common than our literature review has revealed. Importantly, in this chapter I provide evidence for the benefit of using methods that focus on rigorous regression-based experimental designs that incorporate a greater number of densities that range from very low to above carrying capacity. The use of statistics and methods that improve the chances of detecting different forms is important as our models suggest that different DDE forms can cause complex within-patch dynamics that are not observed with DIE or +DDE, for which our model predicts constant population persistence, which is not universally found in nature (e.g., Turchin and Taylor 1992).

As the 5 different forms of DDE have not been theoretically compared for population dynamic changes, we developed a reaction-diffusion model to illustrate how different forms of DDE can affect patch-level populations in different patch sizes and matrix hostilities. I hypothesized that the different DDE forms would have dynamic population persistence consequences, which was the case for -DDE, uDDE, and hDDE. The Allee effect regime in the -DDE and uDDE allows populations to persist in smaller patches formed from a newly fragmented larger patch, which may be why anthropogenic fragmentation is one of the leading causes of demographic Allee effects found in populations (Courchamp et al. 2008). Similarly, the negative slope of -DDE and uDDE changes the reaction norm and produces bi-stability regimes that allows the organism to colonize and persist at a much lower density level. Both Allee effects and alternative stable states are difficult to detect in nature and have limited empirical support; however, our model suggests that these population dynamics are a potential result of fragmentation, but only with populations that have alternative DDE forms.

Chapter 3: A novel system that has interesting aggregative behaviors that results in uDDE

In my third chapter, I address some of the research gaps revealed in my literature review, specifically investigating individual movement and emigration within small, fragmented patches. An individual's response to fragmentation is often the least understood regarding the biology of a species (Evans et al., 2018; Hooten et al., 2017), but understanding individual behavior is important as individual decisions can influence emigration, which in turn changes population and metapopulation dynamics. In this chapter, my study system included the blissid bug *Ischnodemus conicus*, which inhabits *Spartina alterniflora* patches on the coast. To our knowledge, there is no direct manipulation study of *I. conicus* and studies using congeners are primarily concerned with the host plant and not the behavior of the insect (e.g., Johnson and Knapp 1996). Nothing is known concerning its dispersal behavior; thus, this study provides a novel entomological system that can be used to further study dispersal responses to disturbed environments. However, this study is not system dependent as the insect and habitat reflect landscapes used in many theoretical models of a standard patch (monoculture patches of *Spartina alterniflora*) surrounded by a simple, but harsh matrix (bare sand) and bug's responses to fragmentation can be generalized to other populations with similar life history traits to *I. conicus*. As fragmentation is a common disturbance in habitats, understanding how an individual reacts to the edge of a patch as well as to conspecifics is needed.

As predicted, *I. falicus* displayed behavioral responses that are indicative of a gregarious species, such as non-linear uDDE and maintaining a clumped distribution over time. Additionally, as predicted, the emigration of individuals into a harsh, sand matrix was low, and individuals did not remain. This would suggest that *Ischnodemus conicus* populations would be able to persist in large populations, due to their gregarious nature (Bowler and Benton 2005; Kim

et al. 2009; Matthysen 2012). Long-distance dispersal would be limited by the brachypterous population majority and the potential use of aggregating pheromones (e.g., Bartelt et al., 2008; Stevenson et al., 2017). The harsh boundary and hostile nature of the mud matrix further impedes emigration from the habitat as the edge is not very permeable to individuals, who instead move along the boundary and aggregate (e.g., Desrochers et al. 2003).

Chapter 4: A systematic approach to analyzing range expansion dynamics

In my fourth chapter, I examined the eco-evo dynamics of an expanding range using the model organisms *Tribolium confusum* and *T. castaneum*, and applied selection pressure to ten different populations of each species. These populations reflected different selection events that could theoretically occur in the core or the range front. This study encompasses four main additions to the work of range expansion. The first is that I selected for every DCF (dispersal, competition, fecundity) trait and measured the population's response rather than focusing on one trait at a time (e.g., Arnold et al., 2017). Secondly, I placed selection pressures for both competitive ability and the propensity to disperse in a factorial design to account for different population densities than expected from the dense core and space range front, which would fit the contrasting models of Fronhofer and Altermatt (2015) and Benton et al. (2008). Lastly, I measured the response of each selection line to a competitor, which would reflect both the focal specie's expansion into a new habitat that is inhabited by a competitor as well as a competition species invading into the range core population. This systematic approach incorporates several studies of range expansion into one experiment and suggests the interplay of several range expansion responses including founder effects, kin-competition, genetic drift, r - and K -selection, emigration, and spatial sorting of phenotypes.

In this study, I first predicted that the DCF traits would be heritable and thus could be evolutionarily changed. The selection for dispersal supported this hypothesis as there was divergence in dispersal behavior, which is common in many species (e.g., Donohue et al. 2005; Phillips et al. 2006; Roff 2007) as a suite of phenotypes, called dispersal syndromes, often affect dispersal ability (Clobert et al. 2009; Hudina et al. 2014; Sih et al. 2012). Fecundity significantly decreased the number of offspring that survived until pupation by 40% between CFB F_H and F_L lines, but not for RFB, which suggests that fecundity may be selected for in one species (e.g., Long et al. 2009; Quezada-Garcia and Bauce 2014; Sgro and Hoffmann 1998). Alternatively, changes in fecundity can be caused by another heritable trait relating to fitness (e.g., Davis and Landolt 2012; Lansing 1942), the health of the mother (e.g., Benton et al. 2008; Bock et al. 2019). Assessing competition trait heritability in this study was not possible as results are confounded by both genetics as well as environmental differences in resource availability, cannibalism rate, and crowded conditions that could have carried over into the new environment (Hamel et al. 2009; Mousseau and Fox 1988; Van Allen and Rudolf 2013).

For populations representing both the core and front, I expected high competition selection to limit the dispersal of the $D_H C_H$ and $D_L C_H$ lines and high dispersal to limit the competition of $D_H C_H$ and $D_H C_L$ lines as proposed in the theoretical work of Svenning et al. (2014). This happened with dispersal ability, but not to the extent that I predicted. Except for a few dispersal responses, selection for traits concurrently promoted differences, but to the control and opposite selection group (the core or the front). Differences within the core and front were limited; however, these small changes can still have great impact on range expansion speed (e.g., Weiss-Lehman et al. 2017). Additionally, the density-emigration response changed between lines with five of the ten range front lines having a +DDE whereas all other lines were DIE. As

described in my second chapter, both of these DDE forms promote constant population persistence in patches larger than the minimum patch size (Harman et al. 2020); however, the DIE form is theoretically promotes range expansion more than +DDE (Amarasekare 2004) as +DDE populations experience a lag time in dispersal events while waiting for densities to increase (Altwegg et al. 2013). Unexpectedly, RFB F_H lines also emigrated positively with density with the highest rates of emigration at the greatest densities of all lines. As this population was founded by few individuals each generation (6-8 pairs compared to 20), this suggest that kin-competition was a byproduct of the selection process and emigration behavior is preferred to reduce local resource competition (Bach et al. 2006; Ronce et al. 2000).

Lastly, for this chapter, I hypothesized that the high competition lines would better compete against the other species, although to a lesser extent if coincidentally selecting for high dispersal. This, however, was not the case as the high competitor lines emigrated with a 2.2-2.3x greater proportion with the competitor than with conspecifics alone. This suggests that the selection process did not produce a high competing line, at least in the definition of competitive exclusion (Cantrell et a. 2007; Luck and Podoler 1985). Inferior competitive and dispersal ability has been noted in other studies pertaining to habitat quality (e.g., Van Allen and Bhavsar 2014).

Conclusions and future research

Dispersal events proceed through a series of stages that start with an individual's decision to move. This movement can be impacted by the presence of conspecifics (chapter 2), the landscape (chapter 3), and selection pressure (chapter 4) and may influence population persistence (chapter 2), the movement decisions of others (chapter 3), and range expansion (chapter 4). Dispersal is a dynamic process and the use of better methods that measure a range of

variables (chapter 2), different study organisms that give a broader picture of dispersal consequences (chapter 3), and systematic approaches that take into account several facets of dispersal at once (chapter 4) will greatly advance our understanding of population dynamics, species invasions, and conservation biology, just as this dissertation has.

In the near future, I plan to continue my research on dispersal and competition in fragmented landscapes and focus on interspecific competition and range expansion across a landscape. This field of research is very interesting to me and much headway is needed for empirical work to catch up with theoretical.

APPENDIX A. SUPPLEMENTARY MATERIAL FOR CHAPTER 2.

Table A1. List of case studies used in the empirical literature review. Source of data, species identity and taxonomic group, type of study (obs = observational, exp = experimental), number and range of densities (ratio of highest to lowest density) and form of density-dependent emigration reported. Experimental studies marked as exp* are those in which individuals exiting the patch were removed from the system, precluding them from returning to the patch. The possible DDE relationships include density-independent (DIE), positive (+DDE), negative (-DDE), u-shaped (uDDE), and hump-shaped (hDDE). Table continues over the next several pages.

Article	Species Scientific Name	Species Type	Research Type	DDE Form (Original Form)	# of Densities	Density Range
Aars and Ims 2000	<i>Microtus oeconomus</i>	mammal	exp	+DDE	2	3.6
Albrechtsen and Nachman 2001	<i>Paroxyna plantaginis</i>	insect	exp	+DDE	3	-
Allen and Thompson 2010	<i>Ischnura pumilio</i>	insect	obs	-DDE	-	-
Alonso et al 1999	<i>Otis tarda</i>	bird	obs	-DDE	-	-
Altwegg et al 2014	<i>Philetairus socius</i>	insect	obs	-DDE	17	20.0
Altwegg et al 2014	<i>Philetairus socius</i>	bird	obs	uDDE	17	20.0
Andreassen and Ims 2001	<i>Microtus oeconomus</i>	mammal	exp	-DDE	20	25.0
Azandeme Hounnmalon et al 2014	<i>Tetranychus evansi</i>	insect	exp	+DDE	4	80.0
Azandeme Hounnmalon et al 2014	<i>Tetranychus urticae</i>	insect	exp	DIE	4	80.0
Baguette et al 2011	<i>Boloria eunomia</i>	insect	exp	-DDE	-	-
Baines et al 2014	<i>Notonecta undulata</i>	insect	exp	uDDE(+DDE)	3	3.2
Bateman et al 2012	<i>Suricata suricatta</i>	mammal	obs	+DDE	24	9.0
Bengtsson et al 1994	<i>Onychiurus armatus</i>	insect	exp	+DDE	2	3.0

(Table cont'd.)

Article	Species Scientific Name	Species Type	Research Type	DDE Form (Original Form)	# of Densities	Density Range
Bengtsson et al 2002	<i>Onychiurus armatus</i>	insect	exp	+DDE	3	81.0
Berggren and Forsman 2012	<i>Tetrix subulata</i>	insect	exp	DIE	2	1.4
Bret et al 2016	<i>Cornu aspersum</i>	invertebrate	exp	+DDE	3	4.0
Brooke 2010	<i>Brueelia merulensis</i>	insect	obs	DIE	-	-
Broseth et al 1998	<i>Lagopus lagopus</i>	bird	obs	+DDE	2	2.2
Byrom 2002	<i>Mustela furo</i>	mammal	obs	DIE	2	-
Callihan et al 2014	<i>Morone saxatilis</i>	fish	exp	+DDE	-	-
Chaput-Bardy et al 2010	<i>Calopteryx splendens</i>	insect	obs	-DDE	-	3.4
Chatelain and Mathieu 2017	<i>Eisenia andrei</i>	insect	exp	+DDE	4	30.0
Chatelain and Mathieu 2017	<i>Eisenia fetida</i>	insect	exp	hDDE(DIE)	4	30.0
Chatelain and Mathieu 2017	<i>Lumbricus rubellus</i>	insect	exp	hDDE(-DDE)	4	30.0
Cote et al 2011	<i>Gambusia affinis</i>	fish	exp*	DIE	2	2.9
Crisp 1993	<i>Salmo trutta</i>	fish	obs	uDDE(+DDE)	21	20.0
Dahirel et al 2014	<i>Cornu aspersum</i>	invertebrate	exp	DIE	2	2.0
Day et al 2004	<i>Haliotis rubra</i>	invertebrate	exp	+DDE	2	5.0
DeMeester and Bonte 2010	<i>Erigone atra</i>	invertebrate	exp	+DDE	15	15.0
Denno et al 2001	<i>Toya venilia</i>	insect	obs	+DDE	10	70.0
Derosier et al 2007	<i>Petromyzon marinus</i>	fish	exp	DIE	3	6.0
Derosier et al 2007	<i>Petromyzon marinus</i>	fish	exp	-DDE	3	6.0
Doak 2000	<i>Itame andersoni</i>	insect	exp	+DDE	3	5.0

(Table cont'd.)

Article	Species Scientific Name	Species Type	Research Type	DDE Form (Original Form)	# of Densities	Density Range
Donaldson et al 2007	<i>Aphis glycines</i>	insect	exp	+DDE	13	101.0
Drolet et al 2013	<i>Corophium volutator</i>	invertebrate	exp	DIE	3	2.0
Einum and Nislow 2005	<i>Salmo salar</i>	fish	exp	+DDE	10	1.6
Einum and Nislow 2005	<i>Salmo salar</i>	fish	exp	-DDE	10	1.6
Einum et al 2006	<i>Salmo salar</i>	fish	exp	+DDE	9	1.7
Elliott 2003	<i>Baetis rhodani</i>	insect	exp	DIE	6	4.0
Elliott 2003	<i>Ecdyonurus venosus</i>	insect	exp	DIE	6	4.0
Elliott 2003	<i>Gammarus pulex</i>	invertebrate	exp	DIE	6	4.0
Elliott 2003	<i>Hydropsyche siltalai</i>	insect	exp	DIE	6	4.0
Elliott 2003	<i>Isoperla grammatica</i>	insect	exp	DIE	6	4.0
Elliott 2003	<i>Perlodes microcephalus</i>	insect	exp	DIE	6	4.0
Elliott 2003	<i>Potamophylax cingulatus</i>	insect	exp	DIE	6	4.0
Elliott 2003	<i>Protonemura meyeri</i>	insect	exp	DIE	6	4.0
Elliott 2003	<i>Rhithrogena semicolorata</i>	insect	exp	DIE	6	4.0
Elliott 2003	<i>Rhyacophila dorsalis</i>	insect	exp	DIE	6	4.0
Enfjail and Leimar 2005	<i>Melitaea cinxia</i>	insect	exp	+DDE	2	7.0
Etherington et al 2003	<i>Callinectes sapidus</i>	invertebrate	exp	DIE	2	4.0
Etherington et al 2003	<i>Callinectes sapidus</i>	invertebrate	exp	-DDE	2	4.0
Fasola et al 2002	<i>Egretta garzetta</i>	bird	obs	DIE	8	9.7
Fattebert et al 2015	<i>Panthera pardus</i>	mammal	obs	uDDE	20	-
Fattebert et al 2015	<i>Panthera pardus</i>	mammal	obs	-DDE	13	-
Fonseca and Hart 1996	<i>Simulium vittatum</i>	insect	exp*	+DDE	15	15.0
French and Travis 2001	<i>Anisopteromalus calandrae</i>	insect	exp	+DDE	3	10.0

(Table cont'd.)

Article	Species Scientific Name	Species Type	Research Type	DDE Form (Original Form)	# of Densities	Density Range
Fronhofer et al 2015	<i>Tetrahymena</i>	micro-organism	exp	-DDE	5	10.0
Hahne et al 2011	<i>Microtus arvalis</i>	mammal	exp	+DDE	5	12.0
Hammill et al 2015	<i>Paramecium aurelia</i>	micro-organism	exp	+DDE	7	16.0
Hammill et al 2015	<i>Paramecium aurelia</i>	micro-organism	exp	-DDE	7	16.0
Hauzy et al 2007	<i>Dileptus sp.</i>	micro-organism	exp	DIE	3	294.7
Hauzy et al 2007	<i>Tetrahymena pyriformis</i>	micro-organism	exp	+DDE	3	4.0
Hendrickx et al 2013	<i>Pterostichus vernalis</i>	insect	exp	-DDE	7	60.0
Herzig 1995	<i>Trirhabda virgata</i>	insect	exp	+DDE	2	2.0
Hibbard et al 2004	<i>Diabrotica virgifera virgifera</i>	insect	exp	+DDE	5	32.0
Hooft et al 2008	<i>Mastomys natalensis</i>	mammal	obs	-DDE	8	3.5
Huffeldt et al 2012	<i>Tyto alba</i>	bird	obs	DIE	-	-
Humphries 2002	<i>Baetis rhodani</i>	insect	exp	DIE	8	14.0
Ims and Andreassen 2005	<i>Microtus oeconomus</i>	mammal	obs	-DDE	28	49.0
Itonaga et al 2011	<i>Ciconia ciconia</i>	bird	obs	+DDE	3	1.6
Izraylevich and Gerson 1995	<i>Hemisarcoptes coccophagus</i>	insect	exp	+DDE	5	12.0
Jacob et al 2016	<i>Tetrahymena thermophila</i>	micro-organism	exp	hDDE	3	4.0
Jacob et al 2016	<i>Tetrahymena thermophila</i>	micro-organism	exp	uDDE	3	4.0
Johnson and Eggleston 2010	<i>Callinectes sapidus</i>	invertebrate	obs	-DDE	2	12.0
Kerans et al 2000	<i>Hydropsyche slossonae</i>	insect	exp*	+DDE	3	8.0
Keynan and Ridley 2016	<i>Turdoides squamiceps</i>	bird	obs	+DDE	25	8.5
Kim et al 2009	<i>Sula neboxii</i>	bird	obs	uDDE	100	65.0

(Table cont'd.)

Article	Species Scientific Name	Species Type	Research Type	DDE Form (Original Form)	# of Densities	Density Range
Kuefler e al 2012	<i>Brachionus calyciflorus</i>	micro-organism	exp	+DDE	22	30.0
Lancaster et al 2011	<i>Baetis rhodani</i>	insect	exp*	DIE	7	20.0
Le Galliard et al 2003	<i>Lacerta vivipara</i>	reptile	exp*	DIE	2	1.4
Le Galliard et al 2003	<i>Lacerta vivipara</i>	reptile	exp*	+DDE	2	1.4
Loe et al 2009	<i>Cervus elaphus</i>	mammal	obs	DIE	5	4.0
Loe et al 2009	<i>Cervus elaphus</i>	mammal	obs	-DDE	5	4.0
Lutz et al 2015	<i>Odocoileus virginianus</i>	mammal	obs	hDDE(+DDE)	12	102.2
Maag et al 2018	<i>Suricata suricatta</i>	mammal	obs	uDDE	3	6.0
Mabry 2014	<i>Peromyscus boylii</i>	mammal	obs	-DDE	2	1.4
Manteuffel and Eiblmaier 2010	<i>Sceloporus virgatus</i>	reptile	exp*	+DDE	2	3.0
Martin et al 2008	<i>Otis tarda</i>	bird	obs	-DDE	90	-
Mathieu et al 2010	<i>Aporrectodea icterica</i>	insect	exp	+DDE	3	3.3
Mckellar et al 2015	<i>Setophaga ruticilla</i>	bird	obs	-DDE	7	3.6
Meylan et al 2007	<i>Lacerta vivipara</i>	reptile	exp	-DDE	2	-
Michler et al 2011	<i>Parus major</i>	bird	exp	DIE	3	-
Midtgaard 1999	<i>Harpalus rufipes</i>	insect	exp*	DIE	7	15.0
Midtgaard 1999	<i>Pterostichus niger</i>	insect	exp*	DIE	5	9.0
Mishra et al 2018	<i>Drosophila melanogaster</i>	insect	exp	-DDE	4	8.0
Moksnes 2004	<i>Carcinus maenas</i>	invertebrate	exp	uDDE(+DDE)	3	9.0
Molina-Morales et al 2012	<i>Pica pica</i>	bird	obs	+DDE	33	7.5
Morton et al 2018	<i>Falco peregrinus</i>	bird	obs	-DDE	2	-

(Table cont'd.)

Article	Species Scientific Name	Species Type	Research Type	DDE Form (Original Form)	# of Densities	Density Range
Newton 2001	<i>Accipiter nisus</i>	bird	obs	DIE	-	-
Nowicki and Vrabec 2011	<i>Maculinea nausithous</i>	insect	obs	+DDE	7	6.5
Nowicki and Vrabec 2011	<i>Maculinea teleius</i>	insect	obs	+DDE	7	6.5
Ost et al 2011	<i>Somateria mollissima</i>	bird	obs	+DDE	-	200.0
Overholtzer-McLeod 2004	<i>Halichoeres garnoti</i>	fish	exp	DIE	11	3.0
Paris et al 2016	<i>Petroica traversi</i>	bird	obs	+DDE	-	16.0
Pasinelli and Walters 2002	<i>Picoides borealis</i>	bird	obs	+DDE	4	4.0
Payne 1991	<i>Passerina cyanea</i>	bird	obs	DIE	4	4.0
Pennekamp et al 2014	<i>Tetrahymena thermophila</i>	micro-organism	exp	DIE	3	3.0
Pennekamp et al 2014	<i>Tetrahymena thermophila</i>	micro-organism	exp	-DDE	3	3.0
Poniatowski and Fartmann 2011	<i>Metrioptera brachyptera</i>	insect	obs	+DDE	16	16.0
Powers and Peterson 2000	<i>Argopecten irradians concentricus</i>	invertebrate	exp	hDDE(+DDE)	3	5.4
Powers and Peterson 2000	<i>Argopecten irradians concentricus</i>	invertebrate	exp	+DDE	3	5.4
Randall et al 2005	<i>Rhombomys opimus</i>	mammal	obs	-DDE	4	94.0
Rasmussen and Belk 2012	<i>Lepidomeda aliciae</i>	fish	obs	DIE	4	4.7
Reyns and Eggleston 2004	<i>Callinectes sapidus</i>	invertebrate	obs	+DDE	14	-
Rhainds and Messing 2005	<i>Aphis gossypii</i>	insect	obs	DIE	20	3.3
Rhainds et al 2002	<i>Metisa plana</i>	insect	exp*	+DDE	3	20.0
Rhainds et al 2005	<i>Frankliniella occidentalis</i>	insect	exp*	+DDE	2	-

(Table cont'd.)

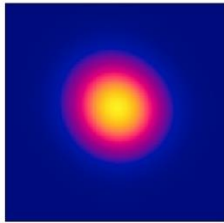
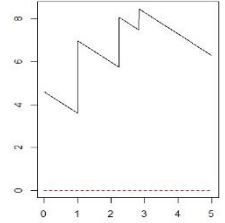
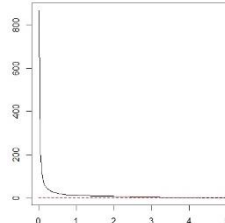
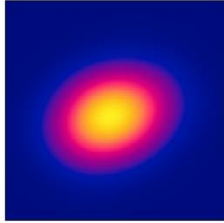
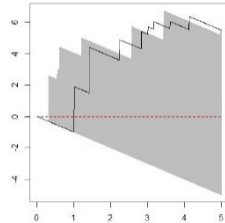
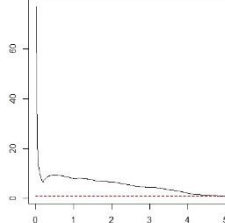
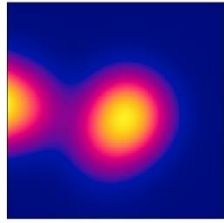
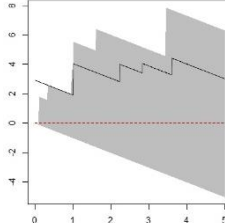
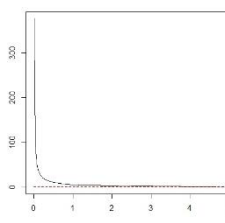
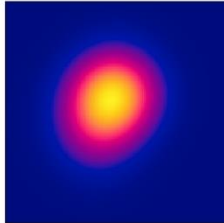
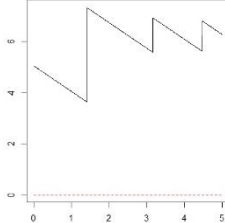
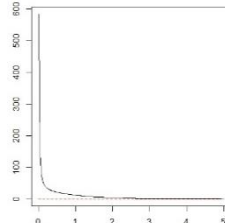
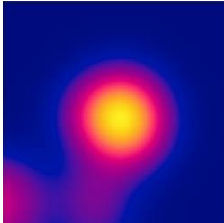
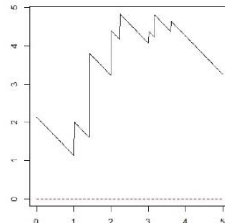
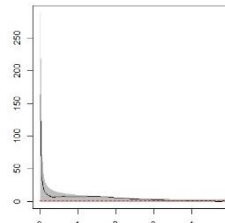
Article	Species Scientific Name	Species Type	Research Type	DDE Form (Original Form)	# of Densities	Density Range
Richardson et al 2010	<i>Notiomystis cincta</i>	bird	obs	-DDE	-	-
Richardson et al 2010	<i>Notiomystis cincta</i>	bird	obs	+DDE	-	-
De Roissart et al 2013	<i>Tetranychus urticae</i>	insect	exp	+DDE	13	6.57
Ronnas et al 2011	<i>Thaumetopoea pinivora</i>	insect	obs	DIE	2	3.33
Rosenberg et al 1997	<i>Amphiura filiformis</i>	invertebrate	exp	+DDE	2	3.4
Rouquette and Thompson 2007	<i>Coenagrion mercuriale</i>	insect	obs	-DDE	3	-
Roy et al 2012	<i>Ursus americanus</i>	mammal	obs	-DDE	2	3.5
Sanderson et al 2002	<i>Leptinotarsa decemlineata</i>	insect	exp	DIE	7	64.0
Sanderson et al 2004	<i>Leptinotarsa decemlineata</i>	insect	exp	uDDE(DIE)	4	16.0
Santoro et al 2013	<i>Plegadis falcinellus</i>	bird	obs	DIE	-	-
Scandolara et al 2014	<i>Hirundo rustica</i>	bird	obs	-DDE	38	34.0
Schulz and Leal 2012	<i>Salminus brasiliensis</i>	fish	exp	+DDE	2	2.2
Smith and Batzli 2006	<i>Microtus ochrogaster</i>	mammal	exp	-DDE	27	25.0
Stasek et al 2017	<i>Agallia constricta</i>	insect	exp	DIE	2	2.0
Stauffer et al 2014	<i>Leptonychotes weddellii</i>	mammal	obs	+DDE	-	2.7
Stoen et al 2006	<i>Ursus arctos</i>	mammal	obs	-DDE	2	4.5
Stevens and Bonsall 2011	<i>Callosobruchus maculatus</i>	insect	exp	+DDE	50	19.0
Tatara et al 2011	<i>Oncorhynchus mykiss</i>	fish	exp	DIE	3	6.0
Tripet et al 2002	<i>Ceratophyllus gallinae</i>	insect	exp	-DDE	16	27.5
Van Allen and Bhavsar 2014	<i>Tribolium</i> sp.	insect	exp*	+DDE	6	18.0
Van Allen and Bhavsar 2014	<i>Tribolium</i> sp.	insect	exp*	DIE	6	18.0

(Table cont'd.)

Article	Species Scientific Name	Species Type	Research Type	DDE Form (Original Form)	# of Densities	Density Range
Ventura et al 2017	<i>Cyrtophora citricola</i>	invertebrate	exp	-DDE	3	8.0
Waser et al 2006	<i>Dipodomys spectabilis</i>	mammal	obs	-DDE	2	3.0
Wauters et al 2004	<i>Sciurus vulgaris</i>	mammal	obs	DIE	13	4.0
Wauters et al 2004	<i>Sciurus vulgaris</i>	mammal	obs	+DDE	13	4.0
Westerberg et al 2008	<i>Protaphorura armata</i>	insect	exp	-DDE	3	16.7
Wojan et al 2015	<i>Peromyscus boylii</i>	mammal	obs	-DDE	5	20.0
Zavorka et al 2015	<i>Salmo trutta</i>	fish	exp	DIE	2	-

APPENDIX B. SUPPLEMENTARY MATERIAL FOR CHAPTER 3.

Table B.1. Outputs for spatial point pattern data for distribution 5 hours after release in habitat landscapes. Table continues on next page

Replicate (# bugs)	Density heat map at 5 hours	Ripley's K transformed $L(r)-r$	Pair-correlation $g(r)$
1 (4)			
2 (6)			
3 (6)			
4 (5)			
5 (8)			

(Table cont'd.)

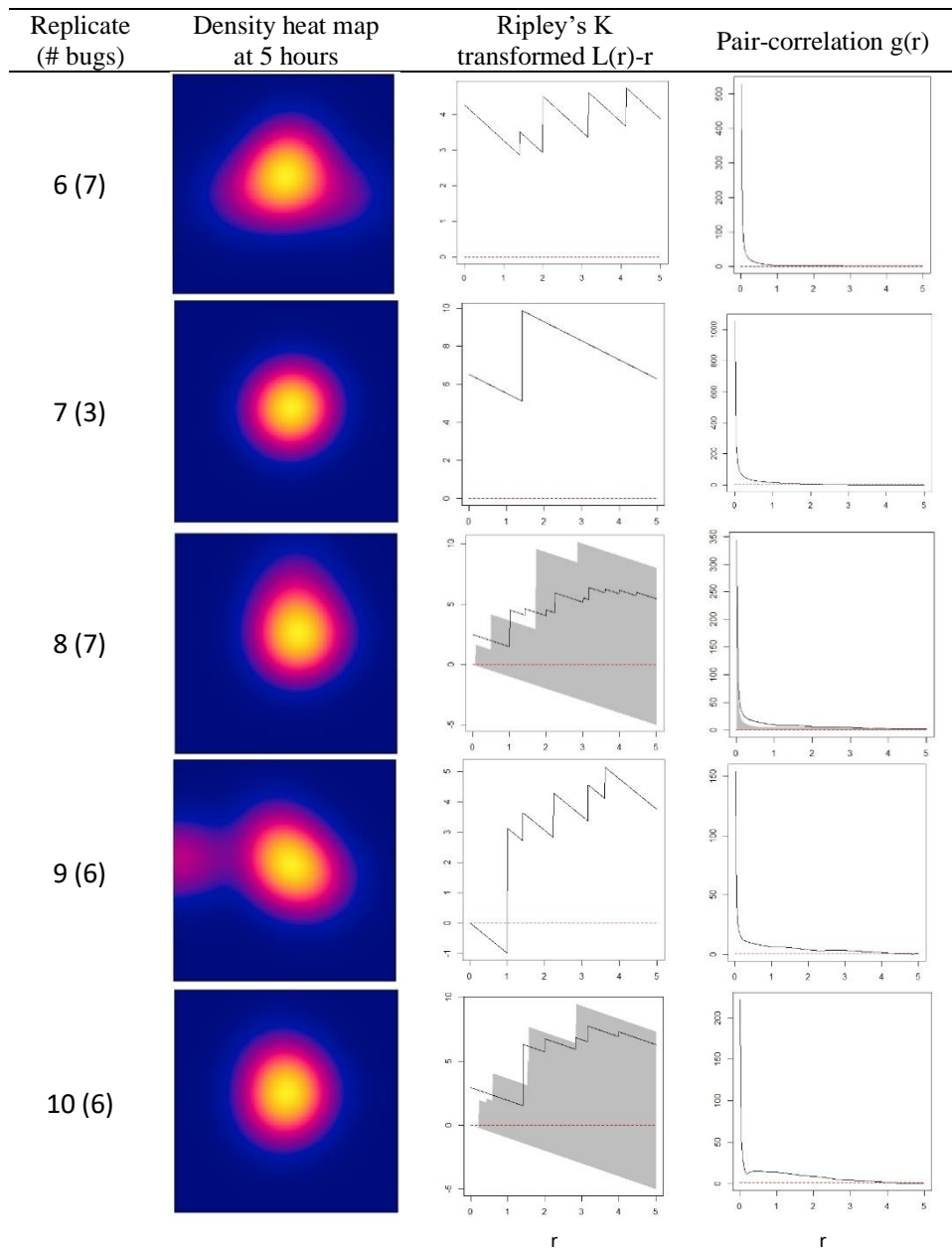
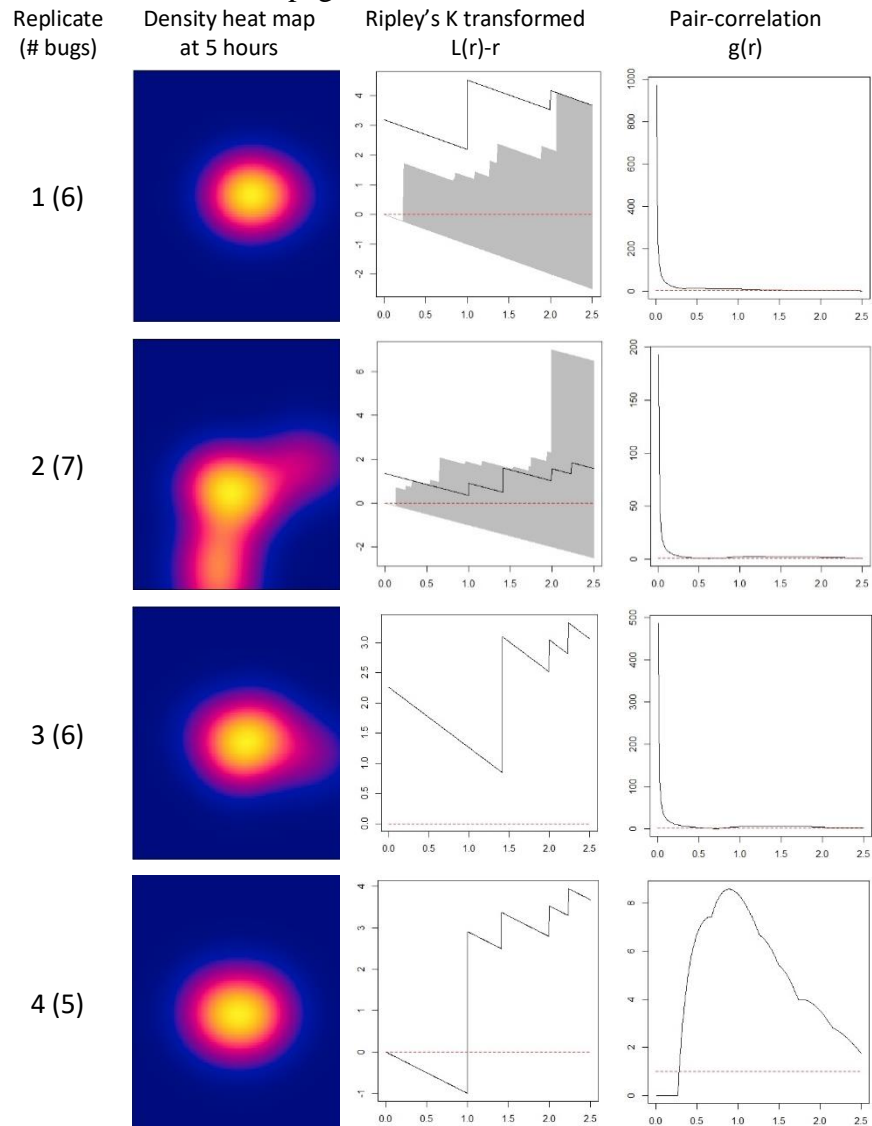
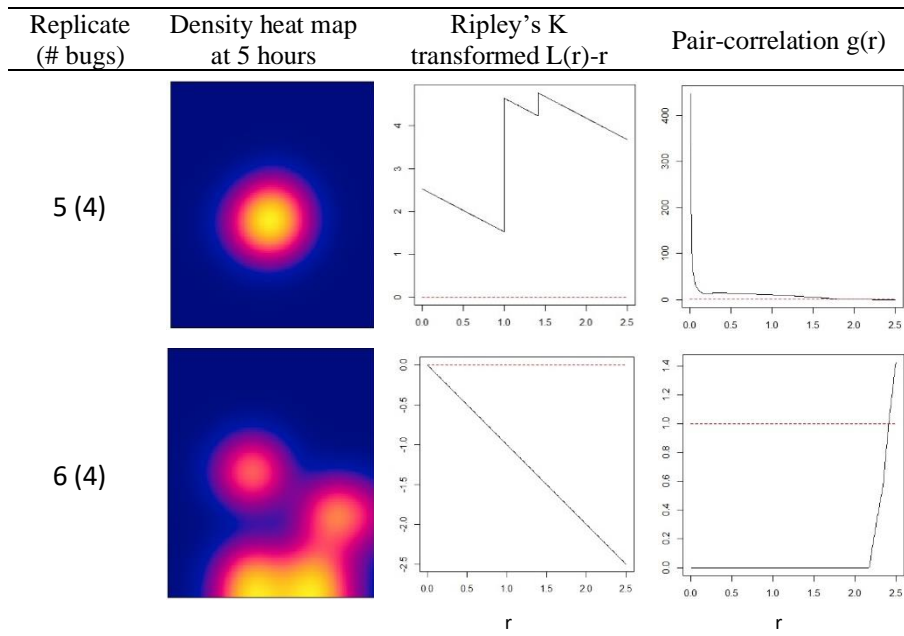


Table B.2. Outputs for spatial point pattern data for distribution 5 hours after release in habitat landscapes. Table continued on next page.



(Table cont'd.)



APPENDIX C. SUPPLEMENTARY MATERIAL FOR CHAPTER 3.

Table C.1. Collection sites for flour beetle species used in range expansion experiments.

Granary	City, State	Species found
Carolina Supply Company	Supply company	RFB, CFB
Sauder Mill	Grabill, IN	RFB, CFB
Monroe Grain & Supply	Monroe, IN	RFB
Atlas Feed Mills	Breaux Bridge, LA	RFB
Summer Farms	Franklin, KY	RFB, CFB
Peppers Hardin County Milling	Elizabethtown, KY	RFB, CFB
Petrus Granary	Alexandria, LA	RFB
Milan Center Feed and Grain	New Haven, IN	RFB, CFB
Miller Feeds	Goshen, IN	CFB

Table C.2. Linear regression and quadratic regression results for density-emigration relationships of the dispersal lines. AICc value comparing the two regressions is provided for comparisons that had differing R² values. (T=control, D=dispersal, C=competition, F=fecundity, L=selection for low ability, H=selection for high ability). DIE under density-emigration relationship represents density-independent.

	Line	Linear regression				Quadratic regression				Linea r AICc	Quadratic AICc
		F	DF	R2	P	F	DF	R2	P		
Red flour beetle	T	0.01	1, 18	0.001	0.93	0.10	2, 17	0.12	0.90		
	D _L	2.6	1, 18	0.13	0.12	1.89	2, 17	0.18	0.18		
	D _H	0.01	1, 18	0.001	0.91	0.03	2, 17	0.01	0.97		
	D _L C _L	0.18	1, 18	0.01	0.68	0.15	2, 17	0.02	0.86		
	D _H C _L	0	1, 18	>0.001	0.99	0.29	2, 17	0.03	0.75		
	D _L C _H	4.13	1, 18	0.19	0.06	1.96	2, 17	0.19	0.17		
	D _H C _H	0.66	1, 18	0.04	0.43	0.45	2, 17	0.05	0.65		
	C _L	11.99	1, 18	0.37	0.003	10.3	2, 17	0.55	0.001	0.75	9.31
	C _H	3.26	1, 18	0.15	0.09	2.35	2, 17	0.22	0.13		
	F _L	1.65	1, 18	0.08	0.22	0.88	2, 17	0.09	0.88		
	F _H	23.92	1, 18	0.57	0.001	14.6	2, 17	0.63	0.001	-4.52	7.79
Confused flour beetle	T	0.12	1, 18	0.01	0.73	0.08	2, 17	0.01	0.92		
	D _L	3.99	1, 18	0.18	0.06	1.99	2, 17	0.19	0.17		
	D _H	1.87	1, 18	0.09	0.19	1.23	2, 17	0.13	0.32		
	D _L C _L	0.26	1, 18	0.01	0.61	0.43	2, 17	0.05	0.66		
	D _H C _L	17.02	1, 18	0.49	0.001	10.88	2, 17	0.56	0.001	-12.1	-2.35
	D _L C _H	0.16	1, 18	0.01	0.7	0.54	2, 17	0.07	0.54		
	D _H C _H	5.65	1, 18	0.24	0.03	2.8	2, 17	0.25	0.09	-3.72	-0.5
	C _L	14.63	1, 18	0.45	0.001	8.08	2, 17	0.49	0.003	-11.3	-10.58
	C _H	0.06	1, 18	0.003	0.81	0.42	2, 17	0.05	0.67		
	F _L	1.16	1, 18	0.06	0.29	0.61	2, 17	0.07	0.55		
	F _H	0.13	1, 18	0.01	0.72	0.11	2, 17	0.01	0.89		

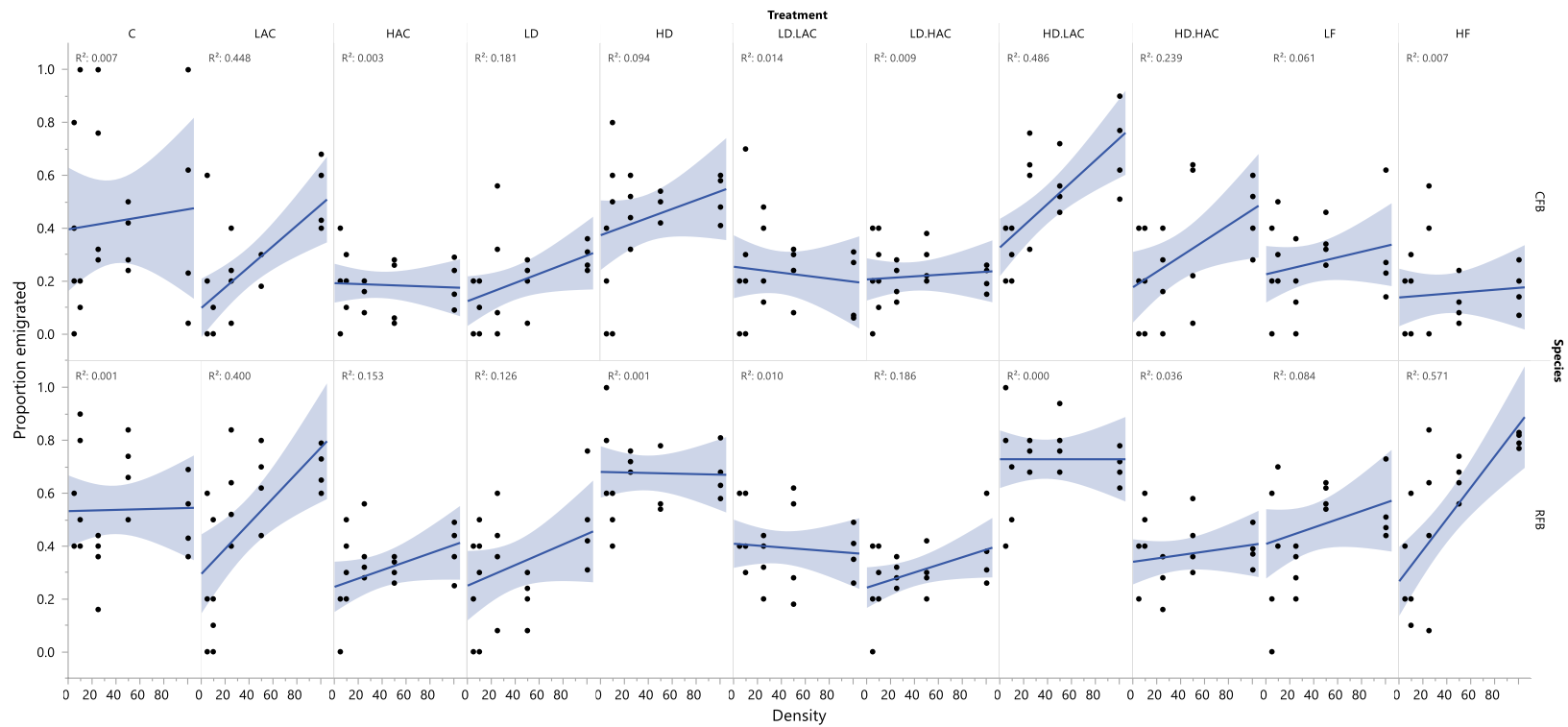


Figure C.1. Linear regression for each selection line and both species. (C=control, D=dispersal, C=competition, F=fecundity, LA=selection for low ability, HA=selection for high ability). DIE under density-emigration relationship represents density-independent.

APPENDIX D. COPYRIGHT INFORMATION.

University of Chicago Press - Journals - License Terms and Conditions

This is a License Agreement between Rachel Harman ("You") and University of Chicago Press - Journals ("Publisher") provided by Copyright Clearance Center ("CCC"). The license consists of your order details, the terms and conditions provided by University of Chicago Press - Journals, and the CCC terms and conditions.

All payments must be made in full to CCC.

Order Date

19-Jun-2020

Order license ID

1042999-1

ISSN

1537-5323

Type of Use

Republish in a thesis/dissertation

Publisher

University of Chicago Press

Portion

Chapter/article

LICENSED CONTENT

Publication Title

The American naturalist

Article Title

Frequency of Occurrence and Population-Dynamic Consequences of Different Forms of Density-Dependent Emigration.

Author/Editor

American Society of Naturalists.

Date

12/31/1866

Language

English

Country

United States of America

Rightsholder

University of Chicago Press - Journals

Publication Type

e-Journal

Start Page

851

End Page

867

Issue

5

Volume

195

URL

<http://www.jstor.org/journals/00030147.html>

REQUEST DETAILS

Portion Type

Chapter/article

Page range(s)

851-867

Total number of pages

16

Format (select all that apply)

Print, Electronic

Who will republish the content?

Author of requested content

Duration of Use

Life of current edition

Lifetime Unit Quantity

Up to 499

Rights Requested

Main product

Distribution

United States

Translation

Original language of publication

Copies for the disabled?

No

Minor editing privileges?

No

Incidental promotional use?

No

Currency

USD

NEW WORK DETAILS

Title

Habitat fragmentation and range margin effects on dispersal and interactions between competitors

Instructor name

Louisiana State Univ Faculty

Institution name

Louisiana State University and Agricultural and Mechanical College

Expected presentation date

2020-06-26

ADDITIONAL DETAILS

Order reference number

cao2722

The requesting person / organization to appear on the license

Rachel Harman

REUSE CONTENT DETAILS

Title, description or numeric reference of the portion(s)

full article

Editor of portion(s)

Cronin, James T.; Shivaji, Ratnasingham; II, Jerome Goddard; Harman, Rachel R.

Volume of serial or monograph

195

Page or page range of portion

851-867

Title of the article/chapter the portion is from

Frequency of Occurrence and Population-Dynamic Consequences of Different Forms of Density-Dependent Emigration.

Author of portion(s)

Rachel Harman

Issue, if republishing an article from a serial

5

Publication date of portion

2020-05-01

CCC Republication Terms and Conditions

1. Description of Service; Defined Terms. This Republication License enables the User to obtain licenses for republication of one or more copyrighted works as described in detail on the relevant Order Confirmation (the "Work(s)"). Copyright Clearance Center, Inc. ("CCC") grants licenses through the Service on behalf of the rightsholder identified on the Order Confirmation (the "Rightsholder"). "Replication", as used herein, generally means the inclusion of a Work, in whole or in part, in a new work or works, also as described on the Order Confirmation. "User", as used herein, means the person or entity making such republication.
2. The terms set forth in the relevant Order Confirmation, and any terms set by the Rightsholder with respect to a particular Work, govern the terms of use of Works in connection with the Service. By using the Service, the person transacting for a republication license on behalf of the User represents and warrants that he/she/it (a) has been duly authorized by the User to accept, and hereby does accept, all such terms and conditions on behalf of User, and (b) shall inform User of all such terms and conditions. In the event such person is a "freelancer" or other third party independent of User and CCC, such party shall be deemed jointly a "User" for purposes of these terms and conditions. In any event, User shall be deemed to have accepted and agreed to all such terms and conditions if User republishes the Work in any fashion.
3. Scope of License; Limitations and Obligations.
 1. All Works and all rights therein, including copyright rights, remain the sole and exclusive property of the Rightsholder. The license created by the exchange of an Order Confirmation (and/or any invoice) and payment by User of the full amount set forth on that document includes only those rights expressly set forth in the Order Confirmation and in these terms and conditions, and conveys no other rights in the Work(s) to User. All rights not expressly granted are hereby reserved.
 2. General Payment Terms: You may pay by credit card or through an account with us payable at the end of the month. If you and we agree that you may establish a standing account with CCC, then the following terms apply: Remit Payment to: Copyright Clearance Center, 29118 Network Place, Chicago, IL 60673-1291. Payments Due: Invoices are payable upon their delivery to you (or upon our notice to you that they are available to you for downloading). After 30 days, outstanding amounts will be subject to a service charge of 1-1/2% per month or, if less, the maximum rate allowed by applicable law. Unless otherwise specifically set forth in the Order Confirmation or in a separate written agreement signed by CCC, invoices are due and payable on "net 30" terms. While User may exercise the rights licensed immediately upon issuance of the Order Confirmation, the license is automatically revoked and is null and void, as if it had never been issued, if complete payment for the license is not received on a timely basis either from User directly or through a payment agent, such as a credit card company.

3. Unless otherwise provided in the Order Confirmation, any grant of rights to User (i) is "one-time" (including the editions and product family specified in the license), (ii) is non-exclusive and non-transferable and (iii) is subject to any and all limitations and restrictions (such as, but not limited to, limitations on duration of use or circulation) included in the Order Confirmation or invoice and/or in these terms and conditions. Upon completion of the licensed use, User shall either secure a new permission for further use of the Work(s) or immediately cease any new use of the Work(s) and shall render inaccessible (such as by deleting or by removing or severing links or other locators) any further copies of the Work (except for copies printed on paper in accordance with this license and still in User's stock at the end of such period).
4. In the event that the material for which a republication license is sought includes third party materials (such as photographs, illustrations, graphs, inserts and similar materials) which are identified in such material as having been used by permission, User is responsible for identifying, and seeking separate licenses (under this Service or otherwise) for, any of such third party materials; without a separate license, such third party materials may not be used.
5. Use of proper copyright notice for a Work is required as a condition of any license granted under the Service. Unless otherwise provided in the Order Confirmation, a proper copyright notice will read substantially as follows: "Republished with permission of [Rightsholder's name], from [Work's title, author, volume, edition number and year of copyright]; permission conveyed through Copyright Clearance Center, Inc. " Such notice must be provided in a reasonably legible font size and must be placed either immediately adjacent to the Work as used (for example, as part of a by-line or footnote but not as a separate electronic link) or in the place where substantially all other credits or notices for the new work containing the republished Work are located. Failure to include the required notice results in loss to the Rightsholder and CCC, and the User shall be liable to pay liquidated damages for each such failure equal to twice the use fee specified in the Order Confirmation, in addition to the use fee itself and any other fees and charges specified.
6. User may only make alterations to the Work if and as expressly set forth in the Order Confirmation. No Work may be used in any way that is defamatory, violates the rights of third parties (including such third parties' rights of copyright, privacy, publicity, or other tangible or intangible property), or is otherwise illegal, sexually explicit or obscene. In addition, User may not conjoin a Work with any other material that may result in damage to the reputation of the Rightsholder. User agrees to inform CCC if it becomes aware of any infringement of any rights in a Work and to cooperate with any reasonable request of CCC or the Rightsholder in connection therewith.
4. Indemnity. User hereby indemnifies and agrees to defend the Rightsholder and CCC, and their respective employees and directors, against all claims, liability, damages, costs and expenses, including legal fees and expenses, arising out of any use of a Work beyond the scope of the rights granted herein, or any use of a Work which has been altered in any unauthorized way by User, including claims of defamation or infringement of rights of copyright, publicity, privacy or other tangible or intangible property.
5. Limitation of Liability. UNDER NO CIRCUMSTANCES WILL CCC OR THE RIGHTSHOLDER BE LIABLE FOR ANY DIRECT, INDIRECT, CONSEQUENTIAL OR INCIDENTAL DAMAGES (INCLUDING WITHOUT LIMITATION DAMAGES FOR LOSS OF BUSINESS PROFITS OR INFORMATION, OR FOR BUSINESS INTERRUPTION) ARISING OUT OF THE USE OR INABILITY TO USE A WORK, EVEN IF ONE OF THEM HAS BEEN ADVISED OF THE POSSIBILITY OF SUCH DAMAGES. In any event, the total liability of the Rightsholder and CCC (including their respective employees and directors) shall not exceed the total amount actually paid by User for this license. User assumes full liability for the actions and omissions of its principals, employees, agents, affiliates, successors and assigns.
6. Limited Warranties. THE WORK(S) AND RIGHT(S) ARE PROVIDED "AS IS". CCC HAS THE RIGHT TO GRANT TO USER THE RIGHTS GRANTED IN THE ORDER CONFIRMATION DOCUMENT. CCC AND THE RIGHTSHOLDER DISCLAIM ALL OTHER WARRANTIES RELATING TO THE WORK(S) AND RIGHT(S), EITHER EXPRESS OR IMPLIED, INCLUDING WITHOUT LIMITATION IMPLIED WARRANTIES OF MERCHANTABILITY OR FITNESS FOR A PARTICULAR PURPOSE. ADDITIONAL RIGHTS MAY BE REQUIRED TO USE ILLUSTRATIONS, GRAPHS, PHOTOGRAPHS, ABSTRACTS, INSERTS OR OTHER PORTIONS OF THE WORK (AS OPPOSED TO THE ENTIRE WORK) IN A MANNER CONTEMPLATED BY USER; USER UNDERSTANDS AND AGREES THAT NEITHER CCC NOR THE RIGHTSHOLDER MAY HAVE SUCH ADDITIONAL RIGHTS TO GRANT.

7. Effect of Breach. Any failure by User to pay any amount when due, or any use by User of a Work beyond the scope of the license set forth in the Order Confirmation and/or these terms and conditions, shall be a material breach of the license created by the Order Confirmation and these terms and conditions. Any breach not cured within 30 days of written notice thereof shall result in immediate termination of such license without further notice. Any unauthorized (but licensable) use of a Work that is terminated immediately upon notice thereof may be liquidated by payment of the Rightsholder's ordinary license price therefor; any unauthorized (and unlicensable) use that is not terminated immediately for any reason (including, for example, because materials containing the Work cannot reasonably be recalled) will be subject to all remedies available at law or in equity, but in no event to a payment of less than three times the Rightsholder's ordinary license price for the most closely analogous licensable use plus Rightsholder's and/or CCC's costs and expenses incurred in collecting such payment.
8. Miscellaneous.
 1. User acknowledges that CCC may, from time to time, make changes or additions to the Service or to these terms and conditions, and CCC reserves the right to send notice to the User by electronic mail or otherwise for the purposes of notifying User of such changes or additions; provided that any such changes or additions shall not apply to permissions already secured and paid for.
 2. Use of User-related information collected through the Service is governed by CCC's privacy policy, available online here: <https://marketplace.copyright.com/rs-ui-web/mp/privacy-policy>
 3. The licensing transaction described in the Order Confirmation is personal to User. Therefore, User may not assign or transfer to any other person (whether a natural person or an organization of any kind) the license created by the Order Confirmation and these terms and conditions or any rights granted hereunder; provided, however, that User may assign such license in its entirety on written notice to CCC in the event of a transfer of all or substantially all of User's rights in the new material which includes the Work(s) licensed under this Service.
 4. No amendment or waiver of any terms is binding unless set forth in writing and signed by the parties. The Rightsholder and CCC hereby object to any terms contained in any writing prepared by the User or its principals, employees, agents or affiliates and purporting to govern or otherwise relate to the licensing transaction described in the Order Confirmation, which terms are in any way inconsistent with any terms set forth in the Order Confirmation and/or in these terms and conditions or CCC's standard operating procedures, whether such writing is prepared prior to, simultaneously with or subsequent to the Order Confirmation, and whether such writing appears on a copy of the Order Confirmation or in a separate instrument.
 5. The licensing transaction described in the Order Confirmation document shall be governed by and construed under the law of the State of New York, USA, without regard to the principles thereof of conflicts of law. Any case, controversy, suit, action, or proceeding arising out of, in connection with, or related to such licensing transaction shall be brought, at CCC's sole discretion, in any federal or state court located in the County of New York, State of New York, USA, or in any federal or state court whose geographical jurisdiction covers the location of the Rightsholder set forth in the Order Confirmation. The parties expressly submit to the personal jurisdiction and venue of each such federal or state court. If you have any comments or questions about the Service or Copyright Clearance Center, please contact us at 978-750-8400 or send an e-mail to support@copyright.com.

REFERENCES

- Addesso, K. M., H. J. McAuslane, and R. Cherry. 2012. Aggregation Behavior of the Southern Chinch Bug (Hemiptera: *Blissidae*). *Environmental Entomology* 41:887-895.
- Agashe, D., and D. I. Bolnick. 2010. Intraspecific genetic variation and competition interact to influence niche expansion. *Proceedings of the Royal Society B-Biological Sciences* 277:2915-2924.
- Alabi, T., J. P. Michaud, L. Arnaud, and E. Haubruge. 2008. A comparative study of cannibalism and predation in seven species of flour beetle. *Ecological Entomology* 33:716-726.
- Allee, W. C., Park, O., Emerson, A. E., Park, T., Schmidt, K. P. 1949. *Principles of Animal Ecology*. WB Saundere Co. Ltd.
- Allen, K. A., and D. J. Thompson. 2010. Movement characteristics of the scarce blue-tailed damselfly, *Ischnura pumilio*. *Insect Conservation and Diversity* 3:5-14.
- Alspach, P. A., and V. G. M. Bus. 1999. Spatial variation of woolly apple aphid (*Eriosoma lanigerum*, Hausmann) in a genetically diverse apple planting. *New Zealand Journal of Ecology* 23:39-44.
- Altamirano, A., G. Valladares, N. Kuzmanich, and A. Salvo. 2016. Galling insects in a fragmented forest: incidence of habitat loss, edge effects and plant availability. *Journal of Insect Conservation* 20:119-127.
- Altwegg, R., C. Doutrelant, M. D. Anderson, C. N. Spottiswoode, and R. Covas. 2014. Climate, social factors and research disturbance influence population dynamics in a declining sociable weaver metapopulation. *Oecologia* 174:413-425.
- Altwegg, R., Y. C. Collingham, B. Erni, and B. Huntley. 2013. Density-dependent dispersal and the speed of range expansions. *Diversity and Distributions* 19:60-68.
- Alzate, A., K. Bisschop, R. S. Etienne, and D. Bonte. 2017. Interspecific competition counteracts negative effects of dispersal on adaptation of an arthropod herbivore to a new host. *Journal of Evolutionary Biology* 30:1966-1977.
- Amarasekare, P. 1998. Interactions between local dynamics and dispersal: insights from single species models. *Theoretical Population Biology* 53:44-59.
- Amarasekare, P. 2004. Spatial variation and density-dependent dispersal in competitive coexistence. *Proceedings of the Royal Society B-Biological Sciences* 271:1497-1506.
- Amarasekare, P. 2004. The role of density-dependent dispersal in source-sink dynamics. *Journal of Theoretical Biology* 226:159-168.

- Anholt, B. R. 1995. Density-dependence resolves the stream drift paradox. *Ecology* 76:2235-2239.
- Armsworth, P. R., and J. E. Roughgarden. 2005. Disturbance induces the contrasting evolution of reinforcement and dispersiveness in directed and random movers. *Evolution* 59:2083-2096.
- Arnold, P. A., P. Cassey, and C. R. White. 2017. Functional traits in red flour beetles: the dispersal phenotype is associated with leg length but not body size nor metabolic rate. *Functional Ecology* 31:653-661.
- Athanassiou, C. G., N. G. Kavallieratos, N. E. Palyvos, A. Sciarretta, and P. Trematerra. 2005. Spatiotemporal distribution of insects and mites in horizontally stored wheat. *Journal of Economic Entomology* 98:1058-1069.
- Bach, L. A., R. Thomsen, C. Pertoldi, and V. Loeschcke. 2006. Kin competition and the evolution of dispersal in an individual-based model. *Ecological Modelling* 192:658-666.
- Baines, C. B., S. J. McCauley, and L. Rowe. 2014. The interactive effects of competition and predation risk on dispersal in an insect. *Biology Letters* 10:20140287.
- Banks, S. C., and D. B. Lindenmayer. 2014. Inbreeding avoidance, patch isolation and matrix permeability influence dispersal and settlement choices by male agile antechinus in a fragmented landscape. *Journal of Animal Ecology* 83:515-524.
- Bartelt, R. J., A. A. Cosse, B. W. Zilkowski, R. N. Wiedenmann, and S. Raghu. 2008. Early-summer pheromone biology of *Galerucella californiensis* and relationship to dispersal and colonization. *Biological Control* 46:409-416.
- Bartholomew, B. 1970. Bare zone between California shrub and grassland communities – role of animals. *Science* 170:1210-1212.
- Barton, K. A., B. L. Phillips, J. M. Morales, and J. M. J. Travis. 2009. The evolution of an 'intelligent' dispersal strategy: biased, correlated random walks in patchy landscapes. *Oikos* 118:309-319.
- Beckerman, A. P., T. G. Benton, C. T. Lapsley, and N. Koesters. 2006. How effective are maternal effects at having effects? *Proceedings of the Royal Society B-Biological Sciences* 273:485-493.
- Belyea, L. R., and J. Lancaster. 1999. Assembly rules within a contingent ecology. *Oikos* 86:402-416.
- Benton, T. G., J. J. H. St Clair, and S. J. Plaistow. 2008. Maternal effects mediated by maternal age: from life histories to population dynamics. *Journal of Animal Ecology* 77:1038-1046.

- Berec, L. 2019. Allee effects under climate change, *Oikos* 128:972-983.
- Bertness, M. D., G. C. Trussell, P. J. Ewanchuk, and B. R. Silliman. 2002. Do alternate stable community states exist in the Gulf of Maine rocky intertidal zone? *Ecology* 83:3434-3448.
- Best, A. S., K. Johst, T. Munkemuller, and J. M. J. Travis. 2007. Which species will successfully track climate change? The influence of intraspecific competition and density dependent dispersal on range shifting dynamics. *Oikos* 116:1531-1539.
- Birch, L. C., T. Park, and M. B. Frank. 1951. The effect of intraspecies and interspecies competition on the fecundity of 2 species of flour beetles. *Evolution* 5:116-132.
- Bitume, E. V., D. Bonte, O. Ronce, F. Bach, E. Flaven, I. Olivieri, and C. M. Nieberding. 2013. Density and genetic relatedness increase dispersal distance in a subsocial organism. *Ecology Letters* 16:430-437.
- Bock, M. J., G. C. Jarvis, E. L. Corey, E. E. Stoner, and K. E. Gribble. 2019. Maternal age alters offspring lifespan, fitness, and lifespan extension under caloric restriction. *Scientific Reports* 9:3138. doi:10.1038/s41598-019-40011-z
- Boesch, D., M. Josselyn, A. Mehta, J. Morris, W. Nuttle, C. Simenstad, and D. Swift. 1994. Scientific assessment of coastal wetland loss, restoration and management in Louisiana, Pages I-103 in *Journal of Coastal Research*.
- Bonte, D., H. Van Dyck, J. M. Bullock, A. Coulon, M. Delgado, M. Gibbs, V. Lehouck et al. 2012. Costs of dispersal. *Biological Reviews* 87:290-312.
- Bowler, D. E., and T. G. Benton. 2005. Causes and consequences of animal dispersal strategies: relating individual behaviour to spatial dynamics. *Biological Reviews* 80:205-225.
- Bowne, D. R., and M. A. Bowers. 2004. Interpatch movements in spatially structured populations: a literature review. *Landscape Ecology* 19:1-20.
- Buoro, M., and S. M. Carlson. 2014. Life-history syndromes: integrating dispersal through space and time. *Ecology Letters* 17:756-767.
- Burnham, K. P., D. R. Anderson, and K. P. Huyvaert. 2011. AIC model selection and multimodel inference in behavioral ecology: some background, observations, and comparisons. *Behavioral Ecology and Sociobiology* 65:23-35.
- Burton, O. J., B. L. Phillips, and J. M. J. Travis. 2010. Trade-offs and the evolution of life-histories during range expansion. *Ecology Letters* 13:1210-1220.

- Butcher, J. A., M. L. Morrison, D. Ransom, R. D. Slack, and R. N. Wilkins. 2010. Evidence of a minimum patch size threshold of reproductive success in an endangered songbird. *Journal of Wildlife Management* 74:133-139.
- Cadotte, M. W., D. V. Mai, S. Jantz, M. D. Collins, M. Keele, and J. A. Drake. 2006. On testing the competition-colonization trade-off in a multispecies assemblage. *American Naturalist* 168:704-709.
- Campbell, J. F., and D. W. Hagstrum. 2002. Patch exploitation by *Tribolium castaneum*: movement patterns, distribution, and oviposition. *Journal of Stored Products Research* 38:55-68.
- Cantrell, R. S., and C. Cosner. 2003. *Spatial ecology via reaction-diffusion equations*. Wiley Series in Mathematical and Computational Biology. Chichester, England; Hoboken, NJ.
- Cantrell, R. S., and C. Cosner. 2007. Density dependent behavior at habitat boundaries and the Allee effect. *Bulletin of Mathematical Biology* 69:2339-2360.
- Cantrell, R. S., C. Cosner, and Y. Lou. 2007. Advection-mediated coexistence of competing species. *Proceedings of the Royal Society of Edinburgh Section a-Mathematics* 137:497-518.
- Caplat, P., P. Edelaar, R. Y. Dudaniec, A. J. Green, B. Okamura, J. Cote, J. Ekroos et al. 2016. Looking beyond the mountain: dispersal barriers in a changing world. *Frontiers in Ecology and the Environment* 14:262-269.
- Chatelain, M., and J. Mathieu. 2017. How good are epigeic earthworms at dispersing? An investigation to compare epigeic to endogeic and anecic groups. *Soil Biology & Biochemistry* 111:115-123.
- Chesson, P. L., and R. R. Warner. 1981. Environmental variability promotes coexistence in lottery competitive-systems. *American Naturalist* 117:923-943.
- Clobert, J., J. F. Le Galliard, J. Cote, S. Meylan, and M. Massot. 2009. Informed dispersal, heterogeneity in animal dispersal syndromes and the dynamics of spatially structured populations. *Ecology Letters* 12:197-209.
- Cocroft, R. B. 1999. Parent-offspring communication in response to predators in a subsocial treehopper (Hemiptera : Membracidae : *Umbonia crassicornis*). *Ethology* 105:553-568.
- Colombo, E. H., and C. Anteneodo. 2018. Nonlinear population dynamics in a bounded habitat. *Journal of Theoretical Biology* 446:11-18.
- Conradt, L., and T. J. Roper. 2006. Nonrandom movement behavior at habitat boundaries in two butterfly species: Implications for dispersal. *Ecology* 87:125-132.

- Cossu, P., F. Scarpa, G. L. Dedola, D. Sanna, T. Lai, B. Cristo, M. Curini-Galletti et al. 2017. Surviving at the edge of a fragmented range: patterns of genetic diversity in isolated populations of the endangered giant Mediterranean limpet (*Patella ferruginea*). *Marine Biology* 164:18.
- Cote, J., E. Bestion, S. Jacob, J. Travis, D. Legrand, and M. Baguette. 2017. Evolution of dispersal strategies and dispersal syndromes in fragmented landscapes. *Ecography* 40:56-73.
- Courchamp, F., L. Berec, and J. Gascoigne. 2008. *Allee effects in ecology and conservation*. Oxford University Press. Oxford, UK.
- Cronin, J. T. 2003. Movement and spatial population structure of a prairie planthopper. *Ecology* 84:1179-1188.
- Cronin, J. T. 2007. From population sources to sieves: the matrix alters host-parasitoid source-sink structure. *Ecology* 88:2966-2976.
- Cronin, J. T. 2009. Habitat edges, within-patch dispersion of hosts, and parasitoid oviposition behavior. *Ecology* 90:196-207.
- Cronin, J. T., and K. J. Haynes. 2004. An invasive plant promotes unstable host-parasitoid patch dynamics. *Ecology* 85:2772-2782.
- Cronin, J. T., J. Goddard II, and R. Shivaji. 2019. Effects of patch matrix and individual movement response on population persistence at the patch-level. *Bulletin of Mathematical Biology*. 81:3933-3975.
- Daehler, C. C., and D. R. Strong. 1994. Variable reproductive output among clones of *Spartina alterniflora* (Poaceae) invading San Francisco Bay, California – the influence of herbivory, pollination, and establishment site. *American Journal of Botany* 81:307-313.
- Dallas, T., R. R. Decker, and A. Hastings. 2017. Species are not most abundant in the centre of their geographic range or climatic niche. *Ecology Letters* 20:1523-1533.
- Davis, H. G. 2005. r-Selected traits in an invasive population. *Evolutionary Ecology* 19:255-274.
- Davis, T. S., and P. J. Landolt. 2012. Body size phenotypes are heritable and mediate fecundity but not fitness in the Lepidopteran frugivore *Cydia pomonella*. *Naturwissenschaften* 99:483-491.
- Dawson, P. S. 1967. Interspecific competition egg cannibalism and length of larval instars in *Tribolium*. *Evolution* 21:857-858.
- De Meester, L., J. Vanoverbeke, L. J. Kilsdonk, and M. C. Urban. 2016. Evolving perspectives on monopolization and priority effects. *Trends in Ecology & Evolution* 31:136-146.

- De Meester, N., S. Derycke, A. Rigaux, and T. Moens. 2015. Active dispersal is differentially affected by inter- and intraspecific competition in closely related nematode species. *Oikos* 124:561-570.
- Debinski, D. M., and R. D. Holt. 2000. A survey and overview of habitat fragmentation experiments. *Conservation Biology* 14:342-355.
- Dennis, B., L. Assas, S. Elaydi, E. Kwessi, and G. Livadiotis. 2016. Allee effects and resilience in stochastic populations. *Theoretical Ecology* 9:323-335.
- Denno, R. F. 1994. The evolution of dispersal polymorphisms in insects – the influence of habitats, host plants and mates. *Researches on Population Ecology* 36:127-135.
- Denno, R. F., D. J. Hawthorne, B. L. Thorne, and C. Gratton. 2001. Reduced flight capability in British Virgin Island populations of a wing-dimorphic insect: the role of habitat isolation, persistence, and structure. *Ecological Entomology* 26:25-36.
- Denno, R. F., G. K. Roderick, K. L. Olmstead, and H. G. Dobel. 1991. Density-related migration in planthoppers (Homoptera, Delphacidae) – the role of habitat persistence. *American Naturalist* 138:1513-1541.
- Derosier, A. L., M. L. Jones, and K. T. Scribner. 2007. Dispersal of sea lamprey larvae during early life: relevance for recruitment dynamics. *Environmental Biology of Fishes* 78:271-284.
- Desrochers, A., I. K. Hanski, and V. Selonen. 2003. Siberian flying squirrel responses to high- and low-contrast forest edges. *Landscape Ecology* 18:543-552.
- Dethier, V. G., and R.H. MacArthur. 1964. A field's capacity to support a butterfly population. *Nature* 201:728-729.
- Dhiman, A., and S. Poria. 2018. Allee effect induced diversity in evolutionary dynamics. *Chaos Solitons & Fractals* 108:32-38.
- Dickens, B. L., and H. L. Brant. 2014. Effects of marking methods and fluorescent dusts on *Aedes aegypti* survival. *Parasites & Vectors* 7:1-16.
- Doak, D. F., P. C. Marino, and P. M. Kareiva. 1992. Spatial scale mediates the influence of habitat fragmentation on dispersal success – implications for conservation. *Theoretical Population Biology* 41:315-336.
- Doerr, V. A. J., and E. D. Doerr. 2004. Fractal analysis can explain, individual variation in dispersal search paths. *Ecology* 85:1428-1438.
- Donahue, M. J. 2006. Allee effects and conspecific cueing jointly lead to conspecific attraction. *Oecologia* 149:33-43.

- Donohue, K., C. R. Polisetty, and N. J. Wender. 2005. Genetic basis and consequences of niche construction: plasticity-induced genetic constraints on the evolution of seed dispersal in *Arabidopsis thaliana*. *American Naturalist* 165:537-550.
- Dunstan, P. K., and N. J. Bax. 2007. How far can marine species go? Influence of population biology and larval movement on future range limits. *Marine Ecology Progress Series* 344:15-28.
- Edmunds, J., J. M. Cushing, R. F. Costantino, S. M. Henson, B. Dennis, and R. A. Desharnais. 2003. Park's *Tribolium* competition experiments: a non-equilibrium species coexistence hypothesis. *Journal of Animal Ecology* 72:703-712.
- Einum, S., and I. A. Fleming. 2000. Highly fecund mothers sacrifice offspring survival to maximize fitness. *Nature* 405:565-567.
- Elkin, C. M., and H. P. Possingham. 2008. The role of landscape-dependent disturbance and dispersal in metapopulation persistence. *American Naturalist* 172:563-575.
- Enfjall, K., and O. Leimar. 2005. Density-dependent dispersal in the Glanville fritillary, *Melitaea cinxia*. *Oikos* 108:465-472.
- Engelen, A., and R. Santos. 2009. Which demographic traits determine population growth in the invasive brown seaweed *Sargassum muticum*? *Journal of Ecology* 97:675-684.
- Evans, M. J., S. C. Banks, P. S. Barton, K. F. Davies, and D. A. Driscoll. 2018. A long-term habitat fragmentation experiment leads to morphological change in a species of carabid beetle. *Ecological Entomology* 43:282-293.
- Fagan, W. E., R. S. Cantrell, and C. Cosner. 1999. How habitat edges change species interactions. *American Naturalist* 153:165-182.
- Fahrig, L. 2003. Effects of habitat fragmentation on biodiversity. *Annual Review of Ecology Evolution and Systematics* 34:487-515.
- Farina, A. 2000. *Landscape ecology in action*. Springer-Science+Business Media, B.V.
- Ferriere, R., and S. Legendre. 2013. Eco-evolutionary feedbacks, adaptive dynamics and evolutionary rescue theory. *Philosophical Transactions of the Royal Society B-Biological Sciences* 368:20120081 (doi: 10.1098/rstb.2012.0081).
- Fisher, R. A. 1937. The wave of advance of advantageous genes. *Annals of Eugenics* 7:355-369.
- Foneska, N., J. Goddard II, Q. Morris, R. Shivaji and B. Son. 2019. On the effects of the exterior matrix hostility and a U-shaped density dependent dispersal on a diffusive logistic growth model. *Discrete & Continuous Dynamical Systems-Series B*. (doi: 10.3934/dcdss.2020245).

- Fowler, N. L., R. D. Overath, and C. M. Pease. 2006. Detection of density dependence requires density manipulations and calculation of lambda. *Ecology* 87:655-664.
- Franke, J. E., and A. A. Yakubu. 2008. Disease-induced mortality in density-dependent discrete-time S-I-S epidemic models. *Journal of Mathematical Biology* 57:755-790.
- Fraser, E. J., X. Lambin, J. M. J. Travis, L. A. Harrington, S. C. F. Palmer, G. Bocedi, and D. W. Macdonald. 2015. Range expansion of an invasive species through a heterogeneous landscape - the case of American mink in Scotland. *Diversity and Distributions* 21:888-900.
- French, D. R., and J. M. J. Travis. 2001. Density-dependent dispersal in host-parasitoid assemblages. *Oikos* 95:125-135.
- Fronhofer, E. A., and F. Altermatt. 2015. Eco-evolutionary feedbacks during experimental range expansions. *Nature Communications* 6:6844.
- Fryer, J. C., and C. L. Meek. 1989. Further-studies on marking an adult mosquito, *Psorophora columbiae*, insitu using fluorescent pigments. *Southwestern Entomologist* 14:409-417.
- Gascoigne, J., L. Berec, S. Gregory, and F. Courchamp. 2009. Dangerously few liaisons: a review of mate-finding Allee effects. *Population Ecology* 51:355-372.
- Gates, J. E., and L. W. Gysel. 1978. Avian nest dispersion and fledgling success in field-forest ecotones. *Ecology* 59:871-883.
- Gilbert, L. E., and M. C. Singer. 1973. Dispersal and gene flow in a butterfly species. *American Naturalist* 107:58-72.
- Goodnight, C. J., and D. M. Craig. 1996. Effect of coexistence on competitive outcome in *Tribolium castaneum* and *Tribolium confusum*. *Evolution* 50:1241-1250.
- Gros, A., T. Hovestadt, and H. J. Poethke. 2008. Evolution of sex-biased dispersal: the role of sex-specific dispersal costs, demographic stochasticity, and inbreeding. *Ecological Modelling* 219:226-233.
- Haddad, N. M. 1999. Corridor and distance effects on interpatch movements: A landscape experiment with butterflies. *Ecological Applications* 9:612-622.
- Hahn, N. G., C. Rodriguez-Saona, and G. C. Hamilton. 2017. Characterizing the spatial distribution of brown marmorated stink bug, *Halyomorpha halys* Stal (Hemiptera: Pentatomidae), populations in peach orchards. *Plos One* 12:e0170889.
- Hallatschek, O., P. Hersen, S. Ramanathan, and D. R. Nelson. 2007. Genetic drift at expanding frontiers promotes gene segregation. *Proceedings of the National Academy of Sciences of the United States of America* 104:19926-19930.

- Hamel, S., J. M. Gaillard, M. Festa-Bianchet, and S. D. Cote. 2009. Individual quality, early-life conditions, and reproductive success in contrasted populations of large herbivores. *Ecology* 90:1981-1995.
- Hamilton, W. D., and R. M. May. 1977. Dispersal in stable habitats. *Nature* 269:578-581.
- Hammill, E., R. G. Fitzjohn, and D. S. Srivastava. 2015. Conspecific density modulates the effect of predation on dispersal rates. *Oecologia* 178:1149-1158.
- Hammond, J. I., B. Luttbeg, T. Brodin, and A. Sih. 2012. Spatial scale influences the outcome of the predator-prey space race between tadpoles and predatory dragonflies. *Functional Ecology* 26:522-531.
- Han, C. S., and R. C. Brooks. 2014. Long-term effect of social interactions on behavioral plasticity and lifetime mating success. *American Naturalist* 183:431-444.
- Han, X. Y. 2016. Persistent alternate abundance states in the coral reef sea urchin *Diadema savignyi*: evidence of alternate attractors. *Marine Ecology - an Evolutionary Perspective* 37:1179-1189.
- Handley, L. J. L., and N. Perrin. 2007. Advances in our understanding of mammalian sex-biased dispersal. *Molecular Ecology* 16:1559-1578.
- Hanski, I. 1998. Metapopulation dynamics. *Nature* 396:41-49.
- Hanski, I., and M. E. Gilpin. 1997. *Metapopulation biology: ecology, genetics, and evolution*. Academic Press, London, England.
- Hanski, I., and M. Gilpin. 1991. Metapopulation dynamics - brief-history and conceptual domain. *Biological Journal of the Linnean Society* 42:3-16.
- Hanski, I., C. Eralahti, M. Kankare, O. Ovaskainen, and H. Siren. 2004. Variation in migration propensity among individuals maintained by landscape structure. *Ecology Letters* 7:958-966.
- Harada, Y., H. Ezoe, Y. Iwasa, H. Matsuda, and K. Sato. 1995. Population persistence and spatially limited social-interaction. *Theoretical Population Biology* 48:65-91.
- Harman, R. R., J. Goddard, R. Shivaji, and J. T. Cronin. 2020. Frequency of occurrence and population-dynamic consequences of different forms of density-dependent emigration. *American Naturalist* 195(5):851-867.
- Harrington, J. E. 1972. Notes on the biology of *Ischnodemus* species of America north of Mexico, Pages 47-56, University of Connecticut Occasional Papers.
- Hassell, M. P. 1986. Detecting density dependence. *Trends in Ecology & Evolution* 1:90-93.

- Hastings, A., K. Cuddington, K. F. Davies, C. J. Dugaw, S. Elmendorf, A. Freestone, S. Harrison et al. 2005. The spatial spread of invasions: new developments in theory and evidence. *Ecology Letters* 8:91-101.
- Hauzy, C., M. Gauduchon, F. D. Hulot, and M. Loreau. 2010. Density-dependent dispersal and relative dispersal affect the stability of predator-prey metacommunities. *Journal of Theoretical Biology* 266:458-469.
- Hawkin, K. J., D. M. Stanbridge, and P. G. Fields. 2013. Sampling *Tribolium castaneum* and *Tribolium confusum* in flour mill roll stands. *Journal of Stored Products Research* 52:7-11.
- Haynes, K. J., and J. T. Cronin. 2003. Matrix composition affects the spatial ecology of a prairie planthopper. *Ecology* 84:2856-2866.
- Haynes, K. J., and J. T. Cronin. 2006. Interpatch movement and edge effects: the role of behavioral responses to the landscape matrix. *Oikos* 113:43-54.
- Henery, M. L., and M. Westoby. 2001. Seed mass and seed nutrient content as predictors of seed output variation between species. *Oikos* 92:479-490.
- Holder, M. W., and S. W. Wilson. 1992. Life-history and descriptions of the immature stages of the planthopper *Prokelisia-crocea* (VanDuzee) (Homoptera, Dephacidae). *Journal of the New York Entomological Society* 100:491-497.
- Holt, R. D. 1987. Population dynamics and evolutionary processes: the manifold roles of habitat selection. *Evolutionary Ecology* 1:331-347.
- Hooten, M. B., D. S. Johnson, B. T. McClintock, and J. M. Morales. 2017, *Animal movement: statistical models for telemetry data*, CRC Press.
- Hovestadt, T., A. Kubisch, and H. J. Poethke. 2010. Information processing in models for density-dependent emigration: a comparison. *Ecological Modelling* 221:405-410.
- Hovestadt, T., and H. J. Poethke. 2006. The control of emigration and its consequences for the survival of populations. *Ecological Modelling* 190:443-453.
- Huang, F. F., S. L. Peng, B. M. Chen, H. X. Liao, Q. Q. Huang, Z. G. Lin, and G. Liu. 2015. Rapid evolution of dispersal-related traits during range expansion of an invasive vine *Mikania micrantha*. *Oikos* 124:1023-1030.
- Hudina, S., K. Hock, and K. Zganec. 2014. The role of aggression in range expansion and biological invasions. *Current Zoology* 60:401-409.

- Hudina, S., K. Zganec, and K. Hock. 2015. Differences in aggressive behaviour along the expanding range of an invasive crayfish: an important component of invasion dynamics. *Biological Invasions* 17:3101-3112.
- Hughes, C. L., C. Dytham, and J. K. Hill. 2007. Modelling and analysing evolution of dispersal in populations at expanding range boundaries. *Ecological Entomology* 32:437-445.
- Ims, R. A., and N. G. Yoccoz. 1997. Studying transfer processes in metapopulations: emigration, migration, and colonization. Pages 247-265 in I. Hanski and M.E. Gilpin, eds. *Metapopulation Biology: Ecology, Genetics, and Evolution*. Academic Press.
- Jacob, J., and J. S. Brown. 2000. Microhabitat use, giving-up densities and temporal activity as short- and long-term anti-predator behaviors in common voles. *Oikos* 91:131-138.
- Jacob, S., A. S. Chaine, N. Schtickzelle, M. Huet, and J. Clobert. 2015. Social information from immigrants: multiple immigrant-based sources of information for dispersal decisions in a ciliate. *Journal of Animal Ecology* 84:1373-1383.
- Jacob, S., E. Laurent, T. Morel-Journel, and N. Schtickzelle. 2020. Fragmentation and the context-dependence of dispersal syndromes: matrix harshness modifies resident-disperser phenotypic differences in microcosms. *Oikos* 129:158-169.
- Jacob, S., P. Wehi, J. Clobert, D. Legrand, N. Schtickzelle, M. Huet, and A. Chaine. 2016. Cooperation-mediated plasticity in dispersal and colonization. *Evolution* 70:2336-2345.
- Jezkova, T. 2020. Founder takes more: interspecific competition affects range expansion of North American mammals into deglaciated areas. *Journal of Biogeography* 47:712-720.
- Johnson, D. M. 2005. Metapopulation models: An empirical test of model assumptions and evaluation methods. *Ecology* 86:3088-3098.
- Johnson, S. R., and A. K. Knapp. 1996. Impact of *Ischnodemus falicus* (Hemiptera: Lygaeidae) on photosynthesis and production of *Spartina pectinata* wetlands. *Environmental Entomology* 25:1122-1127.
- Johst, K., and R. Brandl. 1997. Evolution of dispersal: the importance of the temporal order of reproduction and dispersal. *Proceedings of the Royal Society B-Biological Sciences* 264:23-30.
- Jonsen, I. D., and P. D. Taylor. 2000. Fine-scale movement behaviors of calopterygid damselflies are influenced by landscape structure: an experimental manipulation. *Oikos* 88:553-562.
- Kareiva, P. 1982. Experimental and mathematical analyses of herbivore movement - quantifying the influence of plant spacing and quality on foraging discrimination. *Ecological Monographs* 52:261-282.

- Kareiva, P. 1987. Habitat fragmentation and the stability of predator prey interactions. *Nature* 326:388-390.
- Kareiva, P., and R. Perry. 1989. Leaf overlap and the ability of ladybird beetles to search among plants. *Ecological Entomology* 14:127-129.
- Kellner, J. R., and S. P. Hubbell. 2018. Density-dependent adult recruitment in a low-density tropical tree. *Proceedings of the National Academy of Sciences of the United States of America* 115:11268-11273.
- Kendall, B. E., O. N. Bjornstad, J. Bascompte, T. H. Keitt, and W. F. Fagan. 2000. Dispersal, environmental correlation, and spatial synchrony in population dynamics. *American Naturalist* 155:628-636.
- Kim, S. Y., R. Torres, and H. Drummond. 2009. Simultaneous positive and negative density-dependent dispersal in a colonial bird species. *Ecology* 90:230-239.
- Kokko, H., and D. J. Rankin. 2006. Lonely hearts or sex in the city? Density-dependent effects in mating systems. *Philosophical Transactions of the Royal Society B-Biological Sciences* 361:319-334.
- Korona, R. 1991. Genetic-basis of behavioral strategies - dispersal of female flour beetles, *Tribolium confusum*, in a laboratory system. *Oikos* 62:265-270.
- Kramer, A. M., B. Dennis, A. M. Liebhold, and J. M. Drake. 2009. The evidence for Allee effects. *Population Ecology* 51:341-354.
- Kramer, A. M., L. Berec, and J. M. Drake. 2018. Allee effects in ecology and evolution. *Journal of Animal Ecology* 87:7-10.
- Kubisch, A., R. D. Holt, H. J. Poethke, and E. A. Fronhofer. 2014. Where am I and why? Synthesizing range biology and the eco-evolutionary dynamics of dispersal. *Oikos* 123:5-22.
- Kuussaari, M., I. Saccheri, M. Camara, and I. Hanski. 1998. Allee effect and population dynamics in the Glanville fritillary butterfly. *Oikos* 82:384-392.
- Kuussaari, M., M. Nieminen, and I. Hanski. 1996. An experimental study of migration in the Glanville fritillary butterfly *Melitaea cinxia*. *Journal of Animal Ecology* 65:791-801.
- Lachmuth, S., W. Durka, and F. M. Schurr. 2011. Differentiation of reproductive and competitive ability in the invaded range of *Senecio inaequidens*: the role of genetic Allee effects, adaptive and nonadaptive evolution. *New Phytologist* 192:529-541.
- Lancaster, J., B. J. Downes, and A. Arnold. 2011. Lasting effects of maternal behaviour on the distribution of a dispersive stream insect. *Journal of Animal Ecology* 80:1061-1069.

- 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.
- Lansing, A. I. 1942. Increase of cortical calcium with age in cells of a rotifer *Euchlanis dilatata*, planarian *Phagocata sp* and a toad, *Bufo fowleri* as shown by the microincineration technique. *Biological Bulletin* 82:392-400.
- Laurance, W. F. 1991. Ecological correlates of extinction proneness in Australian tropical rain-forest mammals. *Conservation Biology* 5:79-89.
- Leopold, A. 1933. Game management. Scribner's, New York.
- Levin, S. A. 1974. Dispersion and population interactions. *American Naturalist* 108:207-228.
- Levins, R. 1969. Some demographic and genetic consequences of environmental heterogeneity for biological control. *Bulletin of the Entomological Society of America* 15:237-240.
- Levins, R., and D. Culver. 1971. Regional coexistence of species and competition between rare species (mathematical model/habitable patches). *Proceedings of the National Academy of Sciences of the United States of America* 68:1246-1248.
- Liang, Y., M. J. Duveneck, E. J. Gustafson, J. M. Serra-Diaz, and J. R. Thompson. 2018. How disturbance, competition, and dispersal interact to prevent tree range boundaries from keeping pace with climate change. *Global Change Biology* 24:E335-E351.
- Lindenmayer, D. B., and J. Fischer. 2006, Habitat fragmentation and landscape change: an ecological and conservation synthesis. Washington, DC, Island Press.
- Livingston, G., M. Matias, V. Calcagno, C. Barbera, M. Combe, M. A. Leibold, and N. Mouquet. 2012. Competition-colonization dynamics in experimental bacterial metacommunities. *Nature Communications* 3:1234 (doi:10.1038/ncomms2239).
- Long, T. A. F., P. M. Miller, A. D. Stewart, and W. R. Rice. 2009. Estimating the heritability of female lifetime fecundity in a locally adapted *Drosophila melanogaster* population. *Journal of Evolutionary Biology* 22:637-643.
- Lowe, W. H., and M. A. McPeck. 2014. Is dispersal neutral? *Trends in Ecology & Evolution* 29:444-450.
- Luck, R. F., and H. Podoler. 1985. Competitive-exclusion of *Aphytis-linganensis* by *Aphytis-melinus* - potential role of host size. *Ecology* 66:904-913.
- Lustenhouwer, N., J. L. Williams, and J. M. Levine. 2019. Evolution during population spread affects plant performance in stressful environments. *Journal of Ecology* 107:396-406.

- Maag, N., G. Cozzi, T. Clutton-Brock, and A. Ozgul. 2018. Density-dependent dispersal strategies in a cooperative breeder. *Ecology* 99:1932-1941.
- Maciel, G. A., and F. Lutscher. 2013. How individual movement response to habitat edges affects population persistence and spatial spread. *American Naturalist* 182:42-52.
- Mandelbrot, B. 1967. How long is coast of Britain – statistical self-similarity and fractional dimension. *Science* 156:636-638.
- Margules, C. R., G. A. Milkovits, and G. T. Smith. 1994. Contrasting effects of habitat fragmentation on the scorpion *Cercophonius-squama* and an amphipod. *Ecology* 75:2033-2042.
- Martin, P. R., and T. E. Martin. 2001. Ecological and fitness consequences of species coexistence: a removal experiment with wood warblers. *Ecology* 82:189-206.
- Martinson, S. J., T. Ylioja, B. T. Sullivan, R. F. Billings, and M. P. Ayres. 2013. Alternate attractors in the population dynamics of a tree-killing bark beetle. *Population Ecology* 55:95-106.
- Mas, F., and M. Kolliker. 2008. Maternal care and offspring begging in social insects: chemical signalling, hormonal regulation and evolution. *Animal Behaviour* 76:1121-1131.
- Masson, L., G. Masson, J. N. Beisel, L. F. G. Gutowsky, and M. G. Fox. 2018. Consistent life history shifts along invasion routes? An examination of round goby populations invading on two continents. *Diversity and Distributions* 24:841-852.
- Matthysen, E. 2005. Density-dependent dispersal in birds and mammals. *Ecography* 28:403-416.
- Matthysen, E. 2012. Multicausality of dispersal: a review, Pages 3-18 in J. Clobert, M. Baguette, T. G. Benton, and J. M. Bullock, eds., *Dispersal Ecology and Evolution*. Oxford University Press. Oxford, UK.
- McClintic, L. F., G. M. Wang, J. D. Taylor, and J. C. Jones. 2014. Movement characteristics of American beavers (*Castor canadensis*). *Behaviour* 151:1249-1265.
- McPeck, M. A., and R. D. Holt. 1992. The evolution of dispersal in spatially and temporally varying environments. *American Naturalist* 140:1010-1027.
- Melbourne, B. A., and A. Hastings. 2009. Highly variable spread rates in replicated biological invasions: fundamental limits to predictability. *Science* 325:1536-1539.
- Merchant, M. 2011. Little Spartina bug common now in east Texas, *Insects in the City*, Texas A&M Agrilife Extension.

- Mishra, A., S. Tung, P. M. Shreenidhi, M. A. Sadiq, V. R. S. Sruti, P. P. Chakraborty, and S. Dey. 2018. Sex differences in dispersal syndrome are modulated by environment and evolution. *Philosophical Transactions of the Royal Society B-Biological Sciences* 373: 20170428 (doi: 10.1098/rstb.2017.0428).
- Mishra, A., S. Tung, V. R. S. Sruti, M. A. Sadiq, S. Srivathsa, and S. Dey. 2018. Pre-dispersal context and presence of opposite sex modulate density dependence and sex bias of dispersal. *Oikos* 127:1596-1604.
- Molina-Morales, M., J. G. Martinez, D. Martin-Galvez, and J. M. Aviles. 2012. Factors affecting natal and breeding magpie dispersal in a population parasitized by the great spotted cuckoo. *Animal Behaviour* 84:1082-1082.
- Monty, A., and G. Mahy. 2010. Evolution of dispersal traits along an invasion route in the wind-dispersed *Senecio inaequidens* (Asteraceae). *Oikos* 119:1563-1570.
- Morton, E. R., M. J. McGrady, I. Newton, C. J. Rollie, G. D. Smith, R. Mearns, and M. K. Oli. 2018. Dispersal: a matter of scale. *Ecology* 99:938-946.
- Mouquet, N., M. F. Hoopes, and P. Amarasekare. 2005. The world is patchy and heterogeneous! Trade-off and source-sink dynamics in competitive metacommunities, Pages 237-262, *Metacommunities: Spatial Dynamics and Ecological Communities*. University of Chicago Press.
- Mousseau, T. A., and C. W. Fox. 1998. The adaptive significance of maternal effects. *Trends in Ecology & Evolution* 13:403-407.
- Muller-Landau, H. C. 2010. The tolerance-fecundity trade-off and the maintenance of diversity in seed size. *Proceedings of the National Academy of Sciences of the United States of America* 107:4242-4247.
- Muller-Landau, H. C., S. J. Wright, O. Calderon, R. Condit, and S. P. Hubbell. 2008. Interspecific variation in primary seed dispersal in a tropical forest. *Journal of Ecology* 96:653-667.
- Nelson, W. A., E. McCauley, and F. J. Wrona. 2001. Multiple dynamics in a single predator-prey system: experimental effects of food quality. *Proceedings of the Royal Society B-Biological Sciences* 268:1223-1230.
- Neubert, M. G., and H. Caswell. 2000. Demography and dispersal: calculation and sensitivity analysis of invasion speed for structured populations. *Ecology* 81:1613-1628.
- Nguyen, H. D. D., and C. Nansen. 2018. Edge-biased distributions of insects. A review. *Agronomy for Sustainable Development* 38:11 (doi: <https://doi.org/10.1007/s13593-018-0488-4>).

- Nguyen-Ngoc, D., N. H. Tri, and P. Auger. 2012. Effects of fast density dependent dispersal on pre-emptive competition dynamics. *Ecological Complexity* 10:26-33.
- Nowicki, P., V. Vrabec, B. Binzenhofer, J. Feil, B. Zaksek, T. Hovestadt, and J. Settele. 2014. Butterfly dispersal in inhospitable matrix: rare, risky, but long-distance. *Landscape Ecology* 29:401-412.
- Ochocki, B. M., and T. E. X. Miller. 2017. Rapid evolution of dispersal ability makes biological invasions faster and more variable. *Nature Communications* 8: 14315 (doi: 10.1038/ncomms14315).
- 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 Series B-Biological Sciences* 238:113-125.
- Pacala, S. W., and J. Roughgarden. 1982. Spatial heterogeneity and interspecific competition. *Theoretical Population Biology* 21:92-113.
- Park, T. 1948. Experimental studies of interspecies competition .1. Competition between populations of the flour beetles, *Tribolium-confusum* Duval and *Tribolium-castaneum* Herbst. *Ecological Monographs* 18:265-307.
- Patterson, T. A., A. Parton, R. Langrock, P. G. Blackwell, L. Thomas, and R. King. 2017. Statistical modelling of individual animal movement: an overview of key methods and a discussion of practical challenges. *Asta-Advances in Statistical Analysis* 101:399-438.
- Patterson, T. A., L. Thomas, C. Wilcox, O. Ovaskainen, and J. Matthiopoulos. 2008. State-space models of individual animal movement. *Trends in Ecology & Evolution* 23:87-94.
- Perry, G. L. W., and N. J. Enright. 2006. Spatial modelling of vegetation change in dynamic landscapes: a review of methods and applications. *Progress in Physical Geography* 30:47-72.
- Petraitis, P. S., and S. R. Dudgeon. 1999. Experimental evidence for the origin of alternative communities on rocky intertidal shores. *Oikos* 84:239-245.
- Phillips, B. L. 2015. Evolutionary processes make invasion speed difficult to predict. *Biological Invasions* 17:1949-1960.
- Phillips, B. L., G. P. Brown, J. K. Webb, and R. Shine. 2006. Invasion and the evolution of speed in toads. *Nature* 439:803-803.
- Phillips, B. L., G. P. Brown, J. M. J. Travis, and R. Shine. 2008. Reid's paradox revisited: The evolution of dispersal kernels during range expansion. *American Naturalist* 172:S34-S48.

- Pither, J., and P. D. Taylor. 1998. An experimental assessment of landscape connectivity. *Oikos* 83:166-174.
- Poethke, H. J., and T. Hovestadt. 2002. Evolution of density- and patch-size-dependent dispersal rates. *Proceedings of the Royal Society B-Biological Sciences* 269:637-645.
- Poniatowski, D., and T. Fartmann. 2011. Dispersal capability in a habitat specialist bush cricket: the role of population density and habitat moisture. *Ecological Entomology* 36:717-723.
- Pulliam, H. R. 1988. Sources, sinks, and population regulation. *American Naturalist* 132:652-661.
- Qing, J., Z. S. Yang, K. He, Z. J. Zhang, X. D. Gu, X. Y. Yang, W. Zhang et al. 2016. The minimum area requirements (MAR) for giant panda: an empirical study. *Scientific Reports* 6:37715 (doi: <https://doi.org/10.1038/srep37715>).
- Quezada-Garcia, R., and E. Bauce. 2014. Heritability of life-history traits in the spruce budworm. *Entomological Science* 17:111-117.
- Ravigne, V., I. Olivieri, S. C. Gonzalez-Martinez, and F. Rousset. 2006. Selective interactions between short-distance pollen and seed dispersal in self-compatible species. *Evolution* 60:2257-2271.
- Reeve, J. D., and J. T. Cronin. 2010. Edge behaviour in a minute parasitic wasp. *Journal of Animal Ecology* 79:483-490.
- Reeve, J. D., J. T. Cronin, and K. J. Haynes. 2008. Diffusion models for animals in complex landscapes: incorporating heterogeneity among substrates, individuals and edge behaviours. *Journal of Animal Ecology* 77:898-904.
- Rey, J. R. 1981. Ecological biogeography of arthropods on *Spartina* islands in northwest Florida. *Ecological Monographs* 51:237-265.
- Ricketts, T. H. 2001. The matrix matters: effective isolation in fragmented landscapes. *American Naturalist* 158:87-99.
- Ries, L., and D. M. Debinski. 2001. Butterfly responses to habitat edges in the highly fragmented prairies of Central Iowa. *Journal of Animal Ecology* 70:840-852.
- Ries, L., and T. D. Sisk. 2010. What is an edge species? The implications of sensitivity to habitat edges. *Oikos* 119:1636-1642.
- Ritte, U., and B. Lavie. 1977. Genetic basis of dispersal behavior in flour beetle *Tribolium-castaneum*. *Canadian Journal of Genetics and Cytology* 19:717-722.

- Rivera, J. H. V., J. H. Rappole, W. J. McShea, and C. A. Haas. 1998. Wood Thrush post-fledging movements and habitat use in northern Virginia. *Condor* 100:69-78.
- Rodrigues, A. M. M., and R. A. Johnstone. 2014. Evolution of positive and negative density-dependent dispersal. *Proceedings of the Royal Society B-Biological Sciences* 281:20141226 (doi: 10.1098/rspb.2014.1226).
- Roff, D. A. 1986. The evolution of wing dimorphism in insects. *Evolution* 40:1009-1020.
- Roff, D. A. 1994. Habitat persistence and the evolution of wing dimorphism in insects. *American Naturalist* 144:772-798.
- Roff, D. A. 2007. Contributions of genomics to life-history theory. *Nature Reviews Genetics* 8:116-125.
- Rogers, C. D., K. A. Evans, J. Parker, and V. A. Pappa. 2013. Behavioural response of wheat bulb fly (*Delia coarctata*, Diptera: Anthomyiidae) larvae to the primary plant metabolite carbon dioxide. *Bulletin of Entomological Research* 103:675-682.
- Roland, J., N. Keyghobadi, and S. Fownes. 2000. Alpine *Parnassius* butterfly dispersal: effects of landscape and population size. *Ecology* 81:1642-1653.
- Romero, S., J. F. Campbell, J. R. Nechols, and K. A. With. 2009. Movement behavior in response to landscape structure: the role of functional grain. *Landscape Ecology* 24:39-51.
- Ronce, O. 2007. How does it feel to be like a rolling stone? Ten questions about dispersal evolution. *Annual Review of Ecology Evolution and Systematics* 38:231-253.
- Ronce, O., F. Perret, and I. Olivieri. 2000. Landscape dynamics and evolution of colonizer syndromes: interactions between reproductive effort and dispersal in a metapopulation. *Evolutionary Ecology* 14:233-260.
- Roper, T. J., J. R. Ostler, and L. Conradt. 2003. The process of dispersal in badgers *Meles meles*. *Mammal Review* 33:314-318.
- Russell, R. E., R. K. Swihart, and Z. L. Feng. 2003. Population consequences of movement decisions in a patchy landscape. *Oikos* 103:142-152.
- Sæther, B. E., S. Engen, and R. Lande. 1999. Finite metapopulation models with density-dependent migration and stochastic local dynamics. *Proceedings of the Royal Society B-Biological Sciences* 266:113-118.
- Saunders, D. A., R. J. Hobbs, and C. R. Margules. 1991. Biological consequences of ecosystem fragmentation – a review. *Conservation Biology* 5:18-32.

- Saura, S., O. Bodin, and M. J. Fortin. 2014. Stepping stones are crucial for species' long-distance dispersal and range expansion through habitat networks. *Journal of Applied Ecology* 51:171-182.
- Savolainen, O., M. Lascoux, and J. Merila. 2013. Ecological genomics of local adaptation. *Nature Reviews Genetics* 14:807-820.
- Schroder, A., L. Persson, and A. M. De Roos. 2005. Direct experimental evidence for alternative stable states: A review. *Oikos* 110:3-19.
- Schultz, C. B., and E. E. Crone. 2005. Patch size and connectivity thresholds for butterfly habitat restoration. *Conservation Biology* 19:887-896.
- Senger, S. E., B. D. Roitberg, and H. M. A. Thistlewood. 2007. Relative flight responses of *Rhagoletis indifferens* as influenced by crowding, sex, and resources. *Entomologia Experimentalis Et Applicata* 123:91-100.
- Serrano, D., D. Oro, E. Ursua, and J. L. Tella. 2005. Colony size selection determines adult survival and dispersal preferences: Allee effects in a colonial bird. *American Naturalist* 166:E22-E31.
- Sgro, C. M., and A. A. Hoffmann. 1998. Heritable variation for fecundity in field-collected *Drosophila melanogaster* and their offspring reared under different environmental temperatures. *Evolution* 52:134-143.
- Shaw, R. G., C. J. Geyer, S. Wagenius, H. H. Hangelbroek, and J. R. Etterson. 2008. Unifying life-history analyses for inference of fitness and population growth. *American Naturalist* 172:E35-E47.
- Shine, R., G. P. Brown, and B. L. Phillips. 2011. An evolutionary process that assembles phenotypes through space rather than through time. *Proceedings of the National Academy of Sciences of the United States of America* 108:5708-5711.
- Shmida, A., and S. Ellner. 1984. Coexistence of plant-species with similar niches. *Vegetatio* 58:29-55.
- Sibly, R. M., D. Barker, M. C. Denham, J. Hone, and M. Pagel. 2005. On the regulation of populations of mammals, birds, fish, and insects. *Science* 309:607-610.
- Siddiqui, J. A., X. T. Zou, Q. Liu, H. Zhang, X. L. Lin, and X. L. Huang. 2019. Functional morphology and defensive behavior in a social aphid. *Insects* 10:163 (doi: 10.3390/insects10060163).
- Sih, A., J. Cote, M. Evans, S. Fogarty, and J. Pruitt. 2012. Ecological implications of behavioural syndromes. *Ecology Letters* 15:278-289.

- Simmons, A. D., and C. D. Thomas. 2004. Changes in dispersal during species' range expansions. *American Naturalist* 164:378-395.
- Simonsohn, U. 2018. Two lines: a valid alternative to the invalid testing of U-shaped relationships with quadratic regressions. *Association for Psychological Science* 1:538-555.
- Slater, J. A., and R. M. Baranowski. 1990. Lygaeidae of Florida (Hemiptera: Heteroptera): Arthropods of Florida and Neighboring Land Areas, v. 14, Florida Department of Agriculture and Consumer Services.
- Smith, J. E., and G. O. Batzli. 2006. Dispersal and mortality of prairie voles (*Microtus ochrogaster*) in fragmented landscapes: a field experiment. *Oikos* 112:209-217.
- 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.
- Stevenson, B. J., L. Cai, C. Faucher, M. Michie, A. Berna, Y. Ren, A. Anderson et al. 2017. Walking responses of *Tribolium castaneum* (Coleoptera: Tenebrionidae) to its aggregation pheromone and odors of wheat infestations. *Journal of Economic Entomology* 110:1351-1358.
- Stirling, G., D. J. Fairbairn, S. Jensen, and D. A. Roff. 2001. Does a negative genetic correlation between wing morph and early fecundity imply a functional constraint in *Gryllus firmus*? *Evolutionary Ecology Research* 3:157-177.
- Strona, G. 2015. A spatially explicit model to investigate how dispersal/colonization tradeoffs between short and long distance movement strategies affect species ranges. *Ecological Modelling* 297:80-85.
- Strong, D. R., and P. D. Stiling. 1983. Wing dimorphism changed by experimental density manipulation in a planthopper (*Prokelisia-marginata*, Homoptera, Delphacidae). *Ecology* 64:206-209.
- Suarez, A. V., and N. D. Tsutsui. 2008. The evolutionary consequences of biological invasions. *Molecular Ecology* 17:351-360.
- Subudhi, P. K., and N. Baisakh. 2011. *Spartina alterniflora* Loisel., a halophyte grass model to dissect salt stress tolerance. *In Vitro Cellular & Developmental Biology-Plant* 47:441-457.
- Sugiyama, A., L. S. Comita, T. Masaki, R. Condit, and S. P. Hubbell. 2018. Resolving the paradox of clumped seed dispersal: positive density and distance dependence in a bat-dispersed species. *Ecology* 99:2583-2591.

- Sun, G.-Q., Z.-Y. Wu, Z. Wang, and Z. Jin. 2016. Influence of isolation degree of spatial patterns on persistence of populations 83:811-819.
- Sutherland, J. P. 1990. Perturbations, resistance, and alternative views of the existence of multiple stable points in nature. *American Naturalist* 136:270-275.
- Svenning, J. C., D. Gravel, R. D. Holt, F. M. Schurr, W. Thuiller, T. Munkemuller, K. H. Schippers, D. S. Dullinger, T. C. Edwards, T. Hickler, S. I. Higgins, J. E. M. S. Nabel, J. Pagel, and S. Normand. 2014. The influence of interspecific interactions on species range expansion rates. *Ecography* 37:1198-1209.
- Szucs, M., M. L. Vahsen, B. A. Melbourne, C. Hoover, C. Weiss-Lehman, and R. A. Hufbauer. 2017. Rapid adaptive evolution in novel environments acts as an architect of population range expansion. *Proceedings of the National Academy of Sciences of the United States of America* 114:13501-13506.
- Thompson, J. R., D. R. Foster, R. Scheller, and D. Kittredge. 2011. The influence of land use and climate change on forest biomass and composition in Massachusetts, USA. *Ecological Applications* 21:2425-2444.
- Travis, J. M. J., and C. Dytham. 1999. Habitat persistence, habitat availability and the evolution of dispersal. *Proceedings of the Royal Society B-Biological Sciences* 266:723-728.
- Travis, J. M. J., and C. Dytham. 2002. Dispersal evolution during invasions. *Evolutionary Ecology Research* 4:1119-1129.
- Travis, J. M. J., D. J. Murrell, and C. Dytham. 1999. The evolution of density-dependent dispersal. *Proceedings of the Royal Society B-Biological Sciences* 266:1837-1842.
- Travis, J. M. J., K. Mustin, T. G. Benton, and C. Dytham. 2009. Accelerating invasion rates result from the evolution of density-dependent dispersal. *Journal of Theoretical Biology* 259:151-158.
- Travis, J. M. J., R. W. Brooker, and C. Dytham. 2005. The interplay of positive and negative species interactions across an environmental gradient: insights from an individual-based simulation model. *Biology Letters* 1:5-8.
- Tripet, F., A. Jacot, and H. Richner. 2002. Larval competition affects the life histories and dispersal behavior of an avian ectoparasite. *Ecology* 83:935-945.
- Turchin, P. 1996. Fractal analyses of animal movement: A critique. *Ecology* 77:2086-2090.
- Turchin, P., and A. D. Taylor. 1992. Complex dynamics in ecological time-series. *Ecology* 73:289-305.

- Turchin, P., and W. T. Thoeny. 1993. Quantifying dispersal of southern pine beetles with mark recapture experiments and a diffusion-model. *Ecological Applications* 3:187-198.
- Urban, M. C., B. L. Phillips, D. K. Skelly, and R. Shine. 2007. The cane toad's (*Chaunus Bufo marinus*) increasing ability to invade Australia is revealed by a dynamically updated range model. *Proceedings of the Royal Society B-Biological Sciences* 274:1413-1419.
- Urban, M. C., L. De Meester, M. Vellend, R. Stoks, and J. Vanoverbeke. 2012. A crucial step toward realism: responses to climate change from an evolving metacommunity perspective. *Evolutionary Applications* 5:154-167.
- Van Allen, B. G., and P. Bhavsar. 2014. Natal habitat effects drive density-dependent scaling of dispersal decisions. *Oikos* 123:699-704.
- Van Allen, B. G., and V. H. W. Rudolf. 2013. Ghosts of habitats past: environmental carry-over effects drive population dynamics in novel habitat. *American Naturalist* 181:596-608.
- Van Allen, B. G., and V. H. W. Rudolf. 2016. Carryover effects drive competitive dominance in spatially structured environments. *Proceedings of the National Academy of Sciences of the United States of America* 113:6939-6944.
- Van De Koppel, J., P. M. J. Herman, P. Thoolen, and C. H. R. Heip. 2001. Do alternate stable states occur in natural ecosystems? Evidence from a tidal flat. *Ecology* 82:3449-3461.
- Van de Leemput, I. A., T. P. Hughes, E. H. van Nes, and M. Scheffer. 2016. Multiple feedbacks and the prevalence of alternate stable states on coral reefs. *Coral Reefs* 35:857-865.
- Van der Knaap, W. O., J. F. N. van Leeuwen, W. Finsinger, E. Gobet, R. Pini, A. Schweizer, V. Valsecchi et al. 2005. Migration and population expansion of *Abies*, *Fagus*, *Picea*, and *Quercus* since 15000 years in and across the Alps, based on pollen-percentage threshold values. *Quaternary Science Reviews* 24:645-680.
- Van Duzee, E. P. 1909. Observations on some Hemiptera taken in Florida in the spring of 1908., Pages 149-230, *Bull. Buffalo Soc. Nat. Sci.*
- Van Hooft, P., J. F. Cosson, S. Vibe-Petersen, and H. Leirs. 2008. Dispersal in *Mastomys natalensis* mice: use of fine-scale genetic analyses for pest management. *Hereditas* 145:262-273.
- Van Petegem, K., F. Moerman, M. Dahirel, E. A. Fronhofer, M. L. Vandegheuchte, T. Van Leeuwen, N. Wybouw et al. 2018. Kin competition accelerates experimental range expansion in an arthropod herbivore. *Ecology Letters* 21:225-234.
- Vandermeer, J., and R. Carvajal. 2001. Metapopulation dynamics and the quality of the matrix. *American Naturalist* 158:211-220.

- Walter, J. A., D. M. Johnson, and K. J. Haynes. 2017. Spatial variation in Allee effects influences patterns of range expansion. *Ecography* 40:179-188.
- Wang, W. D. 2016. Population dispersal and Allee effect. *Ricerche Di Matematica* 65:535-548.
- Waters, J. M., C. I. Fraser, and G. M. Hewitt. 2013. Founder takes all: density-dependent processes structure biodiversity. *Trends in Ecology & Evolution* 28:78-85.
- Wehnert, A., and S. Wagner. 2019. Niche partitioning in carabids: single-tree admixtures matter. *Insect Conservation and Diversity* 12:131-146.
- Weigang, H. C., and E. Kisdi. 2015. Evolution of dispersal under a fecundity-dispersal trade-off. *Journal of Theoretical Biology* 371:145-153.
- Weiss-Lehman, C., R. A. Hufbauer, and B. A. Melbourne. 2017. Rapid trait evolution drives increased speed and variance in experimental range expansions. *Nature Communications* 8:14303 (doi: 10.1038/ncomms1430).
- Wheeler, A. G. 1996. *Ischnodemus falicus* (Heteroptera: *Lygaeidae*): First record from ornamental grasses, and seasonality on prairie cordgrass in Pennsylvania. *Proceedings of the Entomological Society of Washington* 98:195-198.
- Wheelwright, N. T. 1993. Fruit size in a tropical tree species - variation, preference by birds, and heritability. *Vegetatio* 108:163-174.
- Wiegand, T., and K. A. Moloney. 2004. Rings, circles, and null-models for point pattern analysis in ecology. *Oikos* 104:209-229.
- Wiegand, T., and K. A. Moloney. 2014. *Handbook of spatial point-pattern analysis in ecology*, CRC Press, New York.
- Wiens, J. A., T. O. Crist, K. A. With, and B. T. Milne. 1995. Fractal patterns of insect movement in microlandscape mosaics. *Ecology* 76:663-666.
- Willi, Y., and M. Fischer. 2005. Genetic rescue in interconnected populations of small and large size of the self-incompatible *Ranunculus reptans*. *Heredity* 95:437-443.
- Wolff, J. O. 1997. Population regulation in mammals: an evolutionary perspective. *Journal of Animal Ecology* 66:1-13.
- Zedler, J. B. 2000. Progress in wetland restoration ecology. *Trends in Ecology & Evolution* 15:402-407.
- Ziegler, J. R. 1976. Evolution of the migratory response: emigration by *Tribolium* and the influence of age. *Evolution* 30:579-592.

VITA

Rachel (Fuelling) Harman was raised in the rural farmlands of Indiana, where she grew up with an appreciation for hard work, a yearning to learn, and a love of nature. Since kindergarten, Rachel has known she wants to be a teacher, but it was not until her first laboratory-based class in middle school that her desire to do research grew. In 2012, Rachel received her bachelor's in biology teaching and associate's in chemical methods from Indiana University-Purdue University Fort Wayne (IPFW). Her undergraduate research on micropropagation of *Sassafras albidum* inspired her to pursue research as a profession. At IPFW, she worked under the advisership of Dr. Jordan Marshall, researching plant communities in fragmented forests, and earned her MS in biology in 2014.

Rachel pursued her doctoral degree at Louisiana State University, where she joined the Dr. James Cronin lab to continue researching the effects of fragmentation. While there, she worked with various insects, including *Ischnodemus conicus*, *Prokelisia marginata*, *Tribolium castaneum*, and *T. confusum*. She worked as a teaching assistant for several laboratory courses, including plant taxonomy and ecology, and enhanced her teaching skills by developing curriculum, organizing lectures, and writing examinations. After graduation, she plans to work as a research post-doc for the immediate future. Her ultimate goal is to combine her passion and skills for teaching and research into a professorial position.