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Context-dependency and sex-specificity of dispersal syndromes

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CONTEXT-DEPEDENCY AND SEX-SPECIFICITY OF DISPERSAL SYNDROMES

DISSERTATION

A dissertation submitted in partial fulfillment of the
Requirements for the degree of Doctor of Philosophy in the
College of Arts and Sciences
at the University of Kentucky

By

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ABSTRACT OF DISSERTATION

CONTEXT-DEPEDENCY AND SEX-SPECIFICITY OF DISPERSAL SYNDROMES

For populations in landscapes with increasingly heterogeneous and fragmented habitat patches (e.g., metapopulations), dispersal is an important behavior that leads to gene flow and connectivity among isolated patches. Because dispersal is a complex process, there are many traits involved. When suites of morphological, behavioral, physiological, and life-history traits covary with dispersal (e.g., a dispersal syndrome), the correlated traits can assist dispersing individuals through the complex process. Furthermore, once dispersal is completed, the correlated traits can influence the fitness of those dispersed individuals. Dispersal syndromes will likely interact with the local environment to produce ecological and evolutionary feedbacks on the metapopulation. Thus, for populations in heterogeneous landscapes, the nature of dispersal syndromes may be an important piece in establishing links between variation within a sub-population and the dynamics of multiple sub-populations within the broader metapopulation. My dissertation uses a seed beetle system to quantify a dispersal syndrome across multiple environmental contexts and between the sexes.

If dispersal syndromes are context-dependent, the direction and magnitude of correlations across a range of contexts may influence how much dispersal syndromes affect population dynamics. I artificially selected for long and short distance dispersal in female seed beetles (*Callosobruchus maculatus*, Coleoptera: Chrysomelidae, Bruchinae) then assessed correlated responses to selection in multiple life-history traits with dispersal behavior to quantify a dispersal syndrome in multiple environments (conspecifics absent, low, and high conspecific density). When looking for correlated responses to selection in life-history traits, only two traits were correlated with dispersal: beetles from dispersal-selected lines exhibited larger body sizes and shorter egg lengths compared to non-dispersal-selected lines. Only one trait (short-term fecundity) showed evidence of context-dependence. In an environment with high conspecific density, females from dispersal-selected lines laid fewer eggs than females from non-dispersal selected lines, but this difference was not detected in any other environment. My results indicate that, in seed beetles, dispersal syndromes and context-dependence of syndromes may be subtle.

To better understand the genetic basis of the traits that comprise dispersal syndromes and assess which traits are genetically correlated within and across the sexes, I measured dispersal behavior, body size, time to reach maturity, and reproductive output in male beetles from the populations artificially selected for long- and short-distance dispersal. For 3 traits, males evolved the same as females in response to selection, but interestingly there were 2 traits that males evolved differently from females: females from dispersal-selected lines made more location changes in a dispersal array than those from non-dispersal selected lines, but males from the lines did not differ; and females from the selection lines had similar fecundity, but males from dispersal-selected lines had a smaller spermatophore than males from non-dispersal-selected lines. Additionally, I found limited evidence that responses to selection are context dependent: males from the dispersal- and non-dispersal-selected lines had similar reproductive output regardless of conspecific density. In contrast, female reproductive output was higher for non-dispersal-selected lines than dispersal-selected lines when conspecifics are present, but this difference disappears when conspecifics are absent. The differences in male and female dispersal syndromes suggests that cross-sex genetic correlations are present but weak, and there is likely a combination of genotypic and environmental effects decoupling the traits in the dispersal syndrome.

By assessing context-dependent and sex-specific dispersal syndromes, I found that there is variation in dispersal syndromes of dispersal and non-dispersers that can depend on the environment. Future work should account for the variation among individuals in dispersal syndromes, beyond simply comparing disperser and resident syndromes. The variation among individuals (e.g., dispersal distance) combined with the complicated suite of traits that comprise a dispersal syndrome and interactions with the environment, makes assessing the impact of dispersal syndromes on metapopulation dynamics difficult. But integrating across biological levels (e.g., individual to subpopulation to metapopulation) is an important next step in metapopulation research.

KEY WORDS: behavioral syndrome, dispersal, life-history, artificial selection, *Callosobruchus*, metapopulation

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CHAPTER 1: INTRODUCTION

As human-induced, rapid environmental change alters the natural world, conducting research that links concepts across biological scales becomes increasingly crucial for understanding and mitigating changes to our global environment. One of the most concerning aspects of human-altered landscapes is the loss and fragmentation of habitat (Veach et al. 2017). The persistence of animal populations in fragmented landscapes relies on movement, which is often studied at the individual level (e.g., movements that occur on short time scales, such as foraging, and on longer time scale, such as dispersal or migration, Morales et al. 2010). However, a common assumption for research at the population scale is that any variation among individuals can simply be averaged (e.g., average dispersal distance, Travis et al. 2012). This simplifying assumption makes studying complex population dynamics more tractable; however, when variation from two or more sub-groups is averaged – such as long-distance dispersers, short-distance dispersers, and non-dispersers – the combined population trend can hide important differences between the groups, and this unobserved heterogeneity can lead to false conclusions about the dynamics of the population (Vaupel and Yashin 1985).

As an additional layer of complexity, the individuals that disperse may also have a variety of other traits (morphological, physiological, behavioral, and life-history) that are phenotypically or genetically correlated with dispersal (e.g., a dispersal syndrome, Roff and Fairbairn 2007, Ronce & Clobert 2012). Frequently, dispersal syndromes are described only when there are individuals that disperse and those that do not (e.g., winged vs non-winged individuals of an insect population Roff & Fairbairn 2007). However, dispersal syndromes may vary among individuals of those subgroups (e.g., disperser males vs disperser females, Legrand et al. 2016) or the context in which traits are measured (high vs low nutrients available in environment, Mishra et al. 2018).

Accounting for additional variation within subgroups is necessary because when the correlated traits interact with the local environment (e.g., increased fecundity if dispersers enter an environment with few competitors; Spiegel et al. 2017, Plard et al. 2019), then variation in dispersal syndromes could produce eco-evolutionary feedbacks that enhance or limit population persistence. For example, individuals disperse across the landscape, correlated traits interact with the local environment and other conspecifics to alter genetics and demography of subpopulations, which in turn feeds back on selection (or not) for dispersal syndromes (Starrfelt & Kokko 2012, Duckworth & Aguillon 2015). The variation among individuals (e.g., dispersers vs non-dispersers) combined with the complicated suite of traits that comprise a dispersal syndrome and interactions with the environment, makes assessing the impact of dispersal syndromes on metapopulation dynamics difficult. But integrating across biological levels (e.g., individual to subpopulation to metapopulation) is an important next step in metapopulation research.

One approach to bridge the individual to population scale is to use an easily manipulated model species. Model species, such as insects maintained in a laboratory, are well suited to addressing questions of individual movements (Friedenberg 2003, Hauzy et al. 2010), dispersal syndromes (Jacob et al. 2019, Jacob et al. 2020), and population dynamics in fragmented landscapes (Warren 1996, Cadotte 2006). Additionally, insects often have short generations, making multi-generational studies feasible (Srivastava et al. 2004, Lee et al. 2015, Mukherjee et al. 2015). In my dissertation, I use a model species that is commonly used in metapopulation research, the seed beetle (*Callosobruchus maculatus*). I begin by quantifying the dispersal syndrome of this species, then assess if this dispersal syndrome is context-dependent or sex-specific. Lastly, I discuss the potential for context-dependent and sex-specific dispersal syndromes to alter the expected outcomes for populations living in fragmented landscapes.

1.1 Seed beetles as a study system

The cowpea seed beetle (hereafter seed beetle; *Callosobruchus maculatus*, Coleoptera: Chrysomelidae, Bruchinae), a cosmopolitan agricultural pest that damages stored legume seeds (Tuda et al. 2006). Seed beetles spend most of their lifecycle inside dried legume seeds, with a generation lasting approximately 35 days (when maintained at 16:8 light:dark, 25.5 ^{o}C). Adults do not need to feed and can rely on energetic reserves obtained during the larval portion of the lifecycle (Messina 1993, Fox et al. 2011). Depending on where a seed beetle population is located, the beetle population will evolve an egg laying behavior that best suits the resources available in their host legume. Populations collected from Tirunelveli, India in 1979 from infested mung bean pods (*Vigna radiata;* Mitchell 1991, Fox et al. 2007) have evolved to be highly competitive as larvae (because the mung bean is small relative to the size of the seed beetles only 1 larvae survives to adulthood in a single bean even if multiple eggs are laid, Messina 1991) and because of high larval competition, females are extremely sensitive to the presence of conspecific eggs and will disperse to find beans without previous exposure to conspecifics (Messina et al. 1991). In contrast, beetles collected from the Maiduguri area of Borno State, Nigeria in 2010 (Berger et al. 2016) from infested pods of black-eyed peas (*Vigna unguiculata*), have evolved to be less competitive as larvae (because the black-eyed pea is a large bean that can support 4-6 larvae that survive to adulthood, Ventury et al. 2022) and thus females are generally insensitive to the presence of conspecific eggs and will not disperse as far to lay their eggs. These differences are well documented and are what make seed beetles ideal for my dissertation.

The well-studied Indian and Nigerian lines show consistent responses to the presence of conspecifics that I leveraged in my dissertation to invoke a dispersal response based on a competitive environment. The Indian line is sensitive to conspecific density and females of this line will leave a high-density area to lay eggs in a low-density location, whereas the Nigerian line is much less sensitive to density and will lay eggs on seeds that bear conspecific eggs (Messina 1991, Messina et al. 1991, Fox et al. 2004).

Prior to beginning my experiments, I crossed beetles from the Nigerian and Indian lines to create a control line with genetic mixing in case there was any fixation of alleles in the stock populations. I isolated beans with a single egg from Nigerian and Indian colonies into 15 mm diameter Falcon petri dishes. Approximately 24 h after the adults emerged, I mated virgin females to virgin males from the opposite line (total 55 mated pairs) to create an F1 hybrid. The next generation, I mated virgin females to virgin males from a different hybrid family (avoided sibling inbreeding). I continued this procedure for 5 generations before the start of the artificial selection experiment, which should have disrupted any existing genetic linkages.

1.2 Dissertation Overview

The goal of my dissertation was to identify dispersal syndromes of the seed beetle and assess if they are consistently expressed or are context-dependent or sex-specific. First, I reviewed the literature to identify how variation among individuals in dispersal syndrome, either due to context-dependence or sex-specificity, could impact populations living in fragmented landscapes. Second, I described the dispersal syndrome of female seed beetles and assessed if this dispersal syndrome is context-dependent. Third, I described the dispersal syndrome of male seed beetles and compared the sexes to determine if seed beetle dispersal syndromes are sex-specific. Lastly, I review the potential impacts of context-dependent and sex-specific dispersal syndromes on population dynamics and identify future research directions to explicitly bridge the individual to population scales.

1.2.1 Chapter 2. Variation among individuals in dispersal syndrome: effect of context-dependency, sex-specificity, and plasticity on metapopulation dynamics

Human activities are creating increasingly fragmented landscapes (Hansen et al. 2013). In these fragmented landscapes, habitat may be surrounded by an inhospitable environment, forming a metapopulation, or a regional population composed of smaller, semi-isolated populations. Metapopulations are a “population of populations” (Levins 1969), or a group of populations in distinct habitat patches that are separated by an uninhabitable matrix (Hanski & Gaggiotti 2004). Subpopulations experience stochastic extinction events, but gene flow among populations and re-colonization of patches is maintained by dispersal.

Dispersal within a metapopulation affects both evolutionary and ecological processes; it affects gene flow (e.g., higher genetic diversity in directionally biased dispersal in dendritic metapopulations, Morrissey & de Kerckhove 2009), local adaptation (e.g., genotype-dependent habitat matching in a heterogeneous landscape, Bolnik & Otto 2013), and can ultimately influence speciation (Gavrilets et al. 2000).

Predicting the outcomes of metapopulation dynamics is complex because dispersal can have a wide array of effects on the regional population persistence. However, dispersal is also a very complex process, which adds an additional layer of complexity. Dispersal consists of three phases: emigration – a decision to depart from the initial location (either leaving a breeding or natal site), transience – moving through the landscape and sampling potential settlement sites, and immigration – settling into the chosen new location (Clobert et al. 2001, Ronce 2007).

Because dispersal is a complex process, there are many traits involved. When suites of morphological, behavioral, physiological, and life-history traits covary with dispersal (e.g., dispersal syndrome, Ronce and Clobert 2012), the correlated traits can assist dispersing individuals through the complex process (e.g., high metabolism, increased wing muscles, decreased ovary size, and body shape; Roff and Fairbairn 2007). And furthermore, once dispersal is completed, the correlated traits can influence the fitness of those dispersed individuals (e.g., when food availability is low, higher aggression of dispersing pied flycatchers, *Ficedula hypoleuca*, increases the number offspring fledged whereas the non-dispersing, less aggressive birds fledge fewer offspring, Nicolaus et al. 2022).

For populations in fragmented landscapes, the nature of dispersal syndromes may be an important piece in establishing links between variation within a sub-population and the dynamics of multiple sub-populations within the broader metapopulation. Here, I review the importance of dispersal within the metapopulation concept and how accounting for among-individual variation changes the long-term population dynamics compared to assuming that all individuals are the same. I then review dispersal syndromes and how dispersal syndromes may differ not only between dispersers and non-dispersers, but how individuals within these two categories can also differ in their dispersal syndromes by sex, the environmental context, and the stage of dispersal. Lastly, I discuss how dispersal syndromes may affect metapopulation dynamics and the complexities of incorporating dispersal syndromes into current metapopulation models.

1.2.2. Chapter 3. Artificial selection reveals a dispersal syndrome with limited context dependency in a seed beetle

Generally, dispersal syndromes are measured in one context, and it is assumed that dispersal syndromes are consistent across time and context. However, it is possible that dispersal syndromes are context-dependent even within species (Hoset et al 2011, Legrand et al. 2016, Jacob et al. 2020, Morel-Journel et al. 2020, Nicolaus et al. 2022). Within-species variation in dispersal syndromes may be due to adaptive plasticity of one or more of the correlated traits (Hoset et al. 2011). If a single behavior is plastic, the direction and magnitude of a correlation between two or more traits in the dispersal syndrome will change based on the environment. If multiple traits in the dispersal syndrome are plastic, the influence of the environment on the correlations between traits in the dispersal syndromes can be complex.

In my third chapter, I quantify seed beetle dispersal syndromes in three environments (conspecifics absent, low, and high density) to evaluate the context-dependence of female dispersal syndromes. I artificially selected on dispersal tendency by creating an environment where females that are sensitive to competition would disperse long distances to locate resources without competition, then used the selected lines to evaluate phenotypic correlations of multiple life-history traits with dispersal behavior.

First, I measure life-history and behavioral traits of females from the selected lines in an ideal environment without conspecifics present. If females from the dispersal-selected lines differ in any trait from the non-dispersal-selected lines, then I infer that there is a correlation between dispersal and that trait, which would indicate those traits are part of a dispersal syndrome. Second, to assess if female dispersal syndromes are context-dependent, I measured life-history and behavioral traits in three environments (conspecifics absent, low conspecific density, and high conspecific density) of females from the dispersal and non-dispersal selection lines. If females from the dispersal selection lines differed from the non-dispersal selection lines in any environment, then that suggests that I detected a dispersal syndrome in that environment. I compare the dispersal syndromes detected in the three environments to determine if dispersal syndromes depend on the environment in which I measure them.

After 8 generations of artificial selection for increased female dispersal, beetles from the dispersal-selected lines dispersed longer distances and had a higher dispersal tendency than beetles from non-dispersal-selected lines. When looking for correlated responses to selection in life-history traits, only two traits were correlated with dispersal: beetles from dispersal-selected lines exhibited larger body sizes and shorter egg lengths compared to non-dispersal-selected lines selected. Only one trait (short-term fecundity) showed evidence of context-dependence. In an environment with high conspecific density, females from dispersal-selected lines laid fewer eggs than females from non-dispersal selected lines, but this difference was not detected in any other environment. In summary, for most traits I measured, there is no evidence of a dispersal syndrome in seed beetles. However, there may be a subtle dispersal syndrome that involved body mass and egg length. Additionally, I have evidence that dispersal syndromes are context-dependent because for one trait, we only detected a correlation when conspecific density was high.

My results indicate that, in seed beetles, dispersal syndromes and context-dependence of syndromes may be subtle. I may have found limited evidence of context-dependency because of the environmental cue used when measuring dispersal syndromes may be most relevant for only one trait that we measured. Future work should evaluate dispersal syndromes across multiple environmental cues to tease apart how various environments affect the detection of dispersal syndromes. Overall, my context-dependent approach to measuring dispersal provides a stronger understanding of the proximate causes of dispersal syndromes and the potential of dispersal syndromes to affect the ecology and evolution of populations in fragmented landscapes.

1.2.3 Chapter 4. Selection for higher dispersal in females reveals cross-sex genetic correlations

Selection on behavior and life-history traits can be different for males and females. Because of differences in natural selection on males and females, each sex can have different phenotypic optima (Lande 1980, Fairbairn et al. 2007, Bonduriansky & Chenoweth 2009). However, the degree to which the sexes can reach their optimum and the rate at which sexes differentiate due to differing natural selection is often constrained by a cross-sex genetic correlation (e.g., the similarity of the additive effects of alleles when expressed in the different sexes) caused by a shared genetic architecture between the sexes (Lande 1980, Pennell and Morrow 2013). This genetic architecture constraint means that differences in natural selection on the sexes can lead to sexual conflict (Dean and Mank 2014).

One trait for which this conflict can occur is dispersal. Dispersal may often be the target of different selection pressures in the two sexes (Smale et al. 1997), leading to different phenotypic optima. Frequently, dispersal has been observed to vary between the sexes, known as sex-biased dispersal, such that males and females have different dispersal behaviors (e.g., distance travelled, propensity to leave natal area; Smale et al. 1997, Li & Kokko 2019a). Dispersal behavior often covaries with other behavioral, morphological, and physiological traits, called a dispersal syndrome (Roff and Fairbairn 2007, Ronce & Clobert 2012). Interestingly, there is some evidence that dispersal syndromes differ between the sexes. Generally, there is a difference in dispersal syndromes, but the sexes do not always have the same traits involved in the dispersal syndrome (Legrand et al. 2016).

The impact of sex-specific dispersal syndromes on the ecology and evolution of spatially fragmented populations is intriguing. Males and females disperse for different reasons, and this means that the same environment can lead to different dispersal behavior between the sexes. Thus, not only is it important to know how dispersal syndromes differ between males and females, but the environment in which dispersal syndromes are measured can interact with the sex-specific dispersal syndrome to alter the population dynamics.

In my fourth chapter, I examine how changing selection on components of female dispersal behavior might affect male traits. My goal was to better understand the genetic basis of the traits that comprise dispersal syndromes and assess which traits are genetically correlated within and across the sexes. Using the selection lines developed for Chapter 3, I measure multiple dispersal (activity and dispersal tendency) and life-history traits (body mass, larval development time, reproductive output) of males. First, I quantify male dispersal syndromes by comparing males from the dispersal and non-dispersal-selected lines. Second, I measure two traits (larval development time and reproductive output) for males from the dispersal and non-dispersal-selected lines in two environments (conspecifics present at high density or absent) to look for context-dependence of male dispersal syndromes. Finally, I compare male dispersal syndromes to female dispersal syndromes, which were measured as part of a previous experiment (Chapter 3 of this dissertation), to determine which traits of the dispersal syndrome are correlated across the sexes.

For 8 generations, I selected female dispersal (with no direct selection on males) for long and short distance dispersal. To address my first aim, I compared males from the dispersal- and non-dispersal-selected lines in an ideal environment (conspecific absent). If there is a cross-sex genetic correlation, then selection on female dispersal would also lead to differences between males from the dispersal- and non-dispersal selected lines. I found that for 3 traits, males evolved the same as females in response to selection: males from long-distance dispersal-selected lines were more active, left the starting patch of a dispersal array faster, and were heavier than males from non-dispersal selected lines. For 2 traits, males evolved differently from females: females from dispersal-selected lines made more location changes in a dispersal array than those from non-dispersal selected lines, but males from the lines did not differ; and females from the selection lines had similar fecundity, but males from dispersal-selected lines had a smaller spermatophore than males from non-dispersal-selected lines.

To assess if responses to selection are context dependent, I measured two traits (larval development time and reproductive output) for males from the dispersal and non-dispersal-selected lines in two environments (conspecifics present at high density or absent). If the trait varies between the selection lines differently in the two environments, then we have evidence for context dependence. I found limited evidence that responses to selection are context dependent: males from the dispersal- and non-dispersal-selected lines had similar reproductive output regardless of conspecific density. In contrast, female reproductive output was higher for non-dispersal-selected lines than dispersal-selected lines when conspecifics are present, but this difference disappears when conspecifics are absent.

My results suggest that the traits within a dispersal syndrome vary in their ability to be decoupled between the sexes. In addition, my results suggest that the sexes have different plasticity, and this result offers interesting insights into how populations of the same species can vary in their sex-specific trait expression (e.g., variation in the degree of sexual dimorphism among populations; Stillwell et al. 2010, Han and Dingemanse 2017).

Most interesting is that my work highlights that the traits correlated with dispersal and that form a dispersal syndrome, can evolve due to cross-sex genetic correlations. Thus, even if only a one sex is experiencing selection on a dispersal syndrome, the cross-sex genetic correlation could cause the other sex's dispersal syndrome to evolve as well. When the sexes have different expression of traits within a dispersal syndrome, these differences could lead to variation in the subpopulations within metapopulations (e.g., regional populations in a spatially fragmented landscape). Variation in individual thresholds to an environmental cue (e.g., conspecific density) will produce a mosaic of population densities in the subpopulations (Benton and Bowler 2012). These individuals then have other traits (e.g., reproductive output, activity) within the dispersal syndrome that will interact with the local environment (e.g., conspecific density, predators, food availability) to shape local evolution within a subpopulation (Ronce and Clobert 2012). Our work begins to link together within- and among-sex genetic correlations for traits that comprise a dispersal syndrome, but there is a dearth of studies that explore the impact of the genetic architecture on the population. While complexity of these topics alone makes integrating them to predict the impact of sex-specific dispersal syndromes on population dynamics difficult, this complexity opens some intriguing avenues of future research into the causes and consequences of sex-specific dispersal syndromes for the ecology and evolution of populations in spatially fragmented landscapes.

CHAPTER 2: DISPERSAL SYNDROMES: EFFECTS OF CONTEXT-DEPEDENCY, SEX-SPECIFICITY, AND PLASTICITY ON METAPOPULATION DYNAMICS

2.1 Abstract

For populations in landscapes with increasingly heterogeneous and fragmented habitat patches (e.g., metapopulations), dispersal is an important behavior that leads to gene flow and connectivity among isolated patches. Because dispersal is a complex process, there are many traits involved. When suites of morphological, behavioral, physiological, and life-history traits covary with dispersal (e.g., a dispersal syndrome), the correlated traits can assist dispersing individuals through the complex process. Furthermore, once dispersal is completed, the correlated traits can influence the fitness of those dispersed individuals. Dispersal syndromes will likely interact with the local environment to produce ecological and evolutionary feedbacks on the metapopulation. Thus, for populations in fragmented landscapes, the nature of dispersal syndromes may be an important piece in establishing links between variation within a sub-population and the dynamics of multiple sub-populations within the broader metapopulation. Here, I review the importance of dispersal within the metapopulation concept; how individuals can differ in their dispersal syndromes by sex, the environmental context, and the stage of dispersal; and how dispersal syndromes may affect metapopulation dynamics. I highlight the need for empirical studies that measure dispersal syndromes across all three stages of dispersal and across multiple environmental contexts, as well as the need for theoretical models to incorporate dispersal syndromes. Although both these recommendations are challenging, we need to bridge the levels of individual to subpopulation to metapopulation to fully understand how the small variations among individual behaviors affect larger scale population dynamics.

2.2 Introduction

Human activities are creating landscapes with increasing habitat heterogeneity (Hansen et al. 2013). In these changing landscapes, habitat may become surrounded by an inhospitable environment, thus spatially isolated some habitats. As the landscape change progresses, eventually, the heterogeneous landscape can fragment a continuous population into a regional population composed of smaller, semi-isolated populations (metapopulation). Metapopulations are a “population of populations” (Levins 1969), or a group of populations in distinct habitat patches that are separated by an uninhabitable matrix (Hanski & Gaggiotti 2004). Subpopulations experience stochastic extinction events, but gene flow among populations and re-colonization of patches is maintained by dispersal.

Dispersal within a metapopulation affects both evolutionary and ecological processes; it affects gene flow (e.g., higher genetic diversity in directionally biased dispersal in dendritic metapopulations, Morrissey & de Kerchkhove 2009), local adaptation (e.g., genotype-dependent habitat matching in a heterogeneous landscape, Bolnik & Otto 2013), counteracting location adaption through gene flow of individuals maladapted to local conditions (Lenormand 2002), and can ultimately influence speciation (Gavrilets et al. 2000). Theoretical models show that dispersal movements can increase colonization of empty patches and can bolster extant populations, thereby preventing global extinction of the metapopulation (Levins 1969, Hanski 1999, Ovaskainen et al. 2016). However, other theoretical models show that too much dispersal can have negative effects on the ecology of a metapopulation; high dispersal rates out of a patch can cause local patch extinction as the last individual leaves or due to Allee effects (Hanski 1999, Ovaskainen et al. 2016), or can cause synchronization of local patch dynamics, ultimately increasing the probability of simultaneous patch extinction and metapopulation extinction (Liebhold et al. 2004). From an evolutionary perspective, metapopulations with low emigration have patches that will become inbred and genetically distinct as genetic drift occurs, whereas metapopulations with high emigration avoid inbreeding but local populations may go extinct if too many individuals disperse (Leibhold et al. 2004).

Predicting the outcomes of metapopulation dynamics is complex because dispersal can have a wide array of effects on the regional population persistence. However, dispersal is also a very complex process, which adds an additional layer of complexity. Dispersal consists of three phases: emigration – a decision to depart from the initial location (either leaving a breeding or natal site), transience – moving through the landscape and sampling potential settlement sites, and immigration – settling into the chosen new location (Clobert et al. 2001, Ronce 2007). Many studies have documented that individuals which disperse and those that do not are different in many traits (reviewed in Zera and Denno 1997, Tigreros and Davidowitz 2019, Renault 2020). Sometimes those differences are obvious, such as winged vs non-winged insects (Zera and Denno 1997), but often the differences are subtle (e.g., fat reserves, O'Riain et al. 1996 or hormones, Holekamp and Smale 1998). Because dispersal is a complex process, there are many traits involved. When suites of morphological, behavioral, physiological, and life-history traits covary with dispersal (e.g., a dispersal syndrome, Ronce and Clobert 2012), the correlated traits can assist dispersing individuals through the complex process (e.g., high metabolism, increased wing muscles, decreased ovary size, and body shape; Roff and Fairbairn 2007). Furthermore, once dispersal is completed, the correlated traits can influence the fitness of those dispersed individuals. For example, when food availability is low, higher aggression of dispersing pied flycatchers, *Ficedula hypoleuca*, increases the number offspring fledged whereas the non-dispersing, less aggressive birds fledge fewer offspring (Nicolaus et al. 2022). Although the traits in dispersal syndromes are species specific, there are some general interspecific patterns. A meta-analysis of 15 terrestrial and semi-terrestrial orders (comprising over 700 species) showed that 1) high dispersal ability is associated with high fecundity and survival, and 2) aerial dispersers and ectotherms have stronger evidence for dispersal syndromes than ground dwellers and endotherms (Stevens et al. 2014).

Dispersal syndromes will likely interact with the local environment to produce ecological and evolutionary feedbacks on the metapopulation. Even in a very simplified 2-patch system, the dispersal syndrome had as much effect on metapopulation dynamics as the spatial/temporal environmental variability (Jacob et al. 2019). Thus, for populations in fragmented landscapes, the nature of dispersal syndromes may be an important piece in establishing links between variation within a sub-population and the dynamics of multiple sub-populations within the broader metapopulation.

The variation among individuals (e.g., dispersers vs non-dispersers) combined with the complicated suite of traits that comprise a dispersal syndrome and interactions with the environment, makes assessing the impact of dispersal syndromes on metapopulation dynamics difficult. But integrating across biological levels (e.g., individual to subpopulation to metapopulation) is an important next step in metapopulation research. Here, I review the importance of dispersal within the metapopulation concept and how accounting for among-individual variation changes the long-term population dynamics compared to assuming that all individuals are the same. I then review dispersal syndromes and how dispersal syndromes may differ not only between dispersers and non-dispersers, but how individuals within these two categories can also differ in their dispersal syndromes by sex, the environmental context, and the stage of dispersal. Lastly, I discuss how dispersal syndromes may affect metapopulation dynamics and the complexities of incorporating dispersal syndromes into current metapopulation models.

2.3 Dispersal is a Key Component of Metapopulation Concept

Metapopulations (a regional grouping of spatially semi-isolated habitat patches connected by dispersal, Levins 1969) rely on dispersal for persistence. Levins model assumes that there are an infinite number of identical (e.g., carrying capacity) habitat patches that are surrounded by a completely inhospitable matrix (e.g., only 2 habitat types), all patches have the same probability of extinction and recolonization, and patch occupancy is the focus (Hanski and Ovaskainen 2003). Because of these assumptions, it has been debated if the classic metapopulation concept (e.g., the Levins model) exists in the natural world. Common criticisms are that empirical examples of classic metapopulations only occur at the margin of a species' distribution, with small local population sizes, or when the population is in decline (Baguette 2004). Empirical examples of a classic metapopulation are rare but span a variety of taxa and the ideal dispersal behavior is often species and context-specific (Harrison and Taylor 1997, Hanksi 1999, Baguette 2004, Olivieri et al. 2015). Although the classic metapopulation paradigm may be rare in nature, the concept still has use for conservation and management of some species (Ale and Howe 2010, Olivieri et al. 2015), and thus continues to be a useful representation for species in spatially fragmented habitats.

Many models have expanded the classic concept, but the conclusions from these theoretical metapopulation models are variable and depend on assumptions about the spatial location of patches within the metapopulation and the description of dispersal. The most common manner of representing dispersal in models is to use a dispersal kernel – a statistical probability density function that defines the distribution of post-dispersal locations relative to a source point (i.e., the distribution of distances dispersed for individuals of a species, Nathan et al. 2012). Most metapopulation models do not track individual behavior or interactions between the individual and the environment (Nathan et al. 2012, Travis et al. 2012): dispersal kernels describe the average dispersal process of all individuals in all environments (Nathan et al. 2012). Kernels can represent some of the complexity of the dispersal process by incorporating the many biological mechanisms that underlie it (emigration, transience, settlement, and survival at each of these steps), however, because those multiple mechanisms are averaged across individuals, one key aspect of the dispersal process is masked: the potential impact of individual variation (Nathan et al. 2012).

When variation from two or more sub-groups is averaged such as long-distance dispersers, short-distance dispersers, and non-dispersers – the combined population trend can hide important differences between the groups, and this unobserved heterogeneity can lead to false conclusions about the dynamics of the population (Vaupel & Yashin 1985, Plard et al. 2019). The dispersal kernel only describes variation for the entire population but does not describe among- and within-individual variation (Morales et al. 2010). Commonly, dispersal kernels are estimated separately by obvious phenotypic differences among individuals, such as sex (Miller and Inouye 2013) or dispersal polymorphism (winged vs non-winged individuals; Zera & Denno 1997, Roff & Fairbairn 2007), but even within these groups, phenotypic variation among individuals can be ecologically significant (Bolnick et al. 2011). Therefore, the use of dispersal kernels, a major component of the metapopulation concept, does not provide a detailed description of intra- and inter-individual variation in behavior as a response to local patch characteristics and the characteristics of other individuals within the local patch. After integrating across all patches, intra- and inter-individual behavior may have a large impact on the global characteristics of the metapopulation.

Many theoretical models have been created to track individual fates (e.g. cellular automata, interacting particle systems, or individual-based; see references and examples in Uchmański 2016). Individual-based models (hereafter, IBMs) better represent individual variation in dispersal because these models simulate each individual within the population, but many IBMs assume that dispersing individuals are randomly selected to leave the local population and randomly move through space (Uchmański 2016). However, we know that individuals are not making the decisions for when to disperse or how to move through the landscape randomly (Matthysen 2012, Cantor et al. 2020). A model designed to explicitly compare the dynamics of a metapopulation when individuals are randomly chosen to leave the local populations and when individuals are not chosen randomly, found that randomly selecting individuals to disperse produces metapopulations with shorter persistence than metapopulations where dispersing individuals were non-randomly selected (such as when lighter individuals that could not obtain resources due to intraspecific competition dispersed; Uchmański 2016).

By allowing individuals to make decisions during dispersal, IBMs can produce different predictions about metapopulation persistence and resilience compared to other metapopulation models. For example, a population of marmot (*Marmota marmota*) in southern Germany with 13 years of data on dispersal was used to parameterize and compare the predicted population viability of 2 analytical models and an IBM that was spatially explicit. The behavior incorporated into the IBM was kept simple (e.g., dispersal decision based on a function that maximizes fitness of the individual) to allow comparison with the population level models (Stephens et al. 2002). The more complex IBM was the only model to detect Allee effects from the marmot population, and further investigation of the IBM allowed the authors to determine three possible mechanisms producing this result (Stephens et al. 2002). The benefit of the more complex IBM model is that it can allow researchers to explore the possible mechanisms behind an observed pattern. Although a general, well-constructed IBM that can be applied to multiple situations is difficult to accomplish (Grimm & Railsback 2005), the effort is well worth it as this type of model allows us to observe emergent properties of individual behaviors that can differ from the observed outcomes of population models that average individual behavior.

Despite the power of IBMs to explore in depth the impact of among-individual variation in dispersal at all three stages, many metapopulation models focus on the first stage of dispersal (emigration, Travis et al. 2012). Travis et al. (2012) created an IBM to explore how explicitly modeling emigration, transience, and the cost associated with these two stages of dispersal will evolve and, ultimately, alter the expected outcomes of metapopulation dynamics. Not unexpectedly, the results show that the trade-offs at one stage of dispersal can impact another stage, which gets even more complex when environmental variation is added (Travis et al. 2012). Even this major effort had to exclude the last stage of dispersal (immigration) to keep the model tractable. This was an excellent example of incorporating multiple stages of dispersal into a model, but Travis et al. (2012) focus on identifying the evolutionary stable dispersal behavior and not the consequences of ignoring among-individual dispersal per se. A useful step to advance our understanding of the impact of among-individual variation in dispersal on metapopulation dynamics, would be to compare the results of two models: one that uses the standard dispersal kernel versus one that allows individuals to have a unique dispersal kernel.

Current modelling approaches can be extended to incorporate variation in dispersal kernels and allow exploration of the effect on metapopulations. For example, the individual-based model created by Shaw et al. (2014) can be extended using an IBM-like approach. Shaw et al.'s (2014) model created a circular world with randomly arranged habitat patches, where size and number of patches was held constant. Following classic metapopulation theory, subpopulations within patches go extinct with a specified probability. The simulated world was populated with organisms that disperse, reproduce, and die in non-overlapping generations. In Shaw et al.'s model, individuals dispersed a distance d – drawn from a dispersal kernel with mean $\hat{d}$ – in a random direction. They used a simplifying assumption that all individuals had the same $\hat{d}$ (which means that dispersal distance – randomly drawn from that distribution – can vary among individuals but at the population level there is no variation in dispersal). A possible extension would be to have $\hat{d}$ vary among individuals, with $\hat{d}$ inherited as the average of both parents' $\hat{d}$ (which introduces variation not only at the individual level, but also at the population level). To assessing how individuality in dispersal affects population structure, we would repeat the simulation using a constant dispersal variable that does not evolve (all individuals have the same $\hat{d}$). By comparing two models that allow dispersal to vary among individuals and those that do not, we can assess the importance of individual and population level variation in dispersal kernels on metapopulation outcomes.

Theoretical models of metapopulations clearly show that long-term outcomes of the metapopulation change based on how dispersal is modelled – random vs non-random emigration or varying for each stage of dispersal. From observational and empirical work, among-individual variation in dispersal is well documented (Matthysen 2012, Tigreros and Davidowitz 2019, Renault 2020). Therefore, it is crucial that metapopulation theory includes among-individual variation in dispersal.

2.4 Dispersal Syndromes

Dispersers carry along any traits genetically correlated with dispersal (e.g., a dispersal syndrome – a suite of life history traits correlated with dispersal). There are a range of traits that have been found to covary with dispersal (Ronce and Clobert 2012). Morphological traits are often very obviously correlated with dispersal, such as winged vs non-winged insects (Roff and Fairbairn 2007, Zera et al. 2007) or cell shape of ciliates (Schtickzelle et al. 2009, Jacob et al. 2019), but sometimes morphological differences can be subtle, such as body fat (O'Rainin et al. 1996) or body size (Woodroffe et al. 1995). Physiological traits, such as hormones, also covary with dispersal. In some cases, the variation in hormones causes variation in morphology (e.g., juvenile hormone causes crickets to develop into winged or non-winged morph, Roff and Fairbairn 2007, Zera et al. 2007), but in other cases, the variation in a physiological trait does not lead to morphological differences but still covary with dispersal behavior. One example is Glanville fritillary butterfly, where there are no distinct morphological differences as part of the dispersal syndrome, but dispersing butterflies have a higher flight metabolic rate and faster enzyme catalytic rate; Marden et al. 2013, Niitepold & Saastamoinen 2017, Pekny et al. 2018, Saastamoinen et al. 2018). Additionally, there is extensive evidence that life-history traits (e.g., lifespan, fecundity, survival) covary with dispersal across many taxa, but so far there is no clear association between dispersal and these traits (Ronce and Clobert 2012). Lastly, behavior can also covary with dispersal in a syndrome. Currently, the most studied behaviors are aggression/sociality, mate calling, and risk-taking behavior (e.g., boldness, exploration, or neophobia; Duckworth 2006, Overveld et al. 2014, Matsumura & Miyatake 2015, Michelangeli et al. 2016, Nicolaus et al. 2022).

Many studies compare traits of dispersing and non-dispersing individuals (Table A1), but this approach describes a species level dispersal syndrome, disregarding any variation among individuals. Research is beginning to document how dispersal syndromes vary among individuals within a species using more of a reaction norm approach. Dispersal is a trait controlled by many developmental and behavioral pathways that can lead to variation among individuals in dispersal ability (Dufty et al. 2002). For example, dispersing individuals experience a physiological change, such as an increase in juvenile hormone in insects or androgens in mammals prior to dispersing (Dufty & Belthoff 2001, Ims & Hjermann 2001). Using the reaction norm approach will allow a better characterization of traits within a dispersal syndrome along an environmental gradient and provide insight into the relative importance of genotype and environment on individual dispersal syndromes (Clobert et al. 2009).

Here, we review the evidence that dispersal syndromes vary among individuals of a species. We highlight how considering variables other than dispersal status (e.g., disperser or resident) can explain the variation observed at the intraspecific level. We focus on sex, the context in which dispersal syndromes are measured, and the stages of dispersal (e.g., departure, transience, or settlement) as interesting avenues for future research into intraspecific variation in dispersal syndromes.

2.4.1 Sex Specificity

Selection on behavior and life-history traits can be different for males and females. Because of differences in natural selection on males and females, each sex can have different phenotypic optima (Lande 1980, Sherman & Westneat 1988, Fairbairn et al. 2007, Bonduriansky & Chenoweth 2009). However, the degree to which the sexes can reach their optimum and the rate at which sexes differentiate due to differing natural selection is often constrained by a cross-sex genetic correlation (e.g., the similarity of the additive effects of alleles when expressed in the different sexes) cause by shared genetic architecture between the sexes (Lande 1980, Pennell and Morrow 2013). A positive intersexual genetic correlation means that when one sex experiences strong selection and evolves, the other sex also evolves in the same direction, but there are also cases where selection on one sex produces no response in the other or an opposite response (Lande 1980, Bonduriansky & Chenoweth 2009, Wyman et al. 2013). This genetic architecture constraint means that differences in natural selection on the sexes can lead to sexual conflict (Dean and Mank 2014).

While sex-specific dispersal syndromes should be relatively easy to measure by adding an additional variable into the analyses, there is limited research that specifically addresses sex-specific dispersal syndromes (Table A1). Consequently, to date there is no clear pattern for how male and female dispersal syndromes will differ. In some cases, the sexes do not differ in their dispersal syndromes (Michelangeli et al. 2016, Steyn et al. 2016), but generally there is a difference in dispersal syndromes, but the sexes do not always have the same traits involved in the dispersal syndrome (Table A1). For example, in the red flour beetle, males that dispersed had a higher frequency of mating than males that did not dispersal, but this trait correlation was not present in females (Matsumura & Miyatake 2015). At this point, the research that considers sex-specific dispersal syndromes primarily focuses on comparing phenotypic correlations of traits for male and female dispersers with male and female non-dispersers, respectively (Table A1). An interesting avenue for future work is to identify genetic correlations that possibly underly the observed phenotypic correlations and to specifically identify how sex-specific dispersal syndromes may impact population dynamics. An excellent example of this approach was done with butterflies (*Pieris brassciae*), where Legrand et al. (2016) concluded that trait covariations in the dispersal syndrome were not due to genetic correlations and that some trait combinations were favored differently in the sexes (e.g., dispersal and lifespan correlated in females but not males).

2.4.2 Context-dependence

Generally, dispersal syndromes are measured in one context (e.g., one environment), and it is assumed that the observed trait correlations are consistent across time and context. However, one or more traits within the dispersal syndromes may be plastic in response to the environment (e.g., predators absent vs present, Cote et al. 2022 or food resources/nutrients high vs low, Mishra et al. 2018; Cote et al. 2022). If a trait within a dispersal syndrome is plastic, this may shift the correlation structure (Scheiner et al. 1991) and change our ability to detect that correlation. A detailed experiment comparing dispersal syndromes across species (n = 15 species including protists, arthropods, mollusks, and vertebrates) found evidence for context-dependence of dispersal syndromes. Across all species tested, when the environment contained limited resources or predators, the individuals that dispersed had a larger body size and locomotory morphology traits (length or width of locomotory apparatus proportional to body size) than individuals that did not disperse, but the differences between dispersers and non-dispersers were reduced in environments with abundant resources or no predators (Cote et al. 2022). The exact cause of the variation between dispersers and residents is not clear at this point but may be due to plasticity induced by local conditions (Cote et al. 2022). If plasticity is the mechanism behind context-dependent dispersal syndromes, then one or more traits that facilitate movement or survival during dispersal should be plastic (e.g., cell shape of ciliates, Junker et al. 2021).

Generating specific hypotheses for context-dependent dispersal may be difficult because the correlation between traits likely depends on multiple cues and the costs of dispersal. For example, body size is frequently correlated with dispersal, but the environmental and social context changes the predicted relationship between the traits for dispersers and residents. If the environment is harsh (e.g., low food resources, high predation, Cote et al. 2022), then only individuals with large body size, indicating high energy reserves or mobility, may be dispersing away from the poor environment to find better habitat (Jenkins et al. 2007). Alternatively, in a harsh environment, the large individuals may be more competitive, thus excluding and forcing smaller individuals to disperse (Baines et al. 2019).

2.4.3 Stages of dispersal

2.4.3.1 Emigration

Emigration, the decision to leave one area, is the most extensively studied stage of dispersal. Because individuals are relatively easy to locate and track before emigration (e.g., capture, mark, and observe juveniles from the nest), there is extensive research on the factors that cause individuals to disperse (reviewed in Clobert et al. 2001, Clobert et al. 2012). The most extensive literature on dispersal syndromes at the emigration stage is focused on insects with distinct dispersal morphs. There is an increase in juvenile hormone and ecdysteroid, two hormones that impact multiple developmental pathways, in disperser morphs that does not occur in non-dispersal morphs (Roff and Fairbairn 2007, Zera et al. 2007). Because of the increase in juvenile hormone, the dispersal morphs develop a different body shape, increased wing muscles, decreased ovary size (females), shorter mate call duration (males), and a crepuscular daily hormone cycle that facilitate their leaving the natal site (Roff and Fairbairn 2007, Zera et al. 2007). In wing polymorphic insects, the differences occur during development and remain throughout the lifetime of the individual. However, in other species, the dispersing individuals do not differentiate from non-dispersing individuals until shortly before dispersal (e.g., gonadal hormone production increasing before emigration, Holekamp et al. 1984).

Interestingly, there is a lot of evidence that maternal effects determine if an individual will disperse or not. Females can control the emigration of their offspring by changing the hormones present during development, which will make some offspring develop with traits that facilitate dispersal (e.g., great tits adjust androgen levels in yolk in response to parasite density, Tschirren et al. 2007). Therefore, dispersal may not necessarily be an active choice of an individual, but a behavior that is determined by its mother. The decision to disperse can be complex and juveniles may be too inexperienced to make an optimal decision (DeWitt et al. 1998) and having an experienced adult individual adjust the offspring behavior can increase fitness for the parent and offspring (Meylan et al. 2012).

2.4.3.2 Transience

The movements of organisms from one location to another is a difficult behavior to study. There are many studies that document the net distance an individual traveled, but there is very little known about the specific movements and behaviors during transience. While difficult, observing the transience stage could reveal some subtle characteristics that may allow some dispersers to survive this stage. One study that has managed to track individuals found that female butterflies travel along valleys instead of over hills, whereas males showed no movement preference (Plazio et al. 2020). Only estimating the net distance obscures variation (e.g., butterflies only moving through valleys, Plazio et al. 2020). One attempt to get around this limitation is the use of circuit theory to estimate the likely path that an organism dispersed, but this method requires the researcher to assign permeability measures to each type of landscape (e.g., to estimate red squirrel dispersal paths, Merrick and Koprowski 2017 simulated 3 different permeability levels using known immigration and emigration data). However, the human perspective on the landscape may not accurately represent the organism's perspective of the landscape and thus the circuit method is useful, but not ideal.

Although challenging, it will be beneficial to invest time and effort into tracking individuals during transience. It is likely that the individuals most likely to disperse (e.g., highly active) may also be at higher risk for predation during transience because increased activity may increase the probability of encountering a predator (Matsumura & Miyatake 2015). However, the other traits that are correlated with dispersal can also affect an individuals during transience. As an example, if the individuals that disperse have a larger body size than those that do not disperse, then although these dispersers may potentially encounter more predators, having a large body size may limit the predators that are a threat to you.

2.4.3.3 Immigration

Although more well studied than the transience stage, there is still a lack of research at the immigration stage. Most of the research that describes how the dispersing individuals differ from the non-dispersing individuals simply compares traits of the individuals that successfully navigated all three stages of dispersal to settle in a new subpopulation against the individuals that did not disperse (e.g., Cote et al. 2022). For example, in bluebirds (*Sialia mexicana*), the males that have completed dispersal and established a territory are more aggressive than males that do not disperse from the natal area (Duckworth 2008). This approach provides some useful insights, but it masks variation across all stages of dispersal. One study that attempted to estimate trait correlations for two dispersal behaviors (distance travelled and exploratory behavior) at each stage of dispersal by tracking juveniles for 1 year after fledging, found that the correlation between traits was highest at the start of first year after fledging (equivalent to the emigration phrase), and decreased as the year progressed (equivalent to the later phases of dispersal, van Overveld et al. 2014).

2.5 Impact of dispersal syndromes on metapopulation dynamics

I have discussed how dispersal is a key component of metapopulation dynamics and that dispersal is often correlated with a suite of other traits, but my goal is to identify how dispersal syndromes (and not simply dispersal alone) could have large impacts on metapopulation dynamics. When an individual disperses, any associated traits (e.g., dispersal syndromes) will interact with the local environment at the settled site and have impacts on the individual's fitness as well as the local population, and ultimately the metapopulation.

In a simple conceptual model of a metapopulation (Figure 1A), let us assume that there is a finite quantity of resources available in each patch and when the resources are depleted, the subpopulation goes extinct (e.g., pests that rely on human stores of dried goods as habitat patches). If we use the same simple assumption of most theoretical metapopulation models (e.g., all individuals have a chance to disperse and there is no variation in dispersal ability), then some individuals from all patches will disperse and possibly survive dispersal to recolonize an empty patch or join an established subpopulation. This will lead to a landscape with varying densities in the patches and the metapopulation dynamics rely on the subpopulation environments only.

By adding variation among individuals in dispersal into our conceptual model, the complexity of the metapopulation emerges and no longer relies entirely on new habitat patches emerging for the persistence of the metapopulation. In this scenario, when conspecific density reaches a threshold, the dispersal phenotype (e.g., a winged insect morph) develops in the next generation and leaves the area before resources become fully depleted (Figure 1B). Additionally, that threshold should vary with the quantity of resources available (more resources available means a higher threshold before disperser phenotypes are produced).

As a final layer of complexity, let’s consider how a trait correlated with dispersal will alter our conceptual metapopulation. An excellent empirical example of this is the Western bluebird (*Sialia mexicana*). Bluebird individuals that disperse are more aggressive – the aggressive individuals are capable of securing territory in areas with few conspecifics because these aggressive individuals that compete with heterospecifics for limited nest boxes (Duckworth 2006, Duckworth and Kruuk 2008). Aggression is important for bluebirds because they are secondary cavity nesters (e.g., they use cavities that are created by natural events or other organisms and thus not capable of creating more nest boxes in a high-density area) specializing in post-fire patches of forest (Duckworth and Aguillon 2015). Therefore, there can be high competition for nesting sites. However, aggressive males are poor parents, and fledge fewer offspring than non-aggressive males (Duckworth 2008). Because of this fitness difference, over time, the aggressive phenotypes in an area decrease and non-aggressive phenotypes comprise most of the subpopulation (Duckworth and Badyaev 2007). And when conspecific density becomes high, females adjust the order in which they lay male eggs – early laid male eggs become aggressive males and late ones become non-aggressive males (Duckworth 2009). Therefore, any empty patches in the metapopulation – an area of forest that was recently opened into meadowland (either human created as in the experiment, Duckworth 2008, or due to natural causes such as fire) – become recolonized by aggressive birds. Bluebirds are one the few empirical examples that explicitly link dispersal syndromes to larger scale metapopulation dynamics (Figure 1C).

From a theoretical perspective, I am not aware of any metapopulation models that explicitly incorporate dispersal syndromes. As an example of how to investigate the ecological and evolutionary consequences of dispersal syndromes on metapopulations, let’s consider again the theoretical model that I described earlier: individuals disperse a distance d – drawn from a dispersal kernel with mean $\hat{d}$ – in a random direction and I would allow $\hat{d}$ to vary among individuals, with $\hat{d}$ inherited as the average of both parents’ $\hat{d}$ (which introduces variation not only at the individual level, but also at the population level). To add dispersal syndromes into this model, I could alter the direction and strength

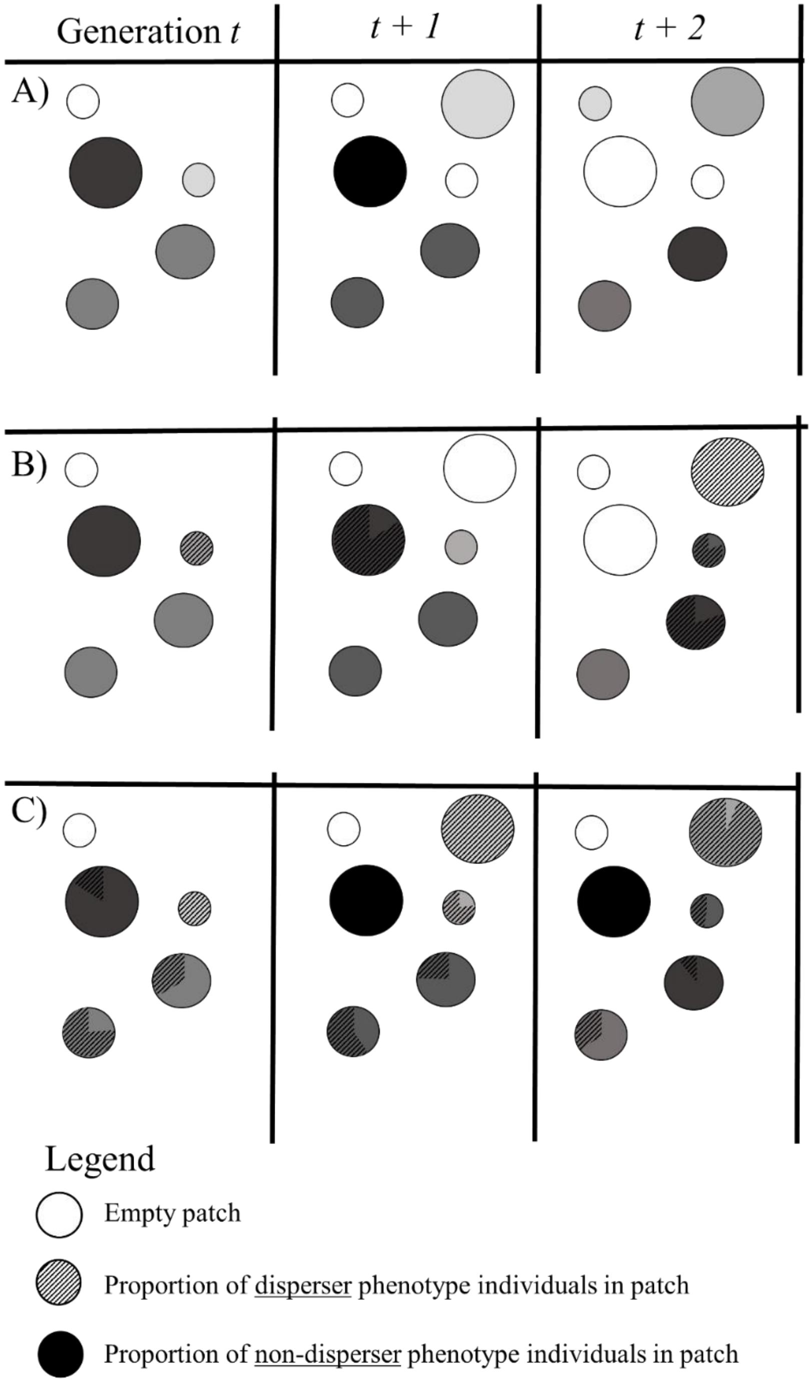

Figure 2.1. Conceptual metapopulation model with increasing levels of complexity at the individual level: no variation in dispersal behavior among individuals (A), a simple dichotomy of dispersal ability (e.g., winged vs non-winged individuals), and a dispersal syndrome where dispersal is correlated with aggression (C). Patch shading represents conspecific density within a patch from low (light grey) to high (black). Metapopulation landscapes are dynamic and new habitat patches may arise (e.g., for a stored product pests, harvest placed into a silo or for birds that nest in open fields, a tree falls opening a gap in the forest) and is represented by a new subpopulation appearing in generation *t*+1.

of covariation between dispersal and other dispersal syndrome traits (e.g., a reproduction variable), by creating a correlation matrix (e.g., a positive correlation between dispersal and fecundity – Duckworth & Aguillon 2015) as an additional variable for the model.

2.6 Conclusion

It is well established both empirically and theoretically that dispersal of individuals among patches is the key to maintaining a metapopulation. However, because of the complex nature of dispersal, we know relatively little about the last two stages of dispersal (transience and immigration). And we know even less about how any traits correlated with dispersal affect each stage of dispersal and thus, metapopulation dynamics. In this review, I show that including among-individual variation is crucial for understanding large scale metapopulation dynamics. The individuals that disperse are different from those that do not, and that variation can impact the metapopulation because dispersers bring along other traits correlated with dispersal that will interact with the environment, at all stages of dispersal.

There are some clear next steps to improve our empirical knowledge of dispersal syndromes and how they impact dispersal, and to incorporate dispersal syndromes into theoretical metapopulation models. Although logistically difficult, empirical work that measures dispersal syndromes across all three stages of dispersal will be an important step in better understanding dispersal syndromes across time and contexts. It is not enough to know the dispersal syndromes of those that successfully complete dispersal, but to accurately incorporate dispersal syndromes into models, we need to know how dispersal syndromes facilitate (or not) all three stages of dispersal. Additionally, theoretical models need to account for individual variation in dispersal by including at least one correlation between dispersal and another trait. I provided an example of how modifying an existing model could begin offering insights into the importance of dispersal syndromes on metapopulation dynamics but given the diverse array of traits that comprise a dispersal syndrome, there are many possible modelling approaches.

Increasing our understanding of the impact of individual variation, even subtle differences, on subpopulation and, ultimately, metapopulation dynamics will bridge scales of biology and link subdisciplines together. Linking across scales of biology will be a valuable direction for research to better understand how increasing change to our natural world may affect populations that have to live in increasingly heterogeneous and fragmented landscapes.

CHAPTER 3: ARTIFICIAL SELECTION REVEALS A DISPERSAL SYNDROME WITH LIMITED CONTEXT DEPENDENCY IN A SEED BEETLE

3.1 Abstract

Dispersal can be correlated with other non-dispersal traits thereby forming a dispersal syndrome. Dispersal syndromes are often measured in one context and assumed to be consistent across contexts. If dispersal syndromes are context-dependent, the direction and magnitude of correlations across a range of contexts may influence how much dispersal syndromes affect population dynamics. Using a seed beetle system, we artificially selected on long and short distance dispersal then assessed among-line phenotypic correlations of multiple life-history traits with dispersal behavior to quantify a dispersal syndrome in multiple environments (conspecifics absent and conspecifics at low or high density). Beetles from the dispersal-selected lines dispersed longer distances and had a higher dispersal tendency than beetles from non-dispersal-selected lines. Artificial selection on dispersal distance influenced some beetle life history traits demonstrating a dispersal syndrome. Beetles from dispersal-selected lines exhibited larger body sizes and shorter egg lengths compared to non-dispersal-selected lines selected. In an environment with high conspecific density, dispersal was negatively correlated with short-term fecundity and larval survivorship, but not in any other environment. There was no evidence that other life-history traits were correlated with dispersal. Our results indicate that seed beetles do exhibit a dispersal syndrome, but the lack of response to the environment for multiple traits suggests that context-dependent dispersal syndromes may be subtle. Our context-dependent approach to measuring dispersal provides a stronger understanding of the proximate causes of dispersal syndromes and the potential of dispersal syndromes to affect the ecology and evolution of populations in fragmented landscapes.

3.2 Introduction

Dispersal syndromes – a correlated suite of behavioral, morphological, and life-history traits associated with dispersal (Roff and Fairbairn 2007, Ronce & Clobert 2012) – could produce eco-evolutionary feedbacks that enhance or limit population persistence. Individuals disperse across the landscape and interact with the local environment. The outcomes of those individual interactions depend on the traits correlated with dispersal (e.g., increased fecundity if dispersing individuals enter an environment with few competitors; Spiegel et al. 2017, Plard et al. 2019). Over time, these individual interactions can alter genetics and demography of subpopulations, which in turn feeds back on selection (or not) for dispersal syndromes (Starrfelt & Kokko 2012, Duckworth & Aguillon 2015). This eco-evolutionary feedback has been demonstrated at the expanding range front of western bluebirds (*Silia mexicana*; Duckworth 2008). Male bluebirds that disperse are the first to recolonize a new habitat patch and have dispersal syndromes that include increased aggression and high fecundity (Duckworth 2008). The aggression and fecundity traits that are part of the dispersal syndrome of male bluebirds interact with the environment leading to a change in the phenotypes present within a patch over time to produce a gradient of dispersal syndrome phenotypes from the range edge to core (Duckworth 2006, Duckworth & Aguillon 2015). Thus, for populations in fragmented landscapes, the nature of dispersal syndromes may be an important piece in establishing links between variation within a sub-population and the dynamics of multiple sub-populations within the broader population.

Generally, dispersal syndromes are measured in one context (e.g., one environment), and it is assumed that dispersal syndromes are consistent across time and context. In this case, dispersal syndromes can be considered canalized – the correlation between traits persists across variation in the environment or over time (e.g., animal 1 always moves longer distances and has higher fecundity than animal 2 regardless of the environment). This would require that there is an additive genetic effect on all components of the syndrome. However, dispersal syndromes may be plastic which allows an individual genotype to adjust to the environment (Murren et al. 2001, Ghalambor et al. 2010). If dispersal syndromes are plastic, then measuring syndromes in multiple environments would reveal the genotype-by-environment effect on genetic correlations underlying traits within a dispersal syndrome (Santana et al. 2017). If context-dependent dispersal syndromes exist in a population, then a better understanding of the direction and magnitude of correlations across a range of contexts is important to evaluate the implications of dispersal syndromes on population dynamics.

Here, we quantify dispersal syndromes in a model organism, the seed beetle (*Callosobruchus maculatus*) in three environments (conspecifics absent, low density and high density) to evaluate the context-dependence of female dispersal syndromes. We focus on females because females are the founders of new populations in this species: female beetles mate, then disperse to find hosts on which to lay their eggs, ultimately having a large impact on population growth and spread (Miller & Inouye 2013). To quantify dispersal syndromes of female seed beetles, we artificially select on dispersal tendency. We created an environment where females that are sensitive to competition would disperse long distances to locate resources lacking competitors. We then evaluated evolved responses of multiple life-history traits (correlated responses to selection on dispersal) in three environments. Our goals were to:

1) Assess if artificial selection alters the dispersal behavior of beetles. After selection, we measured the trait we attempted to select – dispersal distance – and two additional dispersal traits that may co-evolve during selection – activity and dispersal tendency. We hypothesized that female beetles selected for dispersal would have greater dispersal ability in three traits. We predicted that individuals from the dispersal selected lines would disperse longer distances, have a greater activity level, and a higher dispersal tendency than beetles from non-dispersal selection lines.

2) We quantified correlated responses in life-history traits to test for genetic correlations among traits and thus identify dispersal syndromes in seed beetles. We measured the genetic correlations between dispersal and multiple life-history traits: fecundity, egg size, egg distribution, lifespan, and development time to adulthood (reviewed in Ronce & Clobert 2012, Bonte & Saastamoinen 2012, and Stevens et al. 2013). Given that there are several reasonable expectations for the direction and magnitude of correlations between dispersal and our life-history traits of interest (Legrand et al. 2016, Renault 2020), we made no predictions about the specific direction or magnitude of phenotypic correlations in the dispersal syndrome.

3) We evaluated the context-dependence of dispersal syndromes by measuring correlated responses life history traits in three environmental conditions varying in competition for seed resources. If dispersal syndromes are context-dependent, we

expected that the direction (e.g., positive or negative) or magnitude of phenotypic correlations to vary among environments.

3.3 Methods

3.3.1 Study Organism

We studied the cowpea seed beetle (hereafter seed beetle; *Callosobruchus maculatus*, Coleoptera: Chrysomelidae, Bruchinae), a cosmopolitan agricultural pest that damages stored legume seeds (Tuda et al. 2006). Seed beetles spend most of their lifecycle inside dried legume seeds, with a generation lasting approximately 35 days (when maintained at 16:8 light:dark, 25.5 ºC). Adults do not need to feed and can rely on energetic reserves obtained during the larval portion of the lifecycle (Messina 1993, Fox et al. 2011). The seed beetles in our experiment were collected from two locations: Tirunelveli, India in 1979 from infested mung bean pods (*Vigna radiata;* Mitchell 1991, Fox et al. 2007), and the Maiduguri area of Borno State, Nigeria in 2010 (Berger et al. 2016) from infested pods of black-eyed peas (*Vigna unguiculata*). In the lab, the populations have been maintained at large population sizes (> 1000 adults per generation) under standard growth chamber conditions (16:8 light:dark, 25.5 ºC) on mung beans (India population) and black-eyed peas (Nigeria population, Fox et al. 2007).

3.3.2 Study Populations

The well-studied Indian and Nigerian lines show consistent responses to the presence of conspecifics that we leveraged in our experiment to invoke a dispersal response based on a competitive environment. The Indian line is sensitive to conspecific density and females of this line will leave a high-density area to lay eggs in a low-density location, whereas the Nigerian line is much less sensitive to density and will lay eggs on seeds that bear conspecific eggs (Messina 1991, Messina et al. 1991, Fox et al. 2004).

Prior to beginning the experiment, we crossed beetles from the Nigerian and Indian lines to create a control line with genetic mixing in case there was any fixation of alleles in our stock populations. We isolated beans with a single egg from Nigerian and Indian colonies into 15 mm diameter Falcon petri dishes. Approximately 24 h after the adults emerged, we mated virgin females to virgin males from the opposite line (total 55 mated pairs) to create an F1 hybrid. The next generation, we mated virgin females to virgin males from a different hybrid family (avoided sibling inbreeding). We continued this procedure for 5 generations before the start of the artificial selection experiment, which should have disrupted any existing genetic linkages.

3.3.3 Experimental Dispersal Arrays

To quantify dispersal, we created dispersal arrays to control the environment experienced by female seed beetles. A dispersal array consisted of multiple petri dishes (60 mm diameter Falcon) connected by silicon tubing (3 cm long) in a line (Figure 3.1A). Each petri dish represented a different habitat patch of suitable environment in a fragmented landscape. Each petri dish contained 20 mung beans, which were all either pristine or had one previously laid seed beetle egg on each bean. Patches that contained mung beans with previously laid eggs simulated an environment with conspecific competition. Female seed beetles can detect eggs on the surface of beans (Messina & Renwick 1985, Messina et al. 1987) and the presence of conspecific eggs influences their egg-laying decisions (Messina et al. 1991, Guedes & Yack 2016). In patches that contained pristine mung beans, this simulated an environment without competition, which is the ideal environment for females to lay their eggs.

To obtain beans with a single previously laid egg, we placed ~100 adult beetles into a Mason jar with 300 mL of mung beans for 4-6 days under standard growth chamber conditions. We removed adults, placed beans in the incubator for 10 days to allow all laid eggs to hatch, then froze beans to kill any larva that had developed within the beans. The beans were sorted, and we kept only beans that contained a single egg laid on the surface.

Arrays initially consisted of 7 petri dishes; the first 3 dishes contained beans with previously laid eggs and the remaining 4 dishes contained beans without previously laid eggs (Figure 3.1A & B). Throughout the experiment, the non-dispersal lines (see *Selection Lines* below), always had arrays where the first 3 dishes in the array contained beans with previously laid eggs. However, during the selection experiment, we increased the number of dishes with eggs already present on the beans whenever 30% or more of the females from the dispersal lines laid at least one egg in the first patch without eggs present. We increased the length of the array as needed to keep a minimum of 3 dishes that contained beans without eggs present (number of dishes with eggs present/total number of dishes in array; generation 1: 3/7, generation 2: 4/7, generation 3: 5/9, generation 4: 6/9, generation 5: 7/10, generation 6 & 8: 8/12).

To evaluate dispersal ability with the experimental arrays, we mated a virgin female to a non-sibling virgin male from the same line and placed the female singly into the first dish of the array. We allowed females 24 h to disperse and lay eggs, then removed females and counted the number of eggs laid in each patch of the array. We quantified dispersal distance as the farthest dish in the array where the female laid at least 1 one egg.

3.3.4 Selection Experiment

3.3.4.1 Control Lines

The unselected control line (e.g., the hybrid population, Table B2) was maintained in a colony in standard lab conditions on mung beans during the selection experiment. This line provided a baseline against which to compare the selected lines. We measured dispersal ability using our experimental dispersal arrays at the start (generation 0) and end (generation 9) of the selection experiment. In total, we measured dispersal for 182 beetles (generation 0: 121, generation 9: 61).

3.3.4.2 Selection Lines

To setup our selection lines (generation 0), we chose 121 random female emergers from our control line, mated them to a non-sibling male, and placed females alone in the dispersal array for 24 hr. Any female that laid eggs only in the first three dishes was selected as a founder of a non-dispersal selection line (e.g., down-selection line), and any female that laid at least 1 egg in the 4th dish or farther was selected as a founder of a dispersal line (e.g., up-selection line). After selecting and grouping females into dispersal and non-dispersal lines, we split those females into two groups so that we had two replicate lines of each dispersal phenotype (4 lines total, Table B2). We then isolated every bean on which the selected females had laid one or more eggs in a 15 mm petri dish (one bean per dish) to raise the offspring to adulthood. We kept every egg laid by a female (mean ± SD: 11.0 ± 7.5, range: 1-33 eggs). When there were multiple offspring developing in a single bean, we used the first adult offspring to emerge from that bean for the next generation to control for differences among the first and subsequent emergers that could have affected our experiment (Messina 1991). We had a limited number of arrays that could be run each day, so although we kept every egg laid by a female, we only used some of the offspring of each female. We used whichever offspring emerged from a female at the appropriate time which was relative to the availability of an array to run the test. This method arbitrarily mixed offspring with different development times, and arbitrarily mixed the number of offspring used from each female.

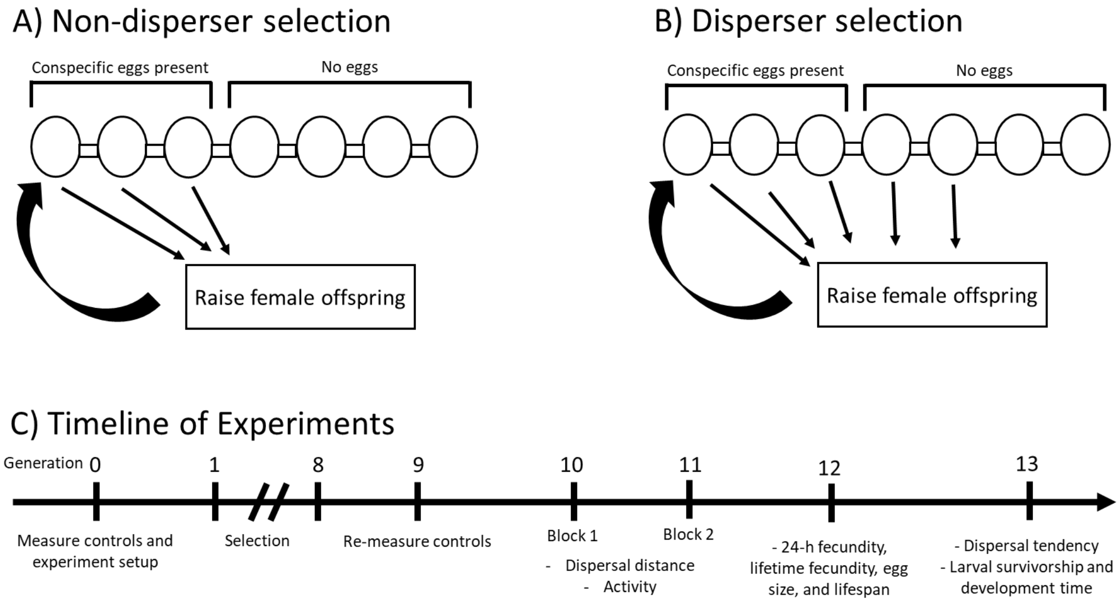

Figure 3.1. General experimental setup for selection (A & B) where dispersal arrays contained 7 petri dishes (black ovals) connected by silicon tubing (black rectangles). Dishes contained 20 mung beans per dish. Mated females were always placed alone in the first dish of the array (far left dish). (A) To select the non-dispersal line, any female that laid eggs only in the first 3 or fewer dishes of the array had her offspring contribute to the next generation. We took all eggs laid by a selected female, mated a female offspring to a non-sibling male from the same replicate, and repeated the selection procedure. (B) To select the dispersal population, females that laid at least one egg in the dishes lacking previously laid eggs (dishes 4 to 7 in generation 0) contributed offspring to the next generation. We repeated the same procedure as described in A. C) Artificial selection was imposed from generations 1 to 8, with generation 7 as a rest month where no selection occurred. Generations 10 to 13, we measured multiple life-history and behavioral traits in three environments to assess correlated responses with dispersal to determine if dispersal syndromes are context-dependent.

For each subsequent generation (generation 1-8, Figure 3.1), we performed the same procedure. Every generation, we ran 70-100 females per selection line through the arrays (Table B2). Due to variation in the number of eggs laid by each female (mean ± SD across all generations of selection: 23.7 ± 10.4, range: 1-51 eggs) and larval survival, we were not able to put the same number of offspring from each female through the arrays (mean ± SD: 4.0 ± 3.1, range: 0-19 female offspring). Therefore, we have calculated effective line size each generation (Table B2). Finally, due to time limitations, we did not impose selection on females in generation 7. To continue lines without selection during generation 7, we randomly mated a 24 h old virgin female to a 24 h old non-sibling virgin male of the same replicate line. We resumed the selection protocol described above for generation 8.

After generation 8, all selection lines and the control line were maintained without imposing selection under a standardized larval density (one beetle per seed) for 2 generations before any additional experiments were conducted. By rearing all lines in a common density, we prevented any confounding issues with larval density (e.g., high larval density can decrease mass and fecundity of developing beetles, Fox 1994).

3.3.5 Assessing response to selection for dispersal

To determine if dispersal behavior varied among populations after selection, we compared dispersal behavior of females from the dispersal and non-dispersal lines after selection was relaxed and larval density standardized (generations 10 and 11). Females were placed singly into 9-dish dispersal arrays (one of three treatments: No conspecifics – all 9 dishes contained mung beans with no previously laid eggs present; Low conspecific density - the first 3 dishes in the array containing beans with previously laid eggs and the remaining 6 dishes containing beans without previously laid eggs; and High conspecific density – every dish of the array contained beans with previously laid eggs). Due to resource limitations, we measured dispersal over 2 generations (hereafter, blocks). To maximize the genetic variation among the individuals tested, we did not put any females through the arrays in block 2 that were related (within 1 generation) to females used in block 1. Additionally, we excluded any female that laid 0 eggs because without laying eggs, we could not assess how far in the dispersal array the female travelled. In total, we collected data for 751 females in generations 10 & 11 (n = 22-29 per block, which was n = 45-54 per line, summary of sample sizes by treatment, block, and selection line provided in Table B1).

We also measured the correlated response to selection for two other dispersal traits that we may have indirectly selected (activity and dispersal tendency). To evaluate the general activity levels of beetles (in generations 10 & 11), we placed virgin females (24-48 h post emergence) alone into a sanitized (90% isopropyl alcohol) 60 mm diameter petri dish without any beans and recorded them for 10 minutes using a handheld camera (Besteker HD 1080P 24 MP 16X Digital Zoom Video Camcorder) mounted on a tripod (Amazon Basics). The camera was maintained at a standard distance of 32 cm from the beetles. We repeated this behavioral test another 2 times (~48 h between every test). We used ToxTrac (Rodriguez et al. 2018) to analyze videos and obtain detailed trajectories for every individual (all tracking settings kept as default except maximum displacement per frame = 75 pixels). Then we calculated the total distance traveled (mm). We excluded the first 0.5 s of tracking to avoid any errors due to irregular tracking as ToxTrac located an individual. To obtain a conversion rate of pixels into mm, we used ImageJ (Rasband 2018) to measure the number of pixels in the 60mm diameter of 30 randomly selected petri dishes in the videos (mean ± SD, 0.15 ± 0.002 mm/pixel). Some data points were lost due to video files getting corrupted, labeling issues, or detection complications (Trial 1 n = 246 usable videos, Trial 2 n = 248, Trial 3 n = 244). We measured beetles over 2 generations (e.g., blocks) and did not test any females in block 2 that were related (within 1 generation) to females tested in block 1 (n = 22-30 per block, which is n = 45-54 per line, summary of sample sizes by treatment, block, and selection line provided in Table B1).

To evaluate dispersal tendency, defined as the probability of leaving the starting patch of a dispersal array, we placed virgin females (Non-dispersal replicate 1: n = 40; Non-dispersal replicate 2: n = 38; Dispersal replicate 1: n = 39; Dispersal replicate 2: n = 39; Control: n = 41) alone into a two-patch dispersal array (two Falcon 60mm diameter petri dishes connected by 30 mm long silicon aquarium tubing) for 3 h without any seeds. Every 30 mins, we recorded the location of the beetles (patch 1, patch 2, or in tubing). We recorded two measures of dispersal tendency. First, we recorded the time it took for a beetle to leave the starting patch, which occurred when a beetle was in the tubing or patch 2. Second, we calculated the total number of location changes during the trial (e.g., a beetle that moved from dish 1, to tubing, back to dish 1 would have 2 total location changes). We repeated this behavioral test another 2 times per beetle (~48 h between every test).

3.3.6 Correlated responses of life-history traits to selection for dispersal

To determine if seed beetles have a dispersal syndrome, we measured multiple life-history traits, tested for differences between lines under the assumption that such differences would reflect correlated responses to selection. We measured all traits in an ideal environment where there were no conspecifics present (e.g., no previously laid eggs). We measured multiple life-history traits (body mass, short- and long-term fecundity, egg size, egg distribution, lifespan, and larval development time from hatching to adulthood) after the selection experiment (Generations 12-13).

In Generation 12, we weighed 227 virgin females (24-48 h post-emergence; Mettler Toledo AT261 Delta Range, 0.1 mg), then mated each female to a virgin male of the same age and population, then placed the female alone into a 15 mm diameter petri dish with 30 mung beans. The mung beans had no previous exposure to seed beetles and represented an ideal environment for females to lay eggs. We left females for 24 h, then placed females into a 60 mm diameter petri dish that contained mung beans (mean ± SD [min-max]; n = 96, 201.2 beans per dish ± 36.9 [96-267]; 16.3 g of beans in dish ± 1.4 [13-20]) that had no previous exposure to seed beetles. This approach provides two measures of female fecundity: 24 h after mating and lifetime. We left females in the large dishes until their deaths and recorded the number of days post-emergence that a female survived. We recorded the number of eggs laid (including both hatched and unhatched) as a measure of fecundity. We also measured the length and width of 3 haphazardly selected eggs from each 24-h fecundity dish. We used an optical micrometer on a 50x dissecting scope (± 0.01 mm precision, Wild Heerbrugg M5A Stereo-microscope) following established protocols (Fox 1993, Fox 1994, Czesak & Fox 2003). If a female laid less than 3 eggs in the 24 h dish (n = 12 females), we measured the length and width of all eggs. While counting the number of eggs laid, we quantified how evenly females distributed their eggs among the 30 beans available in the 15 mm petri dish by counting the number of eggs laid by a female on each bean. We then calculated an index of uniformity (Messina & Mitchell 1989) that is independent of the number of eggs laid by each female. The index ranges from 0 (randomly distributed eggs) to 1 (most uniform distribution possible given the number of eggs laid).

To measure larval development time (e.g., to fully develop from hatching to adulthood; Generation 13), virgin females (24 h after emerging) were mated to non-sibling males, then placed in a petri dish with 4 mung beans for 24 h. We used a scalpel to remove all but one egg from each mung bean. For each female (n = 25-32 per line, sample sizes summarized in Table B1), we had four replicate beans, and each bean was maintained individually in a petri dish in an incubator under standard lab conditions. Beans were monitored every day until adult beetles emerged. If a beetle had not emerged from a bean within 44 days after its egg was laid, we recorded the larva as dead.

3.3.7 Correlated responses to selection across environments

To determine if dispersal syndromes are context-dependent, we examined the correlated response to selection for multiple life-history traits (same traits as measured in the ideal environment to assess the presence of a dispersal syndrome) in two additional environments (low conspecific density, and high conspecific density). If the trait of interest varies between the selection lines differently in the three environments, then we have evidence for context dependence.

To measure short- and long-term fecundity, egg size, egg distribution, and lifespan, we followed the same procedure as the ideal environment: after mating, females were placed along into a small petri dish with 30 mung beans for 24 hr. Females were assigned to one of two environment treatments: low conspecific density – half the beans provided had one previously laid egg on each bean and the remaining beans had no previously laid eggs; and high conspecific density – all beans had one previously laid egg on each bean (n = 40-51 per line, summary of sample sizes environmental treatment and selection line provided in Table B1). After 24 hr in the small petri dish, females were placed in a large dish with mung beans. Regardless of the environmental treatment for the first 24 h, all females were placed into an ideal environment (mung beans with no previous exposure to other beetles) in the large dish.

To measure larval development time in three environments, we again placed mated females (n = 13-20 per line, summary of sample sizes for each environmental treatment and selection line provided in Table B1) in a dish with 4 mung beans for 24 h, then used a scalpel to remove all but the number of eggs required for the female's assigned environmental treatment (no conspecifics present – only one egg on a bean, low conspecific density – 2 eggs per bean, and high conspecific density – 3 eggs per bean).

3.3.8 Analyses

3.3.8.1 Assessing response to selection for dispersal

All analyses were conducted in R software v 4.0.3 (R Core Team 2021). To ensure that our selection experiment had led to the evolution of dispersal, we compared dispersal distance of the lines immediately after selection (generation 8), using a nested

ANOVA with line (e.g., Dispersal replicate 1) nested within treatment (e.g., Dispersal vs Non-Dispersal).

After one generation of relaxed selection with all lines maintained at low density, we compared dispersal (Generations 10 & 11) with a generalized linear model with dispersal selection treatment (n = 2 long-distance dispersal selection lines, and n = 2 non-dispersal selection lines), environmental treatment (dispersal array with no conspecifics present, low conspecific, and high conspecific density), and block as fixed effects, including an interaction between dispersal and environment treatments, and dispersal distance (farthest dish in the array where a female laid at least one egg), as a response (Conway-Maxwell Poisson distribution). To ensure that our model distribution for the response was appropriate, we fitted models with a Poisson, negative binomial, and Conway-Maxwell Poisson distribution and performed a visual inspection of diagnostic plots, compared model AIC values, and tested for overdispersion. After assessing the appropriate model distribution, we used Type 3 Wald Chi-square test ANOVA (package “car”, Fox and Weisberg 2019) and if the interaction was significant, then we performed planned contrasts (R package “emmeans”, Length 2021) to compare selection lines in each environment. For contrasts on a model with a Gaussian distribution, R uses a *t*-score, and for Poisson distributions, a *z*-score (Length 2021). We also quantified dispersal using two other metrics: 1) farthest dish in the array where a female laid the largest proportion of her eggs (Conway-Maxwell Poisson distribution), and 2) location in array after 24 h (Gaussian because beetles could be in the tubing connecting dishes e.g., dish 1.5). Results for these additional measures of dispersal are presented in the supplemental material (Figure B1, Tables B3 and B4).

For assessing the correlated response of activity to our selection for dispersal distance, we used a linear mixed model with line and block as fixed effects, individual identity as a random effect, and total distance traveled (mm) as the response (log-transformed to meet regression assumptions). A second trait that could be correlated with dispersal distance is dispersal tendency. We compared dispersal tendency between lines, measured as the time it took for a beetle to leave the starting patch, with a grouped time-survival model with a Chi-square test (package “rms”, Harrell 2022). We also assessed line differences in dispersal tendency as the total number of location changes by using generalized linear mixed model with a Poisson distribution, with line as a fixed effect and individual identity as a random effect.

3.3.8.2 Correlated responses of life-history traits to selection for dispersal

From each statistical model for every trait of interest, we addressed multiple aims. First, we assess the response to selection by comparing the dispersal- and non-dispersal-selected lines (e.g., main effect of selection treatment). Next, we look for a context-dependent genetic correlation (e.g., interaction of sex and selection treatment) by assessing if the dispersal- and non-dispersal selected lines have differing responses in different environments. All models used data where beetles were in an ideal environment (3.3.6) and the two environments with conspecifics present (3.3.7).

For body mass, 24-h fecundity, lifetime fecundity, and lifespan, we used generalized linear models with a Poisson distribution. For the egg size models (two response variables – length and width), we used a linear mixed model that included female identity as a random effect, and for egg distribution, we used a linear model. In the model for body mass, we only include selection line as a fixed effect because all beetles were raised in an environment without conspecific competition. In all other models, we first fit a model that included only selection treatment, environment, and their interaction as fixed effects, and, if the interaction was significant, we re-ran the model and included female body mass as a covariate to determine if the difference among lines was due to body mass. Body mass can affect fecundity, egg size, and lifespan: large seed beetles produce more eggs (Messina 1993), larger eggs (Fox 1994, Yanagi & Tuda 2012), and can have a slightly longer lifespan (Møller et al. 1989, Messina & Fry 2003) than small beetles (but see Fox et al. 2003). Body mass was included in the final model for 24-h and lifetime fecundity.

After final model selection (with or without body mass), if the interaction was significant, we performed contrasts to compare dispersal and non-dispersal selected lines in all three environments. There were 24 females that did not lay any eggs during the first 24 h and did so later in the experiment; these females were kept in the fecundity datasets but excluded from the egg size and distribution datasets. For 24-h fecundity and lifetime fecundity, we present results for the total number of eggs laid.

For development time to adulthood, we calculated the time to adult emergence as the number of days an offspring emerged after the egg was laid. We used a generalized linear mixed model with selection treatment, environment treatment, and their interaction as fixed effects, number of days to adult emergence as the response variable, bean identity nested within female identity as the random effects, and Poisson distribution.

All results present the mean ± SE and full ANOVA results are given in the supplemental material. Figures present the raw data (mean ± SE, calculated with R package “Rmisc”, Hope 2022).

3.4 Results

3.4.1 Did artificial selection alter dispersal behavior?

After 7 generations of selection, females from the two lines selected for long-distance dispersal traveled, on average, just over twice as far in our dispersal arrays (approximately 3 dishes farther), than did females from the two lines selected for short-distance dispersal (nested ANOVA comparing lines in Generation 8: $F_{1,340} = 418.2$, $p < 0.001$; mean ± SE; averaged among dispersal-selected lines: 5.9 ± 0.15 dishes; non-dispersal-selected lines: 2.6 ± 0.08 dishes; Figure 3.2).

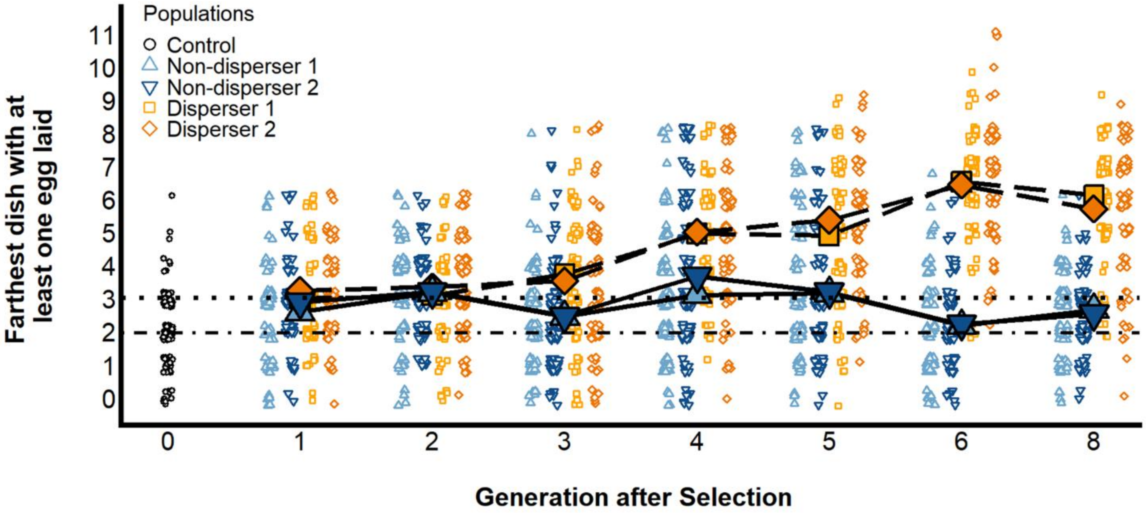

Figure 3.2. Dispersal response to artificial selection, measured as the farthest dish in which a female laid at least one egg, for the control line before selection and for each experimental population during selection. Results for individual females put through the arrays are shown as jittered unfilled points and line averages are shown as filled points. The generation after the start of selection is shown across the X-axis. Generation 7 is skipped in the figure because this was a rest month where no selection was conducted, and beetles were not put through the arrays. Horizontal lines show the average dish in which a female laid at least one egg (distance traveled) in the control line at the start (dot-dash line) and end of the experiment (dotted line).

At the end of the selection experiment (Generation 8 in Figure 3.2), the dispersal- and non-dispersal-selected lines were being tested in different length arrays because the arrays were extended during the experiment for the dispersal lines but not for the non-dispersal lines. We thus re-measured dispersal at the end of the experiment in arrays of common length and in three environments (conspecific eggs absent, conspecific eggs present at low density, and high density of conspecific eggs) for all selection lines. In all environments, the dispersal lines laid their most distant egg farther in the array than non-dispersal lines (GLM with Conway-Maxwell Poisson distribution – main effect of selection: $\chi^2_1 = 33.6$, $p < 0.001$). The distance in the array where females laid their farthest egg increased as conspecific density increased (GLM with Conway-Maxwell Poisson distribution – main effect of environment: $\chi^2_2 = 239.5$, $p < 0.001$). Interestingly, the difference between the dispersal and non-dispersal selection lines in how far females moved to lay eggs – our measure of dispersal distance – varied with the environment (Interaction between selection and density treatments: $\chi^2_2 = 11.4$, $p < 0.01$). However, the difference between selection lines was only marginally different among environmental treatments: when conspecifics were absent, or were present a low density, females from dispersal-selected lines laid their farthest egg approximately 1 dish farther in the array than females from the non-dispersal-selected lines, but when at high conspecific density females from dispersal-selected lines laid their farthest egg in the array approximately 1.5 dishes farther than females from non-dispersal-selected lines. (Figure 3.3, Table B3).

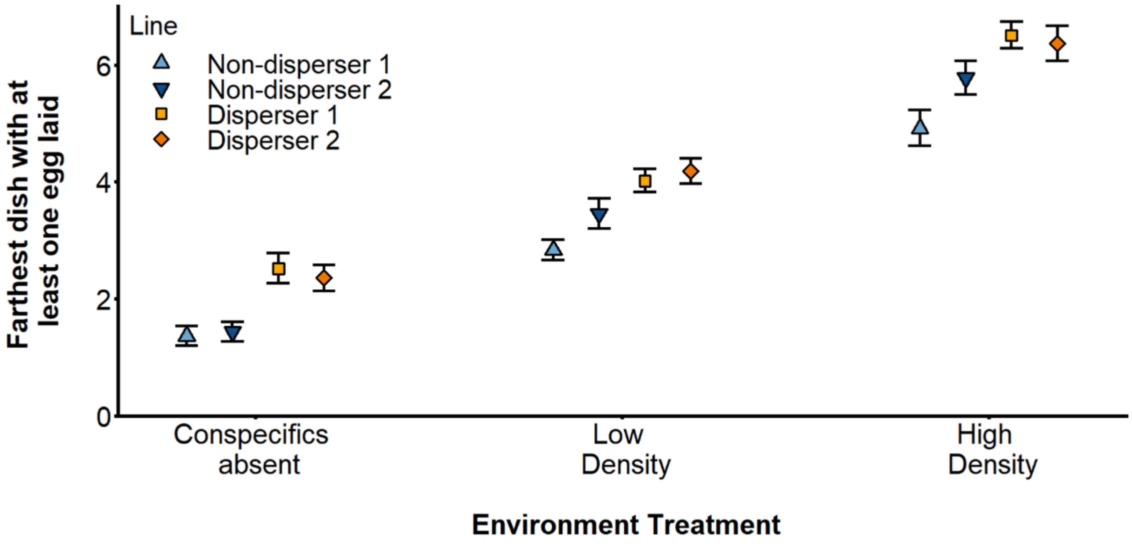

Figure 3.3. Female dispersal distance (mean ± SE) - the farthest dish where a female laid at least one egg. As conspecific density increased, all lines increased the distance they dispersed, but females from dispersal selected lines always dispersed farther than females from the non-dispersal selected lines. ANOVA results are available in Table B2, contrasts in Table B3.

We predicted that selecting on dispersal distance would indirectly select for both higher activity and increased dispersal tendency. Our evidence for this was mixed. There was a trend towards females from dispersal-selected lines being more active - moving longer distances in the empty petri dish during the 10 min activity behavior test (mean ± SE; averaged among dispersal lines, 906.7 mm ± 44.4; averaged among non-dispersal lines, 795.6 mm ± 38.2), but the difference among selection lines was not statistically significant (contrast between selection treatments: mean difference 73.6 ± 41.0 SE, $t_{199} = 1.8$, $p = 0.07$; Figure 3.4A). We found stronger evidence that dispersal tendency co-evolved with dispersal distance. For one measure of dispersal tendency (number of location changes in a 2-patch array), females from dispersal-selected lines made more location changes during the 3 h test than females from non-dispersal-selected lines (dispersal-selected lines: 1.4 changes ± 0.1, non-dispersal-selected lines: 0.9 ± 0.09; contrast: mean difference 0.4 ± 0.1 SE, $z = 3.4$, $p < 0.001$; Figure 3.4B). For a second measure of dispersal tendency (time to leave the first patch of a dispersal array), we found that females from dispersal-selected lines left faster than females from non-dispersal-selected lines (contrast: mean difference 0.5 ± 0.1 SE, $z = 3.3$, $p < 0.001$; Figure 3.4C).

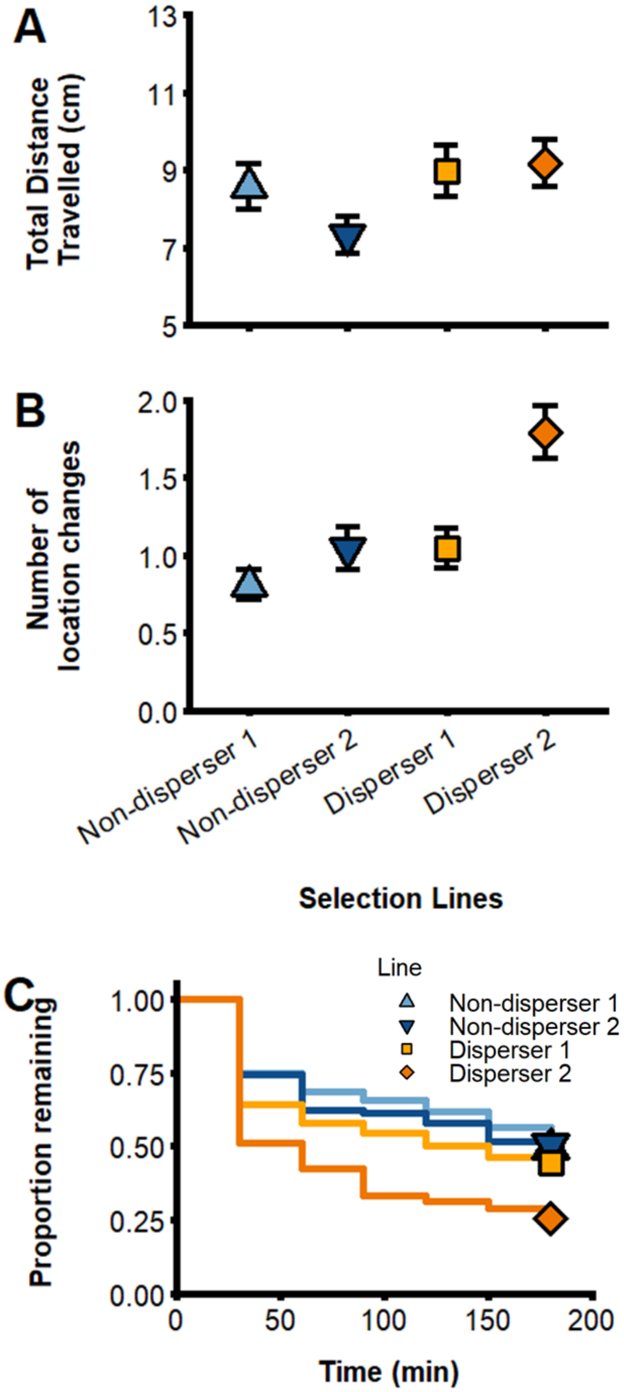

Figure 3.4. Female activity (panel A - total distance travelled in an empty petri dish during the 10 min activity behavior test), and dispersal tendency (panel B - number of location changes, and panel C - time to leave the starting patch of a dispersal array) evolved as correlated responses to dispersal distance. We averaged total distance and number of location changes across 3 trials for each individual, then averaged across individuals within lines to present mean ± SE. Confidence intervals for survival curves are not shown to improve visibility of line trends. ANOVA results are available in Table B3.

3.4.2 Correlated responses of life-history traits to selection for dispersal

To determine if life-history traits are genetically correlated with dispersal in female seed beetles, we measured multiple life-history traits in an ideal environment where there are no conspecifics present. We interpret differences between the dispersal and non-dispersal selection lines as evidence that the trait of interest evolved as a correlated response.

Females from the dispersal-selected lines had larger bodies ($F_{1,185} = 15.9$, $p < 0.001$; dispersal-selected lines: 6.8 mg ± 0.07, non-dispersal-selected lines: 6.4 ± 0.07; Figure 3.5A), and laid longer eggs ($\chi^2_1 = 6.1$, $p = 0.01$; dispersal-selected lines: 0.67 mm ± 0.002, non-dispersal-selected lines: 0.68 ± 0.002, Figure 3.5D) than females from the non-dispersal-selected lines.

However, females from the dispersal-selected and non-dispersal-selected lines laid a similar number of eggs the first 24 h after mating (e.g., short term fecundity; $\chi^2_1 = 0.5$, $p = 0.4$; Figure 3.5B) and during their lifetime $\chi^2_1 = 0.03$, $p = 0.9$; Figure 3.5F). Additionally, regardless of the selection line a female came from, all eggs were the same width ($\chi^2_1 = 1.04$, $p = 0.3$; Figure 3.5E) and females evenly distributed their eggs among the available mung beans ($F_{1,\,541} = 0.01$, $p = 0.9$; Figure 3.5C). Females from all lines also had a similar lifespan ($\chi^2_1 = 1.08$, $p = 0.3$; Figure 3.5G) and took a similar number of days to develop into adults ($\chi^2_1 = 0.01$, $p = 0.9$; Figure 3.5H).

3.4.3 Correlated responses of life-history traits across environments

We predicted that if dispersal syndromes were context-dependent, then the direction (e.g., positive or negative) or magnitude of correlated responses would vary across an environmental gradient (e.g., no conspecifics present, low conspecific density and high conspecific density). Therefore, if the dispersal- and non-dispersal-selected lines have differing responses in different environments, then we would conclude that correlated responses are context-dependent.

The difference in short-term fecundity between selection lines depended on the environment a female experienced (Interaction between selection and density treatments: $\chi^2_2 = 13.7$, $p < 0.01$). In an environment without conspecifics present, females from the dispersal-selected lines laid a similar number of eggs as females from the non-dispersal-selected lines (contrast dispersal versus non-dispersal lines: mean difference -0.05 ± 0.04 SE, $z = -1.2$, $p = 0.2$), but as conspecific density increased, females from the dispersal-selected lines laid fewer eggs than females from the non-dispersal-selected lines, with the difference increasing as density increased (Low conspecific density – -0.09 ± 0.04 SE, $z = -1.9$, $p = 0.05$; High conspecific density – -0.2 ± 0.04 SE, $z = -4.9$, $p < 0.001$, Figure 3.5B). There was no interaction between selection and the environment for any other trait, which means that the correlated responses of egg distribution ($F_{2,\,541} = 1.7$, $p = 0.2$; Figure 3.5C), egg length ($\chi^2_2 = 1.9$, $p = 0.4$; Figure 3.5D), egg width ($\chi^2_2 = 3.8$, $p = 0.2$; Figure 3.5E), lifetime fecundity ($\chi^2_2 = 3.8$, $p = 0.2$; Figure 3.5F), lifespan ($\chi^2_2 = 1.2$, $p = 0.6$; Figure 3.5G), and larval development time ($\chi^2_2 = 0.4$, $p = 0.8$; Figure 3.5H) are not context-dependent.

For all traits that did not have a significant selection by environment interaction, we looked at the main effect of the environment on those traits to determine if the trait was sensitive to density, regardless of the selection line. All females changed how they

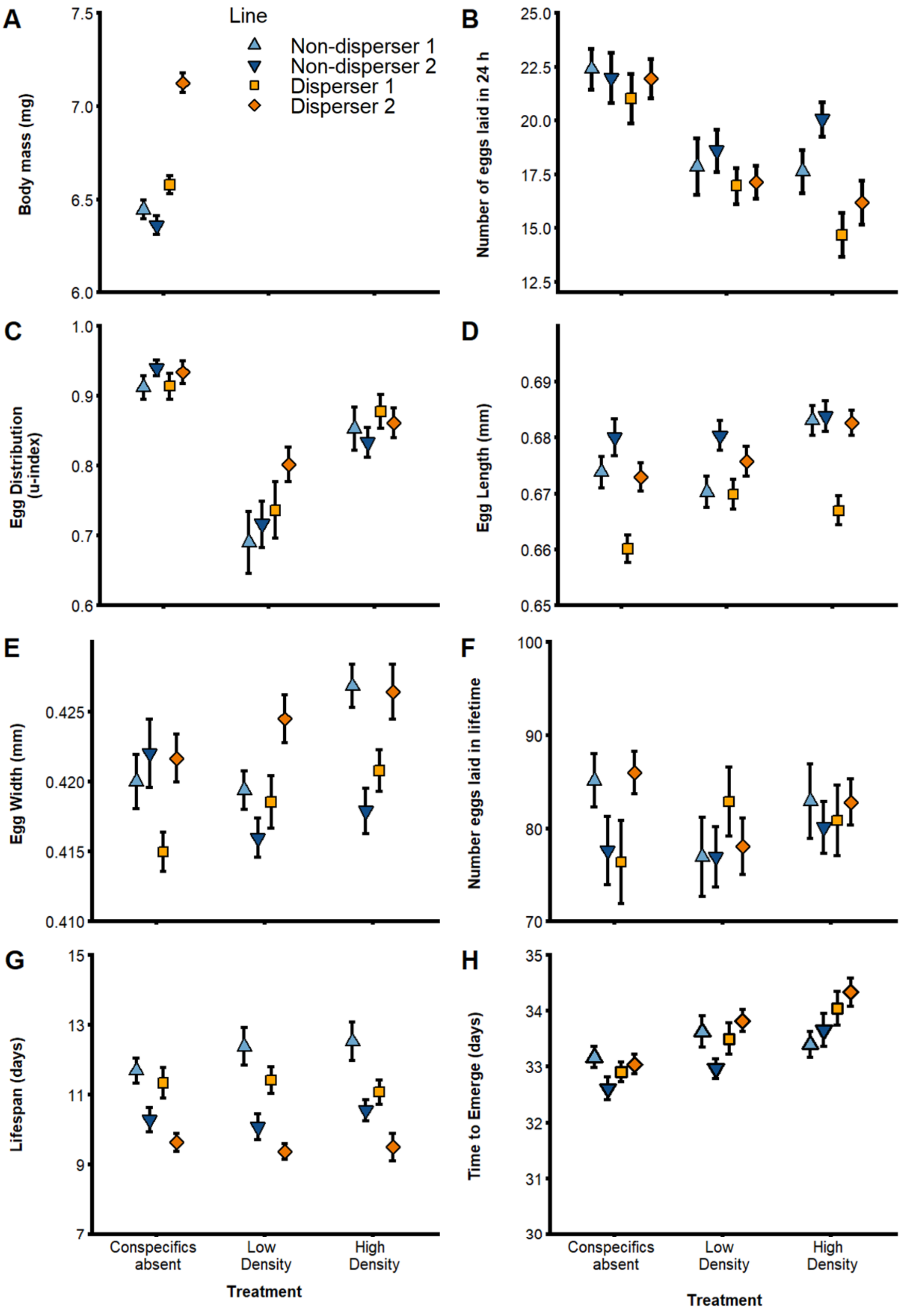

Figure 3.5. Life history differences between lines selected for long distance dispersal (orange diamonds and squares) or non-dispersal (blue triangles) in three environments (conspecifics absent, low conspecific density, and high conspecific density). The interaction between selection line and the environment was significant only for 24h

fecundity – females from lines selected for increased dispersal distance had a higher fecundity over 24 h in environments with conspecifics present (B). Selection lines did not differ in how they distributed eggs among the available beans, but females from all lines were very sensitive to the conspecific environment (C). Across all environments, females from dispersal-selected lines were heavier (A) and laid slightly shorter eggs than females from non-dispersal-selected lines (D). There was no selection-by-environment interaction for egg width (E), lifetime fecundity (F), lifespan (G), or development time to adulthood (H). ANOVA results available in Table B5.

distributed eggs based on the environment (main effect of environment treatment: $F_{2, 541} = 17.9$, $p < 0.001$). In the environment without conspecifics, females distributed their eggs more uniformly than in the other two environments (u-index is an index of uniformity that is independent of the number of eggs laid by each female and ranges from 0 [randomly distributed eggs] to 1 [most uniform distribution possible given the number of eggs laid]; contrast conspecifics absent versus low density: 0.188 ± 0.00187 SE, $t_{541} = 10.04$, $p < 0.001$; contrast conspecifics absent versus high density: 0.069 ± 0.00184 SE, $t_{541} = 3.77$, $p < 0.001$) and in the low-density environment, females laid their eggs in a more random distribution than in the high density environment (-0.118 ± 0.00186 SE, $t_{541} = -6.35$, $p < 0.001$). No other traits responded to conspecific density (egg length: $\chi^2_2 = 4.56$, $p = 0.1$; egg width: $\chi^2_2 = 4.66$, $p = 0.1$; lifetime fecundity: $\chi^2_2 = 1.47$, $p = 0.5$; lifespan: $\chi^2_2 = 0.13$, $p = 0.9$; or larval development time: $\chi^2_2 = 3.32$, $p = 0.2$; Figure 3.5D-H).

3.5 Discussion

In this experiment, our goals were to: 1) assess if artificial selection alters the dispersal behavior of beetles, 2) identify correlated responses to selection between dispersal and life-history traits to test for a dispersal syndrome in seed beetles, and 3) evaluate the context-dependence of dispersal syndromes by comparing correlated responses across three environmental conditions relating to competition for seed resources. After 8 generations of artificial selection for increased female dispersal, beetles from the dispersal-selected lines dispersed longer distances and had a higher dispersal tendency than beetles from non-dispersal-selected lines. When looking for correlated responses to selection in life-history traits, only two traits were correlated with dispersal: beetles from dispersal-selected lines exhibited larger body sizes and shorter egg lengths compared to non-dispersal-selected lines selected (Table 3.1). Only one trait (short-term fecundity) showed evidence of context-dependence. In an environment with high conspecific density, females from dispersal-selected lines laid fewer eggs than females from non-dispersal selected lines, but this difference was not detected in any other environment (Table 3.1).

In summary, for most traits we measured, there is no evidence of a dispersal syndrome in seed beetles. However, there may be a subtle dispersal syndrome that involved body mass and egg length. Additionally, we have evidence that dispersal syndromes are context-dependent because for one trait, we only detected a correlation when conspecific density was high.

Table 3.1. Summary of the relationships between dispersal behavior and multiple life-history traits in an ideal environment with no conspecifics present (we assume that if a trait is correlated with dispersal, then a dispersal syndrome exists) and how relationships change across three contexts (conspecifics absent, low and high conspecific density). Mean ± SE for dispersal (D) and non-dispersal (ND) selected lines are summarized in each environment. ANOVA results for all models available in Table B5.

Response	**Correlated with dispersal (ideal environment)?**	**Correlation with dispersal changes based on environment?**	**Conspecifics Absent**	**Low density**	**High density**
Body mass (mg)	**Yes**	NA	D: 6.8 ± 0.07 ND: 6.4 ± 0.07	D: 6.9 ± 0.06 ND: 6.4 ± 0.06	D: 6.8 ± 0.07 ND: 6.4 ± 0.06
24-h Fecundity (total num. laid)	No	**Yes**	D: 21.5 ± 0.7 ND: 22.2 ± 0.8	D: 17.0 ± 0.6 ND: 18.3 ± 0.8	D: 15.4 ± 0.7 ND: 18.9 ± 0.7
Egg Distribution (u-index)	No	No	D: 0.92 ± 0.02 ND: 0.93 ± 0.02	D: 0.77 ± 0.02 ND: 0.70 ± 0.02	D: 0.87 ± 0.02 ND: 0.84 ± 0.02
Egg Length (mm)	**Yes**	No	D: 0.667 ± 0.0018 ND: 0.677 ± 0.0022	D: 0.673 ± 0.0019 ND: 0.676 ± 0.0020	D: 0.675 ± 0.0018 ND: 0.683 ± 0.0019
Egg Width (mm)	No	No	D: 0.419 ± 0.0011 ND: 0.421 ± 0.0016	D: 0.422 ± 0.0013 ND: 0.418 ± 0.0010	D: 0.424 ± 0.0012 ND: 0.422 ± 0.0011
Lifetime Fecundity (total num. laid)	No	No	D: 81.4 ± 2.5 ND: 81.2 ± 2.4	D: 80.3 ± 2.4 ND: 76.9 ± 2.6	D: 81.8 ± 2.3 ND: 81.5 ± 2.4
Lifespan (days)	No	No	D: 10.3 ± 0.3 ND: 11.5 ± 0.3	D: 10.3 ± 0.2 ND: 11.1 ± 0.3	D: 10.4 ± 0.3 ND: 10.9 ± 0.3
Larval Development Time (days)	No	No	D: 33.0 ± 0.1 ND: 32.9 ± 0.1	D: 33.7 ± 0.2 ND: 33.3 ± 0.2	D: 34.2 ± 0.2 ND: 33.5 ± 0.2

3.5.1 Correlated responses to selection for dispersal: body mass and egg length

Dispersal syndromes, often measured as phenotypic correlation between traits, could evolve due to genetic correlations among traits, which would result in dispersing individuals having different phenotypic traits than non-dispersing individuals (Ronce & Clobert 2012, Stevens et al. 2014). Our results support this explanation because selection on dispersal distance of female seed beetles led to the evolution of dispersal tendency, body mass, and egg length. Interestingly, many traits that we expected to evolve as part of the dispersal syndrome – short- and long-term fecundity, lifespan, and larval development time – did not.

The correlations between dispersal and life-history traits are highly variable among species. Female nematodes (*Caenorhabditis remanei*) artificially selected for high dispersal tendency had a lower lifetime fecundity and shorter lifespan than females selected for low dispersal tendency (Zwoinska et al. 2020), but in fruit flies (*Drosophila melanogaster*, Tung et al. 2018) and mites (*Tetranychus urticae*, Tien et al. 2011), there was no change in life-history traits (body size, fecundity, oviposition rate, lifespan, larval development) after selection for high and low dispersal. And in studies that examined dispersal syndromes by looking for correlations in natural populations, there was variation among species in the direction and magnitude of correlations between dispersal and life-history traits (reviewed in Stevens et al. 2013, Ronce & Clobert 2012, and Bonte & Saastamoinen 2012).

Our finding that body size and egg length co-evolved in response to selection for dispersal suggests that these traits are genetically correlated with dispersal. Although our experiment focused on phenotypic correlations, phenotypic correlations often mirror genetic correlations (Cheverud 1988). While our experiment does not allow us to explicitly determine how dispersal, body size, and egg length are correlated, possible mechanisms include linkage disequilibrium and pleiotropy. One example of a syndrome controlled by genetic pleiotropy is the rover/sitter gene, initially discovered in fruit flies but conserved across a range of taxa from insects to humans. Rover flies travel longer distances in a feeding substrate, adults disperse longer distances, move away from food after feeding, have higher responsiveness to sucrose and increased food intake, and better short-term memory but poorer long-term memory than sitters (Anreiter & Sokolowski 2019). In this case, the gene which creates large differences among flies, is pleiotropic, with 4 promoters that produce 21 transcripts and encode 12 protein isoforms, and this gene is expressed in different tissues at different times (Anreiter & Sokolowski 2019).

3.5.2 Correlated responses to selection for dispersal across environmental contexts

The difference between dispersal- and non-dispersal selected lines differ by environment (e.g., detecting the correlation was context-dependent) for only one trait (short-term fecundity). This suggests that there is limited context-dependence of dispersal syndromes in seed beetles in response to the presence of conspecific eggs. A more detailed experiment comparing dispersal syndromes across species (n = 15 species including protists, arthropods, mollusks, and vertebrates) found evidence for context-dependence of dispersal syndromes (Cote et al. 2022). Across all species tested, when the environment contained limited resources or predators, the individuals that dispersed had a larger body size and locomotion morphology traits (length or width of locomotory apparatus proportional to body size) than individuals that did not disperse, but the differences between dispersers and non-dispersers was reduced in environments with abundant resources or no predators (Cote et al. 2022). In our experiment, increasing larval density does represent a decrease in resources for a focal female's offspring, however, it is possible that adult females are using cues of larval density other than the presence of eggs to make egg laying and dispersal decisions. It is possible that our experiment did not accurately capture the specific cue that beetles assess.

We are just beginning to understand the complex environmental landscape that produces observed behaviors. Our experiment focused on a univariate environmental factor (presence of conspecific eggs), but organisms are experiencing multidimensional environments, even in laboratory settings. For seed beetles maintained in colonies in the lab, not only are females assessing the presence of conspecific eggs (via tactile sensory organs that can detect the shape of the egg raised on the surface of the bean, Messina & Renwick 1985, Messina et al. 1987), but also through olfactory (females release a pheromone when they lay an egg that other females can detect, Credland & Wright 1990, Messina & Renwick 1985, Messina et al. 1987) and vibrational signals (larvae developing inside a bean create vibrations that can be detected by female beetles, Guedes and Yack 2018). Our experimental design did not include vibrational signals because beans with previously laid eggs had been frozen to kill larvae. While we did not explicitly wash beans to eliminate oviposition pheromones, we sanitized petri dishes between each trial to eliminate any pheromone trails left from previous beetles. Although we designed our experiment to isolate and select a single trait, female seed beetles have evolved for many generations with multiple cues to indicate if they need to disperse to new oviposition sites. It is possible that seed beetles are adjusting their behavioral response to multiple environmental factors to produce multidimensional plasticity (e.g., simultaneous integration of cues, Westneat et al. 2019), even in the relatively simplified lab environment. If dispersal syndromes are influenced by multidimensional phenotypic plasticity, detecting dispersal syndromes may strongly depend on the traits that we measure and the context in which those traits are measured (e.g., trait variation found in one context may be due to sensitivity to an unmeasured context, Westneat et al. 2019).

Dispersal, while often discussed as a binary (e.g., dispersed or not, Matthysen 2012), is a complex trait that varies among individuals. For example, individuals that disperse vary in the timing of emigration (Dufty & Belthoff 2001), distance traveled (Brown & Crone 2016), and number of areas sampled before settling (Mabry & Stamps 2008, Selonen & Hanski 2009). In some species, dispersal behavior and development of the physical traits associated with it depend on hormone levels (Dufty & Belthoff 2001, Ims & Hjermann 2001). Another layer of rigor to provide more detail on within-species variation in dispersal syndromes would include multiple measurements of traits for each individual (e.g., before and after dispersal, Nicolaus et al. 2022). Ideally, traits would be repeatedly measured on individuals across contexts (at least two environments or time-points surrounding a dispersal event), but this kind of data collection for behavioral, morphological, and physiological traits can be extremely time intensive. The effort will pay off however, because the repeated measures approach will make the data suitable for a reaction norm analysis to better estimate the plasticity and timing of dispersal syndromes of individuals across contexts.

3.5.3 Implications of Context-dependent Dispersal Syndromes

For populations living in spatially fragmented landscapes, the ecological and evolutionary consequences of context-dependent dispersal syndromes are intriguing. The ability to disperse between semi-isolated subpopulations is crucial for the long-term survival of the regional population (Levins 1969) because dispersal leads to gene flow among subpopulations (Cote et al. 2017). However, because landscapes are becoming increasingly heterogeneous, gene flow among populations may either enhance or counteract selection and local adaptation (Lenormand 2002, Edelaar and Bolnick 2012). Individuals with dispersal syndromes that are not plastic can improve their fitness by matching their phenotype to their environment (e.g., preferentially settling in habitat that suits their phenotype, Edelaar et al. 2008). Habitat-matching dispersal could lead to increased local adaptation as individuals mate with similar phenotypes and seek out specific habitats during dispersal (Edelaar et al. 2008). And if dispersal is plastic, then the degree of local adaptation may depend on the other traits correlated with dispersal (e.g., fecundity) and how those correlated traits interact with the environment. Our experiment focused on quantifying the species-specific dispersal syndrome, but local adaptation and non-random gene flow is one example of how dispersal syndromes could differ among populations of the same species (Clobert et al. 2009, Ronce and Clobert 2012).

In general, selection within a subpopulation will eventually feedback on the evolution of dispersal (Cote et al. 2017), and ultimately impact the regional metapopulation (Raffard et al. 2022). Dispersal syndromes that are subtly context-dependent, such as those in female seed beetles, could have unpredictable and complex effects on the long-term dynamics of populations living in heterogeneous and fragmented landscapes. Correlations between fecundity and dispersal is a common pair of traits examined in dispersal syndrome research, but we highlight how the traits measured and the environment in which traits are measured can affect the ability to detect dispersal syndromes. Our work adds to a growing body of literature that identifies the importance of dispersal syndromes as a link between variation within a sub-population (e.g., dispersers vs non-dispersers) and the large-scale population dynamics (Raffard et al. 2022).

CHAPTER 4: SELECTION FOR HIGHER DISPERSAL IN FEMALES REVEALS CROSS-SEX GENETIC CORRELATIONS

4.1 Abstract

Differences in selection on dispersal between males and females can produce sex-biased dispersal, where one sex disperses more than the other. Differences in selection on dispersal could also lead to sex-differences in dispersal syndromes – suites of morphological and life-history traits correlated with dispersal. Our goal was to better understand the genetic basis of the traits that comprise dispersal syndromes and assess which traits are genetically correlated within and across the sexes. We artificially selected for long and short distance dispersal in female seed beetles (*Callosobruchus maculatus,* Coleoptera: Chrysomelidae, Bruchinae), and then measured dispersal behavior, body size, time to reach maturity, and reproductive output in male beetles. We found that for 3 traits, males evolved the same as females in response to the selection on females: males from lines selected for higher dispersal were more active, left the starting patch of a dispersal array faster, and were heavier than males from non-dispersal selected lines. For 2 other traits, males evolved differently from females: females from dispersal-selected lines made more location changes in a dispersal array than those from non-dispersal selected lines, but males from the lines did not differ; and females from the selection lines had similar fecundity, but males from dispersal-selected lines had a smaller spermatophore than males from non-dispersal-selected lines. We did not find any direct evidence that responses of male traits to selection were context dependent: males from the dispersal- and non-dispersal-selected lines had similar reproductive output regardless of conspecific density. In contrast, female reproductive output was higher for non-dispersal-selected lines than dispersal-selected lines when conspecifics are present, but this difference disappears when conspecifics are absent. The differences in male and female dispersal syndromes suggest that cross-sex genetic correlations are present but weak, and there is likely a combination of genotypic and environmental effects decoupling the traits in the dispersal syndrome.

4.2 Introduction

Selection on behavior and life-history traits can be different for males and females. Because of differences in natural selection on males and females, each sex can have different phenotypic optima (Lande 1980, Sherman & Westneat 1988, Fairbairn et al. 2007, Bonduriansky & Chenoweth 2009). However, the degree to which the sexes can reach their optimum and the rate at which sexes differentiate due to differing natural selection is often constrained by a cross-sex genetic correlation (e.g., the similarity of the additive effects of alleles when expressed in the different sexes) cause by shared genetic architecture between the sexes (Lande 1980, Pennell and Morrow 2013). A positive intersexual genetic correlation means that when one sex experiences strong selection and evolves, the other sex also evolves in the same direction, but there are also cases where selection on one sex produces no response in the other or an opposite response (Lande 1980, Bonduriansky & Chenoweth 2009, Wyman et al. 2013). This genetic architecture constraint means that differences in natural selection on the sexes can lead to sexual conflict (Dean and Mank 2014).

One trait for which this conflict can occur is dispersal. Dispersal, broadly defined as the movement of individuals from one location to another, is a key process in ecology and evolution. Dispersal allows individuals to leave an area with high competition, low-quality resources, or predators for areas with increased access to non-kin mates (Hamilton & May 1977, Bengtsson 1978), lower competition from conspecifics (for mates – Hamilton 1967; for local resources – Clark 1978), or fewer predators (Sloggett & Weisser 2002). Dispersal may often be the target of different selection pressures in the two sexes (Smale et al. 1997), leading to different phenotypic optima. For example, female butterflies (*Maculinea nausithous* and *M. teleius*) follow valleys and avoid moving across hills during dispersal, whereas males ignore landscape topography during dispersal (Plazio et al. 2020). This difference in dispersal likely occurs because females are searching for places to lay eggs, and host plants are located in wet meadows in valley beds, whereas males disperse to find females and increase mating opportunities and thus disperse in efficient straight-line distances among habitat patches (Plazio et al. 2020). Frequently, dispersal has been observed to vary between the sexes, known as sex-biased dispersal, such that males and females have different dispersal behaviors (e.g., distance travelled, propensity to leave natal area; Smale et al. 1997, Li & Kokko 2019a). In general, male-biased dispersal occurs in mammals, female-biased in birds, and a mix of male/female-biased dispersal in fish, reptiles, and insects (Li & Kokko 2019a).

Dispersal behavior often covaries with other behavioral, morphological, and physiological traits, called a dispersal syndrome (Roff and Fairbairn 2007, Ronce & Clobert 2012). Dispersal syndromes have been described across multiple taxonomic groups, but results vary in the magnitude and direction of relationships between traits (Stevens et al. 2014). Meta-analysis across multiple taxon revealed a general pattern that higher dispersal ability is associated with high fecundity and survival (Stevens et al. 2013, Stevens et al. 2014). Interestingly, there is some evidence that dispersal syndromes differ between the sexes. Generally, there is a difference in dispersal syndromes, but the sexes do not always have the same traits involved in the dispersal syndrome. For example, in butterflies, female dispersers had a phenotypic correlation between dispersal and lifespan (disperser females had a longer lifespan than non-disperser females), but in males, there was a phenotypic correlation between dispersal and mating opportunities (disperser males had increased mating opportunities than non-disperser males, Legrand et al. 2016).

The impact of sex-specific dispersal syndromes on the ecology and evolution of spatially fragmented populations is intriguing. Males and females disperse for different reasons, and this means that the same environment can lead to different dispersal behavior between the sexes. For example, in a species where one sex is larger than the other, the smaller sex may need to disperse because the larger sex deplete food/resources in the area and thus outcompete the smaller sex (Li and Kokko 2019b). Furthermore, the sexes may differ in other stages of dispersal that can cause the sexes to differ in dispersal. In male flour beetles (*Tribolium castaneum*) that were artificially selected for long- or short-distance dispersal, males from the long-distance-selected lines had increased mating success and more frequent encounters with predators than males from the short-distance-selected lines, but females from the selection lines did not differ (Matsumura & Miyatake 2015). In this case, the increased probability of interacting with a predator would increase the mortality of male dispersers compared to female dispersers. Thus, not only is it important to know how dispersal syndromes differ between males and females, but the environment in which dispersal syndromes are measured can interact with the sex-specific dispersal syndrome to alter the population dynamics.

To assess how changing selection on components of female dispersal behavior might affect the dispersal and life-history traits of males in multiple environments, we studied the cowpea seed beetle (hereafter seed beetle; *Callosobruchus maculatus*, Coleoptera: Chrysomelidae, Bruchinae), a cosmopolitan agricultural pest that damages stored legume seeds (Tuda et al. 2006). This beetle is widely used as a model for sexual selection and life history evolution (Fox and Savalli 1998, Edvardsson & Tregenza 2005, Maklakov et al. 2007, Vasudeva et al. 2014, Canal et al 2021). Both sexes of seed beetles disperse at high conspecific density, but males move longer distances from their natal area than females (e.g., male-biased dispersal, Miller & Inouye 2013). Female dispersal is influenced by local density, but this context-specificity of dispersal varies among populations; females vary within and among populations in their sensitivity to the presence of conspecific eggs (e.g., density-dependent dispersal), and females that are sensitive to conspecific density will leave a high-density area to lay eggs in a low-density location, whereas females that are insensitive to density will lay eggs regardless of the presence of conspecific eggs (Messina 1991, Messina et al. 1992, Fox et al. 2004, Chapter 3 of this dissertation). We leveraged female density-dependent dispersal to artificially select for females that dispersed farther in search of oviposition sites and for females that did not disperse. Afterwards, we measured male dispersal and other life-history traits to compare with females from the same lines (e.g., dispersal or non-dispersal selected).

In a previous study, we found that after 8 generations of selecting for long or short dispersal distance in female beetles, female beetles from the dispersal-selected lines dispersed longer distances in a dispersal array and left the starting patch of a dispersal array faster than females from non-dispersal-selected lines. Additionally, there was a trend towards females from dispersal-selected lines being more active and making more location changes in a dispersal array than females from non-dispersal-selected lines. In an ideal environment without conspecifics, female beetles from the dispersal-selected lines exhibited larger body sizes compared to non-dispersal-selected lines selected (Chapter 3 Table 3.1). For two other traits (fecundity and larval development time), females from the selection lines did not differ (Chapter 3 Table 3.1). Only one trait (short-term fecundity) showed evidence of context-dependence. In an environment with high conspecific density, females from dispersal-selected lines laid fewer eggs than females from non-dispersal selected lines, but this difference was not detected in any other environment

Our overall goal was to better understand the genetic basis of the traits that comprise dispersal syndromes and assess which traits are genetically correlated within and across the sexes. To that end, we had three specific aims:

First, we quantified carry over effects of selection on females by comparing an array of male traits from the dispersal and non-dispersal-selected lines. We assume that if males from the different lines differ in a trait, then that trait is genetically correlated with dispersal, and thus is part of a dispersal syndrome. We considered this exploratory as there are many factors that could push correlation structures to be either positive or negative (Legrand et al. 2016, Renault 2020), and so we tested no specific predictions.

Second, we measured two traits (larval development time and reproductive output) for males from the dispersal and non-dispersal-selected lines in two environments (conspecifics present at high density or absent) to look for context-dependence of dispersal syndromes. If the trait varies between the selection lines differently in the two environments, then we would have evidence that male dispersal syndromes are context dependent.

Finally, we compared male dispersal syndromes to female dispersal syndromes, which were measured as part of a previous experiment (Chapter 3 of this dissertation), to determine which traits of the dispersal syndrome are correlated across the sexes.

4.3 Methods

4.3.1 Study Organism

Seed beetles spend most of their lifecycle inside dried legume seeds, with a generation lasting approximately 45 days (when maintained at 16:8 light:dark, 25.5 ºC). Adults do not need to feed and can rely on energetic reserves obtained during the larval portion of the lifecycle (Messina 1993, Fox et al. 2011). The seed beetles in our experiment were collected from two locations: Tirunelveli, India (Mitchell 1991, Fox et al. 2007) India in 1979 from infested mung bean pods (*Vigna radiata*), and the Maiduguri area of Borno State, Nigeria in 2010 (Berger et. al 2016). from infested pods of black-eyed peas (*Vigna unguiculata*). Our populations are maintained at large population sizes (> 1000 adults per generation) under standard laboratory growth chamber conditions (16:8 light:dark, 25.5 ºC) on mung beans (India population) and black-eyed peas (Nigeria population, Fox et al. 2007). Prior to beginning the experiment, we bred a hybrid of the India and Nigeria populations to create a population with greater genetic variation (total 6 generations).

4.3.2 Selection Experiment

To artificially select on female dispersal distance, we choose 121 random female emergers from our hybrid source population, mated them to a random male, and measured dispersal using a dispersal array. A dispersal array consisted of multiple petri dishes (60 mm diameter Falcon) connected by silicon tubing (3 cm long) in a line. Each petri dish contained 20 mung beans, which were all either pristine or had one previously laid seed beetle egg on each bean.

Arrays initially consisted of 7 petri dishes; the first 3 dishes contained beans with previously laid eggs and the remaining 4 dishes contained beans without previously laid eggs. Throughout the experiment, the non-dispersal lines always had arrays where the first 3 dishes in the array contained beans with previously laid eggs. For dispersal selected lines, we increased the number of dishes with eggs already present on the beans whenever >30% of the females from the dispersal lines laid at least one egg in the first patch without eggs present.

After mating, females were placed singly into the first dish of the array and allowed 24 h to disperse and lay eggs, then removed. We counted the number of eggs laid in each patch of the array, and quantified dispersal distance as the farthest dish in the array where the female laid at least 1 one egg. Any female that laid eggs only in the first three dishes was selected as a founder of a non-dispersal selection line (e.g., down-selection line), and any female that laid at least 1 egg in the 4th dish or farther was selected as a founder of a dispersal line (e.g., up-selection line). After selecting and grouping females into dispersal and non-dispersal lines, we split those females into two groups so that we had two replicate lines of each dispersal phenotype (4 lines total). We then isolated every bean on which the selected females had laid one or more eggs in a 15 mm petri dish (one bean per dish) to raise the offspring to adulthood.

For each subsequent generation, we performed the same dispersal array procedure, ensuring that females mated with a non-sibling male from the same selection line. Every generation, we ran 70-100 females per selection line through the arrays. During the selection experiment, the unselected control line (e.g., the hybrid population) was maintained in a colony in standard lab conditions on mung beans. After 8 generations, all selection lines and the control line were maintained without imposing selection under a standardized larval density (one beetle per seed) for 2 generations before any additional experiments were conducted. Additional details on the selection experiment setup and dispersal arrays are provided in Chapter 3.

4.3.3 Post-Selection Experiments

After eight generations of selection on female dispersal, we performed a series of experiments to evaluate dispersal (activity and dispersal tendency) and life-history traits (body size, larval development time, reproductive output) of male beetles. Body size was only measured when conspecifics are absent (a single beetle developing in one bean) and larval development time and reproductive output were evaluated in two environments: conspecifics absent, and high conspecific density. Previous work on dispersal syndromes of female seed beetles found that only at high conspecific density did females from the selection lines differ in their reproductive output (Chapter 3); therefore, we assessed male traits at multiple density treatments to make the results here comparable to our previous experiments.

4.3.3.1 Dispersal Traits

To quantify dispersal behavior of seed beetles, we made two measures of dispersal, activity and dispersal tendency, in an environment without conspecifics. For activity, we placed virgin beetles (24-48 h post emergence) alone into a sanitized (90% isopropyl alcohol) 60 mm diameter petri dish without any bean resources and recorded them for 10 minutes using a handheld camera (Besteker HD 1080P 24 MP 16X Digital Zoom Video Camcorder) mounted on a tripod (Amazon Basics) 32 cm above the beetles. We repeated this behavioral test another 2 times (~48 h between every test). We used ToxTrac (Rodriguez et al. 2018) to analyze videos and obtain detailed trajectories for every individual (all tracking settings kept as default except maximum displacement per frame = 75 pixels). Then we calculated the total distance traveled (mm). We excluded the first 0.5 s of tracking to avoid any errors due to irregular tracking as ToxTrac located an individual. To obtain a conversion rate of pixels into mm, we used ImageJ (Rasband 2018) to measure the number of pixels in the 60mm diameter of 30 randomly selected petri dishes in the videos (mean ± SD, 0.15 ± 0.002 mm/pixel). Some data points were lost due to video files getting corrupted, labeling issues, or detection complications. We measured beetles over 2 generations (e.g., blocks) and did not use any beetles in block 2 that were related (within 1 generation) to beetles used in block 1 (n = 22-31 beetles of each sex per selection line each block; summary of sample sizes by sex, block, and selection line provided in Table C1).

Activity is only one potential behavioral element of dispersal ability. Another contributor may be dispersal tendency, or the probability of an individual leaving a specified area, the first step in dispersal. To evaluate the dispersal tendency of beetles, we placed virgin adults into a two-patch dispersal array (two Falcon 60mm diameter petri dishes connected by 30 mm long silicon aquarium tubing) for 3 h without any seeds. Every 30 mins, we recorded the location of the beetles (patch 1, patch 2, or in tubing). We recorded two measures of dispersal tendency. First, we recorded the time it took for a beetle to leave the starting patch, which occurred when a beetle was in the tubing or patch 2. Second, we calculated the total number of location changes during the trial (e.g., a beetle that moved from dish 1, to tubing, back to dish 1 would have 2 total location changes). We repeated this behavioral test another 2 times per beetle (~48 h between every test; n = 38-44 individuals of each sex per selection line, summary of sample sizes by sex, selection line, and behavioral test provided in Table C1).

4.3.3.2 Life-History Traits

Body mass of males and females was measured prior to mating for a separate experiment assessing female dispersal distance. Beetles were weighed (Mettler Toledo AT261 Delta Range, 0.1 mg) 24-48 h post-emergence (n = 69-89 beetles of each sex per selection line, sample sizes in Table C1). Due to time limitations with the previous experiment, we sampled over 2 generations (hereafter, blocks; Chapter 3) and thus body mass was also measured over 2 generations. To maximize genetic variation, we did not weigh any females in block 2 that were related (within 1 generation) to females used in block 1; however, the focus of the experiment was females and not males, therefore we did not avoid males related to beetles in the previous block. Body mass results are similar if we exclude block 2 data or if we include both blocks of data (data not shown).

The time for a larva to fully develop from hatching to adulthood was measured as in Chapter 3. Briefly, virgin females were mated to non-sibling males from the same selection line, then placed in a petri dish with 4 mung beans for 24 h. We used a scalpel to remove all but the number of eggs required for the female’s assigned environmental treatment (no conspecifics present – only one egg on a bean, low conspecific density – two eggs per bean, and high conspecific density – 3 eggs per bean). For each female (n = 13-32 females per selection line for each conspecific density treatment, detailed samples sizes in Table C1), we had four replicate beans, and each bean was maintained individually in a petri dish in an incubator under standard lab conditions and monitored daily until adult beetles emerged. After adult beetles emerged, we recorded the sex of the individual. If a beetle had not emerged from a bean within 46 days after eggs were laid, we recorded the larva as dead, and were unable to identify the sex.

Using a subset of the males that emerged from the conspecifics absent and high-density treatments of the larval development time experiment, we measured male reproductive output as nuptial gift size (e.g., a spermatophore). Spermatophores are nutrient packages provided to the female and, in addition to sperm, contain water, proteins and hormones (Vahed 1998), which increase female fecundity (Fox and Savalli 1998), but creating this nuptial gift can be energetically costly for the male (Paukku and Kotiaho 2005). We weighed males (24-48 h post-emergence) two times and if the weights differed by greater than 0.02 mg, then weighed again. If the third weight is not intermediate to the first two weights, then we weighed beetles a 4th time. Males were mated to a non-sibling, virgin female from the same selection line, then weighed again following the same procedure as pre-mating. For each male, we averaged all weights before mating and after mating to compensate for any measurement errors (Fox and Savalli 1998, Savalli et al. 2000). The change in weight before and after mating represents the total spermatophore transferred to the female. We measured spermatophores for 233 males in the no conspecifics environment (n = 35-61 males per selection line) and 143 males from the high-density environment (n = 24-41 males per selection line, sample sizes for each population in Table C1).

To assess female reproductive output, we used data from Chapter 3, that assessed total number of eggs laid. In brief, we mated a virgin female (~24-48 h post-emergence) to a virgin male of the same selection line and placed the female alone into a 15 mm diameter petri dish with 30 mung beans for 24 h. Females were assigned to one of two treatments: conspecifics absent (n = 40-50 females per selection line) – where there were no previously laid eggs by conspecifics; and high conspecific density (n = 41-49 females per selection line; sample sizes for each population available in Table C1) – where each bean had one egg previously laid by a different female. We recorded the number of eggs laid (including both hatched and unhatched).

4.3.4 Analyses

All analyses were conducted in R software v 4.0.3 (R Core Team 2021). First, we tested for correlated response of male dispersal to selection on female dispersal by comparing males from dispersal and non-dispersal-selected lines. Then, we determined if male life-history traits evolved in response to selection for female dispersal by comparing males from dispersal-and non-dispersal-selected lines. These models used data where beetles were in an ideal environment (conspecific absent).

For dispersal, we first compared activity by using a linear mixed model (package “lme4”, Bates et al. 2015) with selection treatment (dispersal or non-dispersal) and block as fixed effects, individual identity as a random effect, and total distance traveled (mm; (log-transformed) as the response. We also quantified dispersal tendency – the probability of leaving an area – in two ways: the time it took a beetle to leave the first patch of a dispersal array and the number of location changes made between two patches of a dispersal array. We analyzed dispersal tendency, with a grouped time-survival model that included selection treatment as a fixed effect and beetle identity as a random effect to control for the three trials administered per individual (package “survival”, Harrell 2022). We used a generalized linear mixed model with a Poisson distribution to analyze dispersal tendency, with selection treatment as a fixed effect and individual identity as a random effect.

We analyzed body size with a linear mixed model with selection treatment as a fixed effect, block number as a covariate, and maternal identity as a random effect. For development time to adulthood, we calculated the time to adult emergence as the number of days an offspring emerged after the maternal female was placed on the beans to lay eggs as the response in a generalized linear model with selection treatment as a fixed effect, and a Poisson distribution. Initially, our model included bean identity nested within female identity as the random effects, but model analysis revealed that this model was singular and there was no significant difference in the AIC of the simpler generalized linear model and the mixed model, so we present the results of the latter. Lastly, to compare male nuptial gifts, we used a linear mixed model with selection treatment as a fixed effect, body mass as a covariate, and maternal identity as a random effect.

Our second aim was to determine if the environment altered the response of male life-history traits to selection for female dispersal. To do this, we combined the male data (analyzed above) with female data and included information from trait measurements in two other environments (conspecifics present a low density and high density). Our generalized linear model with a Poisson distribution for development time to adulthood, had the number of days an offspring emerged after the maternal female was placed on the beans to lay eggs as the response with selection treatment, sex, environment (conspecifics absent, present at low density, and present at high density), and all interactions as fixed effects. To compare reproductive output of the sexes, we standardized male spermatophore and female fecundity and treated them as a single response variable. We analyzed this metric with a linear mixed model with selection treatment, environment treatment (conspecifics absent or high density), and sex plus all interactions as fixed effects, body mass as a covariate, and maternal identity as a random effect.

For all analyses, we used Type 3 Wald Chi-square test ANOVA (package “car”, Fox and Weisberg 2019) and if the interaction was significant (context-dependent models only), then we performed planned contrasts (R package “emmeans”, Length 2021) to compare selection lines within each sex. For contrasts on a model with a Gaussian distribution, R uses a *t*-score, and for Poisson distributions, a *z*-score (Length 2021). All results present the mean ± SE and full ANOVA results are given in the supplemental material. Figures present the raw data (mean ± SE, calculated with R package “Rmisc”, Hope 2022).

4.4 Results

4.4.1 Did male dispersal evolve in response to selection for female dispersal?

To determine how selection for female dispersal affected male dispersal, we compared dispersal traits of males from dispersal-selected lines to males from non-dispersal-selected lines in an ideal environment (no competition from conspecifics). Some male traits showed evidence of having evolved in response to female dispersal. Males from dispersal-selected lines showed higher general activity; they travelled 18% longer distances during 10 min in an empty petri dish than males from non-dispersal-selected lines (mean ± SE; total distance traveled: dispersal-selected – 12.3 cm ± 4.8, non-dispersal-selected – 10.4 ± 4.4; Main effect – Selection line: $\chi^2_1 = 9.9$, $p < 0.01$; Figure 4.1A). Males from dispersal-selected lines also left the first patch of a dispersal array faster than males from non-dispersal-selected lines (Main effect – Selection line: $\chi^2_1 = 7.3$, $p < 0.001$; dispersal-selected lines – 16% remaining in first dish after 3 h, non-dispersal-selected line – 28%; Figure 4.1C-D), but the selection lines did not differ in the number of location changes made during 3 h in the dispersal array ($\chi^2_1 = 2.0$, $p = 0.16$; dispersal-selected lines – 2.0 changes ± 0.09, non-dispersal-selected lines – 1.8 ± 0.1; Figure 4.1B).

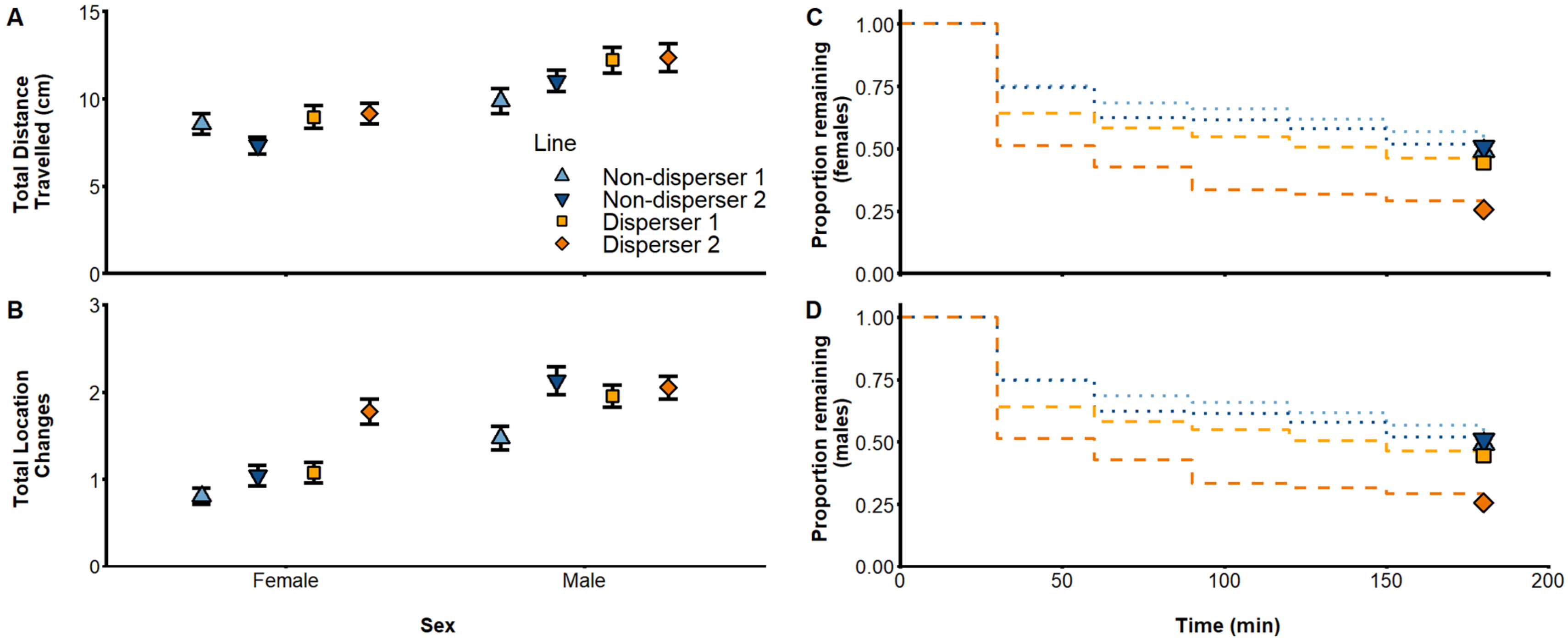

Figure 4.1. Activity, measured as total distance travelled (A) and dispersal tendency – measured as number of location changes (B) and time to leave the starting patch (C - females, D - males), evolved as correlated responses to selection on dispersal distance of female beetles. We averaged total distance (A) and number of location changes (B) across 3 trials for each individual, then averaged across individuals (mean ± SE). Confidence intervals for survival curves (C, D) are not shown to improve visibility of line trends (non-dispersal-selected – blue dotted lines, control – solid black line, dispersal-selected – orange dashed lines). ANOVA results for models available in Table C2.

4.4.2 Did male life-history traits respond to selection for female dispersal?

Selection on dispersal in females affected some male life history traits. Males from dispersal-selected lines weighed 15% more (Main effect – Selection line: χ^2_1 = 111.3, $p < 0.001$, dispersal-selected – 4.4 mg ± 0.05, non-dispersal-selected – 3.8 ± 0.03; Figure 4.2) and had 17% smaller spermatophore (χ^2_1 = 6.0, p = 0.01, dispersal-selected – 0.29 mg ± 0.007, non-dispersal-selected – 0.24 ± 0.007; Figure 4.3B) than males from non-dispersal-selected lines. However, we found no difference between the selection lines in male larval development time (χ^2_1 = 0.004, p = 0.9; Figure 4.3A).

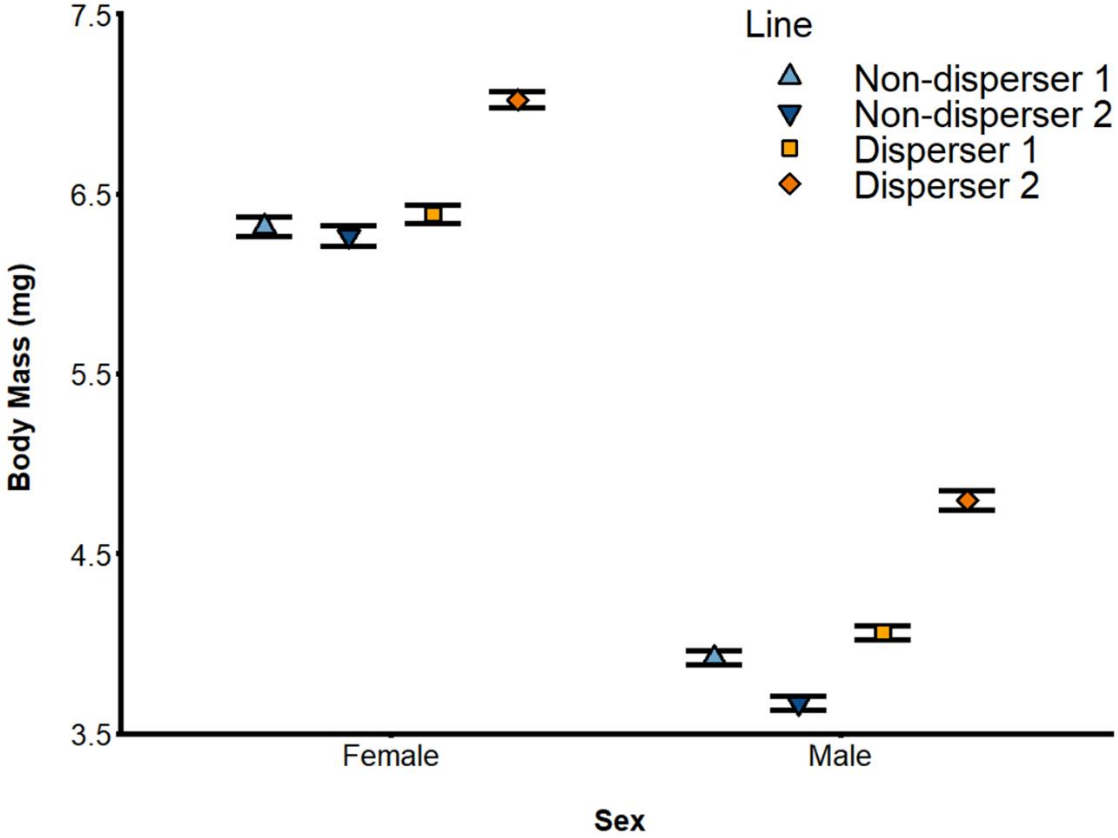

Figure 4.2. Body mass of male beetles (mean ± SE) evolved as a correlated response to selection of females for dispersal distance. ANOVA results for models available in Table C2.

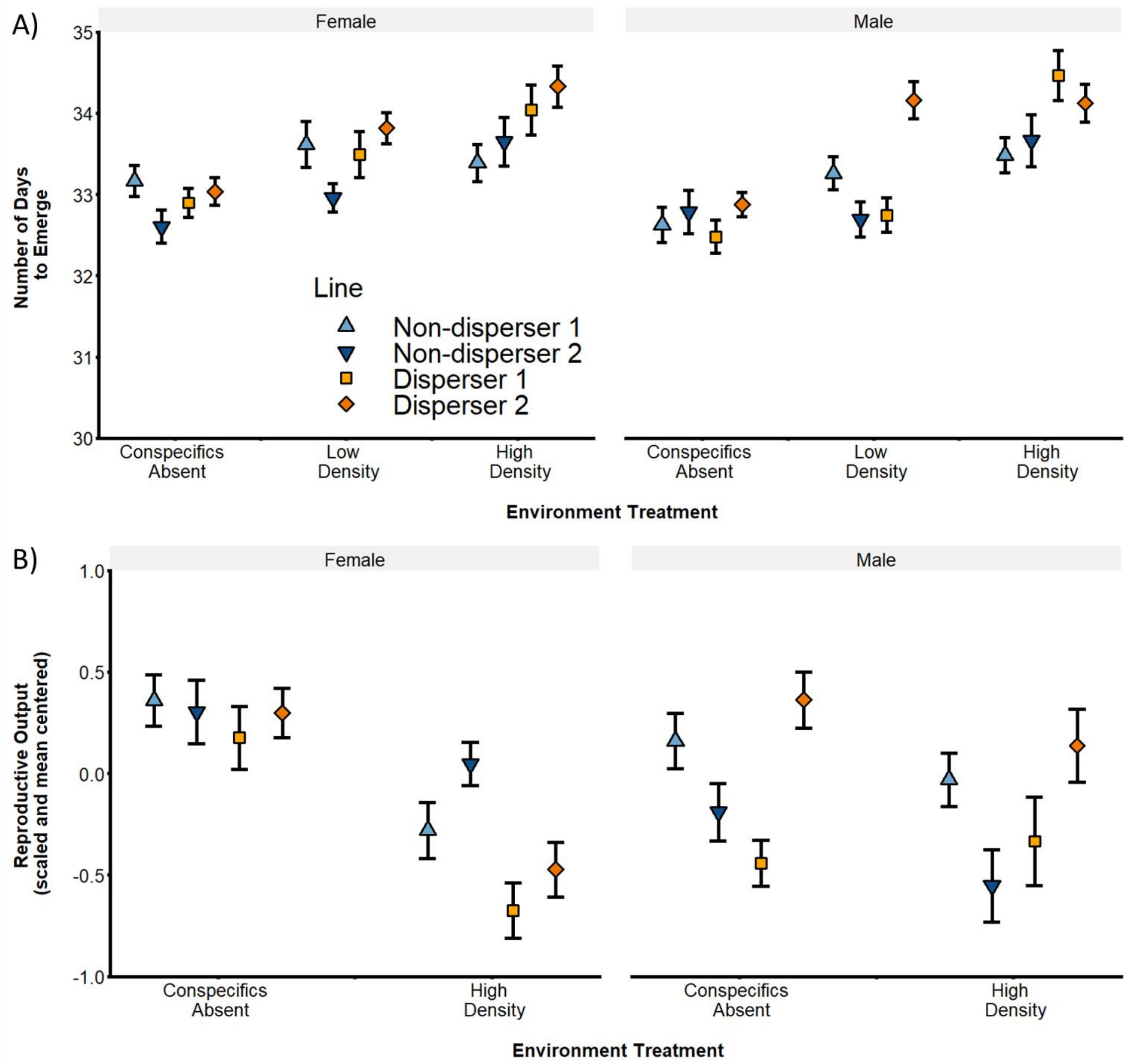

Figure 4.3. Larval development time (mean ± SE) from egg to adulthood (A) – measured as the number of day from laying to adult emergence – does not differ by selection line or sex of the larvae. For female beetles, reproductive output (B) – measured as the number of eggs laid within 24 h after mating (mean ± SE) – depends on the selection treatment (dispersal or non-dispersal selected lines) and the environment in which a beetle is raised (conspecifics absent or present at high density). For male beetles, reproductive output – measured as the weight of the spermatophore transferred to a female during mating – does not differ by selection line or environmental treatment. Fecundity and spermatophore weight were mean-centered and scaled by standard deviation. ANOVA results for models available in Table C2.

4.4.3 Was the response to selection context-dependent?

If the male response to selection for female dispersal was context-dependent, then we expected to see the difference between lines to depend on how the trait was measured. Moreover, if one sex was subject to different effects of context, then we expected a three-way interaction between selection line, context, and sex. We showed in a separate paper (Chapter 3) that only one trait (short-term fecundity) showed evidence of context-dependence. In an environment with high conspecific density, females from dispersal-selected lines laid fewer eggs than females from non-dispersal selected lines, but this difference was not detected in any other environment. We asked here if the response in males differed from that in females.

Context had an effect on larval survival (80% survival in the conspecifics absent treatment, 46% in the low-density treatment, and 30% survival in the high-density treatment). In the survivors, we found no evidence for context-dependence on the effect of selection on female dispersal and the time from egg to adulthood (Main effect – Environment: $\chi^2_2 = 3.3$, $p = 0.2$). We also found no significant selection line-by-sex-by-environment interaction ($\chi^2_2 = 0.04$, $p = 0.9$; Figure 4.3A).

However, selection on female dispersal had a complex effect on the response of reproductive output (number of eggs laid for females and weight of spermatophore for males) to selection that depended on the environment (conspecifics absent or present at high density). For both sexes from all selection lines, reproductive output was 323% lower when conspecific density was high than when conspecifics were absent (Main effect – Environment: $\chi^2_1 = 46.36$, $p < 0.001$, conspecifics absent – 0.13 ± 0.05, conspecifics present – -0.29 ± 0.06). Most interesting, is that there was a significant sex-by-environment-by-selection effect (Interaction: $\chi^2_1 = 4.9$, $p = 0.03$). Males produced spermatophores that did not differ in size regardless of the selection line or environment. In contrast, females from all selection lines laid fewer eggs when conspecific density was high, and when conspecific density was high, females from the dispersal-selected lines laid fewer eggs than females from the non-dispersal-selected lines (Figure 4.3B).

4.5 Discussion

Genetic correlations between the sexes in dispersal traits have some major implications for the evolution of sex differences and for the effects of dispersal on population structure. We indirectly examined the effects of selecting on female dispersal on an array of male traits, including dispersal and possible life history traits that might be correlated with dispersal. We found that for 3 traits, males evolved the same as females in response to the selection on females: males from lines selected for higher dispersal were more active, left the starting patch of a dispersal array faster, and were heavier than males from non-dispersal selected lines. For 2 other traits, males evolved differently from females: females from dispersal-selected lines made more location changes in a dispersal array than those from non-dispersal selected lines, but males from the lines did not differ; and females from the selection lines had similar fecundity, but males from dispersal-selected lines had a smaller spermatophore than males from non-dispersal-selected lines. We did not find any direct evidence that responses of ale traits to selection were context dependent: males from the dispersal- and non-dispersal-selected lines had similar reproductive output regardless of conspecific density. In contrast, female reproductive output was higher for non-dispersal-selected lines than dispersal-selected lines when conspecifics are present, but this difference disappears when conspecifics are absent. The details in each case are relevant to an array of questions about dispersal per se and the ways in which dispersing individuals might carry other trait expressions to new areas.

4.5.1 Some male traits evolved in response to selection on female dispersal

Our experiment specifically selected on female dispersal and had no direct selection on males. From this experimental design, we can ask if there is a shared genetic architecture that would also lead to the evolution of male traits. Of most interest are the traits that differ between the sexes (number of location changes made in a dispersal array and reproductive output). This difference may occur because sex-specific selection imposed by our experimental design has decoupled this genetic correlation. Because it should be more difficult to decouple traits that are controlled by a common mechanism (e.g., pleiotropic gene), it may be that dispersal tendency, measured here as the number of location changes made in a dispersal array, and dispersal distance are traits governed by independent mechanisms (e.g., located on different chromosomes; Sih et al. 2004). Another explanation for our result is that male and female beetles have evolved in response to different selection pressures than males and our experiment did not alter that selection. The timing of dispersal and mating can lead to very different selection on the sexes. If mating occurs before dispersal and oviposition occurs after dispersal (which it does in our experiment), this can impact selection on the sexes because females must disperse and assume any associated costs whereas males can avoid dispersal and the associated costs by staying in once place to mate (Bonte et al. 2012). If timing of dispersal and reproduction alters selection, then experiments that manipulate these factors can yield important insights into the evolution of dispersal syndromes (Massol and Débarre 2015, Canal et al. 2022).

4.5.2 Male reproductive output is not context-dependent, but female reproductive output is

Studies that examine sex-specific genetic correlations in multiple conditions are rare (Poissant et al. 2010) but offer interesting insights into how populations of the same species can vary in their sex-specific trait expression (e.g., variation in the degree of sexual dimorphism among populations; Stillwell et al. 2010, Han and Dingemanse 2017). The importance of measuring sex-specific trait expression across multiple contexts is well highlighted by our results. In the ideal environment (conspecifics absent), when we analyzed male traits separately from female traits, we found that females from the dispersal- and non-dispersal selected lines had similar reproductive effort, whereas males from dispersal-selected lines had a lower reproductive investment than those from non-dispersal-selected lines. However, when we remeasured reproductive investment in a different environment (conspecifics present at high density), males from the two selection lines did not differ, but females from the dispersal-selected lines laid fewer eggs than females from the non-dispersal-selected lines (Chapter 3). If we had measured reproductive effort in only one of these two environments, our conclusions would vary greatly.

Plasticity, the ability of an organism to express different phenotypes in different environments, is well documented (Agrawal 2001, Stillwell et al. 2010). And the sexes may differ in plasticity, which may explain the observation that the magnitude of sexual dimorphism can vary among populations of a species (Stillwell et al. 2010). Our finding that expression of the correlation between reproduction and dispersal is context-dependent for females only is consistent with theoretical predictions that female-biased plasticity should occur when a population is demographically dominated by females (e.g., population growth is more sensitive to female survival and fecundity than males', Hangartner et al. 2021). Female seed beetles are the founders of new populations in this species: females' mate, then disperse to find hosts on which to lay their eggs, ultimately having a large impact on population growth and spread (Miller & Inouye 2013).

4.5.3 Sex-specificity of dispersal syndromes

Because male and female beetles have different traits correlated with dispersal, this suggests that seed beetles have sex-specific dispersal syndromes. Dispersal is commonly sex-biased (Li and Kokko 2019a), and it follows logically, that if dispersal is sexually dimorphic, then dispersal syndromes – the suite of traits correlated with dispersal – can also be sexually dimorphic. Our work adds to the small but growing literature that documents sexually dimorphic dispersal syndromes (reviewed in Chapter 2). Currently, evidence from other studies suggests that sex-specific dispersal syndromes are subtle. For example, in fruit flies (*Drosophila melanogaster*), flies artificially selected for dispersal had lower desiccation than flies from non-dispersal selected lines and this difference was more pronounced in females than males (Mishra et al. 2018). Our results also identified subtle differences in male and female dispersal syndromes. Even subtle differences in dispersal syndromes means that the sexes will interact with each other and the environment differently (Blanckenhorn 2005).

Interestingly, our work highlights that the traits correlated with dispersal and that form a dispersal syndrome, can evolve due to cross-sex genetic correlations. Thus, even if only a one sex is experiencing selection on a dispersal syndrome, the cross-sex genetic correlation could cause the other sex's dispersal syndrome to evolve as well. Currently, theory predictions that the effect of selection in one sex could either restrict or enhance evolution of correlated traits in the other sex (Bonduiansky and Chenoweth 2009). An intriguing avenue for future research is to measure dispersal syndromes of males and females across multiple environmental contexts to explore the interplay of cross-sex correlations, plasticity, and sex-specific dispersal syndromes (see Choy et al. 2023 for an example).

4.5.4 Implications of context-dependent cross-sex genetic correlations for metapopulation dynamics

When the sexes have different expression of traits within a dispersal syndrome, these differences could lead to variation in the subpopulations within metapopulations (e.g., regional populations in a spatially fragmented landscape). Variation in individual thresholds to an environmental cue (e.g., conspecific density) will produce a mosaic of population densities in the subpopulations (Benton and Bowler 2012). These individuals then have other traits (e.g., reproductive output, activity) within the dispersal syndrome that will interact with the local environment (e.g., conspecific density, predators, food availability) to shape local evolution within a subpopulation (Ronce and Clobert 2012). Our work begins to link together within- and among-sex genetic correlations for traits that comprise a dispersal syndrome, but there is a dearth of studies that explore the impact of the genetic architecture on the population. While complexity of these topics alone makes integrating them to predict the impact of sex-specific dispersal syndromes on population dynamics difficult, this complexity opens some intriguing avenues of future research into the causes and consequences of sex-specific dispersal syndromes for the ecology and evolution of populations in spatially fragmented landscapes.

APPENDICES

APPENDIX A. VARIATION AMONG INDIVIDUALS IN DISPERSAL SYNDROME: EFFECTS OF CONTEXT-DEPEDENCY, SEX-SPECIFICITY, AND PLASTICITY ON METAPOPULATION DYNAMICS

Table A1. Summary of literature describing dispersal syndromes and how dispersal syndromes can vary by sex, environmental context, or during stages of dispersal.

Species	**Traits Evaluated**	**Results**	**Data Type**	**Reference**
A) Dispersal Syndromes				
Common skink (*Lampropholis delicata*)	activity, sociability, exploration	Active lizards are more exploratory and social than less active lizards	wild captured, behavior tested in laboratory	Michelangeli et al. 2016
Gran fritillary (*Melitaea cinxia*)	flight, reproduction, and lifespan	Disperser females laid eggs at a younger age, laid more clutches, and had higher fecundity than non-dispersing females	wild caught, 1 generation in lab before testing	Hanski et al. 2006; Saastamoinen 2007; Niitepõld 2019
Pied flycatcher (*Ficedula hypoleuca*)	aggression, dispersal	Individuals that dispersed (both those that settled empty patches and immigrated to established populations) were more aggressive than philopatric individuals	wild population	Nicolaus et al. 2022
Meditteranean fruit fly (*Ceratitis capitata*)	dispersal distance, body mass, abdomen mass, thorax mass, thorax mass to body mass ratio, and abdomen mass to body mass ratio	Flies that dispersed long distances had a larger body mass, abdomen mass, thorax mass, thorax to body mass ratio, and abdomen to body mass ratio than flies that did not disperse	laboratory bred population tested in semi-natural enclosure	Steyn et al. 2016

Sand cricket (*Gryllus firmus*)	wing morph (long vs short), juvenile hormone, reproduction, mate calling	1) Long wing crickets (disperser morph) had a clear cycle of juvenile hormone with crepuscular peaks, whereas short wing (non-disperser morph) had no daily cycle of juvenile hormone 2) Long wing morph females are lighter and lay fewer eggs than short wing morphs 3) Long wing morph males have a shorter mate call duration than short wing males	wild and laboratory populations	Zera and Bottsford 2001; Zera and Cisper 2001; Roff and Fairbairn 2007; Zera et al. 2007
European badger (*Meles meles*)	dispersal, body size, testosterone	Disperser males had a larger body, higher testosterone and maintained testicular activity longer than non-dispersing males	wild population	Woodroffe et al. 1995
Naked mole rat (*Heterocephalus glaber*)	dispersal, body size, aggression towards conspecifics, and luteinizing hormone	Non-dispersing individuals have less body fat, increased aggression towards conspecifics from other colonies, and decreased luteinizing hormone than dispersing individuals	wild population	O'Riain et al. 1996
Beldings ground squirrel (*Spermophilius beldingi*)	dispersal, testosterone	Females treated with testosterone propionate had a higher dispersal tendency than females not treated with testosterone	wild population	Holekamp et al. 1984
Parasitoid wasp (*Melittobia australica*)	dispersal, wing length, abdomen size, fecundity	Dispersal morph females have longer wings, smaller abdomen, decreased dispersal tendency, and decreased fecundity compared to non-dispersal morphs	laboratory bred population	Innocent et al. 2010

Western bluebird (*Sialia mexicana*)	dispersal, aggression	Disperser males were more aggressive than non-disperser males	wild population	Duckworth 2006
Ciliate (*Tetrahymena thermophila*)	dispersal, aggregation, cell shape	Ciliates that were aggregated also had lower growth rates, smaller more elongated cell shapes, and were less dispersive	laboratory culture	Schtickzelle et al. 2009
Ciliate (*Tetrahymena thermophila*)	dispersal, cell shape, sensitivity to patch quality, growth rate	1) Ciliates that dispersed had an increased dispersal propensity, smaller more elongated cells, and high sensitivity to patch quality 2) Dispersal was not correlated with reproduction	laboratory culture	Jacob et al. 2019
B) Sex-specific Dispersal Syndromes				
Fruit flies (*Drosophilia melanogaster*)	body size, desiccation resistance, exploration	1) Across sexes, dispersal selected flies had lower desiccation than non-dispersal selection flies, but this difference was more pronounced in females than males 2) Disperser males and females had similar exploration and body mass as non-disperser individuals	laboratory populations, artificial selection for dispersal	Mishra et al. 2018
Butterflies (*Pieris brassicae*)	flight performance, lifespan, offspring production, mating success	1) Disperser males (high flight performance) had high mating success and offspring production 2) Disperser females (high flight performance) had long lifespan 3) Non-disperser females (low flight performance) had increased offspring production	semi-natural experiment with laboratory breed individuals	Legrand et al. 2016

Common skink (*Lampropholis delicata*)	activity, sociability, exploration	Disperser and non-disperser individuals did not vary by sex	wild captured, behavior tested in laboratory	Michelangeli et al. 2016
Mediterranean fruit fly (*Ceratitis capitata*)	dispersal distance, body mass, abdomen mass, thorax mass, thorax mass to body mass ratio, abdomen mass to body mass ratio, and relative wing size	Disperser and non-disperser individuals did not vary by sex	laboratory bred population tested in semi-natural enclosure	Steyn et al. 2016
Red flour beetle (*Tribolium castaneum*)	dispersal distance, mating frequency, predation	1) Males from lines selected for long-distance dispersal had an increased mating success and higher risk of predation than males from the lines selected for short distance dispersal 2) Females from lines selected for long-distance dispersal had increased risk of predation compared to females from lines selected for short-distance dispersal 3) Females from short- and long-distance dispersal selection lines did not differ in their mating frequency	artificial selection	Matsumura & Miyatake 2015
Great tit (*Parus major*)	dispersal, exploratory behavior	1) In females, dispersal distances and exploratory behavior were correlated 2) No correlation in males	wild population	van Overveld et al. 2014
Seed beetles (*Callosobruchus maculatus*)	activity, dispersal tendency, reproductive output	1) Disperser females have lower reproductive output and higher dispersal tendency than non-disperser females 2) Disperser and non-disperser males show no difference	artificial selection	Chapter 4, this dissertation

C) Context-dependent Dispersal Syndromes				
Fruit flies (*Drosophilia melanogaster*)	dispersal, body size, dessication resistance, exploration	1) Flies that developed in high nutrition environment, dispersive females where heavier than non-dispersive females, no difference among males. No difference among sex and dispersers/non-dispersers in low nutrition environment 2) In both environments, disperser females were more resistance to desiccation than non-disperser females, but males did not differ 3) Flies that developed in a low nutrition environment, disperser males were less exploratory than non-disperser males, no difference among females. No difference among sex and dispersers/non-dispersers in high nutrition	laboratory populations	Mishra et al. 2018
Gran fritillary (*Melitaea cinxia*)	dispersal distance, overwinter survival of offspring	1) overwinter survival of clutches from long-distance disperser females were higher if the female colonized an empty patch than if the disperser female immigrated to an occupied patch. This pattern is the opposite for clutches of short-distance disperser females, and there was no relationship for non-dispersers. 2) clutches of disperser females were less likely to survive overwinter when laid in habitat patches with high grazing than clutches of residents in patches with grazing	wild population	Dileo et al. 2022
Gran fritillary (*Melitaea cinxia*)	flight, reproduction, and lifespan	1) dispersing females given reduced food laid fewer eggs and smaller clutches than dispersing females given ad libitum food 2) Dispersing females with unlimited food had a shorter lifespan than dispersing females with restricted food and non-dispersing females	wild caught, 1 generation in lab before testing	Niitepõld 2019

Pied flycatcher (*Ficedula hypoleuca*)	aggression, dispersal	In a year with harsh environmental conditions, the dispersers were more aggressive than dispersers in a year with good conditions	wild population	Nicolaus et al. 2022
pea aphids (*Acyrthosiphon pisum*)	dispersal morph, reproduction, symbiont association	1) Aphids that evolved on pea and broad bean plants produced winged males exclusively, high investment into reproduction, and had *S. symbiotica* and *Rickettsia* symbionts 2) Apids that evolved on red clover produced wingless males, reduced sexual reproduction, and instead reproduced asexually, and had *H. defensa* and *Spiroplasma* symbionts	laboratory populations	Frantz et al. 2009
ciliate (*Tetrahymena thermophila*)	dispersal, cell shape, movement	Ciliates that dispersed were more elongated, and moved faster and straighter than ciliates that did not disperse, and the difference in these traits between dispersers and non-dispersers were larger when the matrix between habitat patches was harsh compared to a control matrix that was the same the habitat patches.	laboratory culture	Jacob et al. 2020
D) Timing of Dispersal Syndromes				
Spotted hyena (*Crocuta crocuta*)	dispersal, testosterone	In a social group, natal males (young males that had not dispersed) and recently immigrated males had lower testosterone than long-term resident immigrant males	wild population	Holekamp & Sisk 2003
Common lizard (*Lacerta vivipara*)	dispersal, sociality	1) Individuals that are highly attracted to conspecifics, dispersed when conspecific density was low. In contrast, individuals that were not attracted to conspecifics, did not emigrate when conspecific density was low 2) At high conspecific density, the opposite was true: individuals attracted to conspecifics stayed and individuals unattracted to conspecifics dispersed	wild caught animals, tested in a semi-natural enclosure	Cote and Clobert 2007

		3) Individuals that dispersed from low density natal areas settled in areas with high conspecific density more often than areas with low conspecific density		
Great tit (*Parus major*)	dispersal, exploratory behavior	1) Males the immigrated (e.g., those that had dispersed) had a higher exploratory behavior shortly after dispersal (summer and autumn), but in the winter, there was no difference between the immigrant and resident birds 2) In females, there was no difference between immigrant and resident birds in any season	wild population	van Overveld et al. 2014

APPENDIX B. ARTIFICIAL SELECTION REVEALS A DISPERSAL SYNDROME WITH LIMITED CONTEXT DEPENDENCY IN A SEED BEETLE

Table B1. Sample sizes for all measures of dispersal and life-history traits of female seed beetles. Dispersal distance and general activity were measured in a single environment, and the activity test was repeated for each individual 3 times (Trial 1, Trial 2, and Trial 3). Any trait used to assess correlated responses to selection were measured in 1 of three environments (conspecific eggs absent, conspecific eggs present at low density, or high density of conspecific eggs).

Dispersal Distance

		Non-dispersal 1	Non-dispersal 2	Control	Dispersal 1	Dispersal 2
Conspecifics Absent	Block 1	22	23	22	24	24
	Block 2	27	27	23	27	29
Low Density	Block 1	23	24	23	24	24
	Block 2	26	26	24	27	30
High Density	Block 1	24	22	23	24	23
	Block 2	26	28	23	29	29

General Activity

	Non-dispersal 1	Non-dispersal 2	Control	Dispersal 1	Dispersal 2
Block 1	23	24	23	24	24
Block 2	26	24	24	28	30

Correlated response to selection across multiple environments (body mass, 24 hr fecundity, lifetime fecundity, egg length and width, egg distribution traits)

	Non-dispersal 1	Non-dispersal 2	Control	Dispersal 1	Dispersal 2
Conspecifics Absent	43	48	40	46	50
Low density	41	47	41	45	51
High density	45	46	41	49	49

Correlated response to selection across multiple environments (larval development time)

	Non-dispersal 1	Non-dispersal 2	Control	Dispersal 1	Dispersal 2
Conspecifics Absent	27	27	25	26	32
Low density	21	19	13	24	30
High density	27	24	23	26	30

Table B2. Summary of artificial spatial sorting experiment for four experimental lines and three lines of seed beetles (*Callosobruchus maculatus*, Coleoptera: Chrysomelidae, Bruchinae). In the Control and Parent populations, there are no data available for selected female variables or effective line size because the control lines were only measured at the beginning and end of the experiment and there was no selection between those two measures. Effective line size (N_e) calculated with harmonic mean using the number of females selected each generation as the line size. Because the Control line in generation 0 is the start of the experiment, the summary statistics for the Control line in generation 0 are the same for every experimental line in generation 0.

Population	Generation	Number Females Run Through Arrays	Numbers Females Selected to Continue Lines	Farthest Dish with at Least 1 Egg Laid - All Females	Farthest Dish with at Least 1 Egg Laid - Selected Females	Effective line Size (N_e)	Effective Selection Differential	Response to Selection	Cumulative Effective Selection Differential	Cumulative Response to Selection
Non-disperser Replicate 1	0	121	40	2.0 ± 1.1	1.5 ± 0.7	121	-	-	-	-
	1	69	28	2.6 ± 1.5	1.4 ± 1.1	32.9	-0.4	0.6	-0.4	0.6
	2	84	22	3.2 ± 1.4	1.2 ± 0.8	28.3	-1.2	0.6	-1.6	1.2
	3	99	20	2.4 ± 1.4	2.0 ± 0.0	25.6	-1.8	-0.7	-3.5	0.5
	4	100	18	3.1 ± 1.9	2.0 ± 0.0	23.6	-0.4	0.7	-3.9	1.1
	5	80	16	3.2 ± 2.0	2.0 ± 0.0	21.9	-1.1	0.1	-5.0	1.2
	6	82	32	2.2 ± 1.5	0.8 ± 0.5	22.9	-1.2	-1.0	-6.2	0.2
	8	86	20	2.7 ± 1.2	1.1 ± 0.6	22.5	-1.4	0.5	-7.6	0.7
Non-disperser Replicate 2	0	121	50	2.0 ± 1.1	1.5 ± 0.7	121	-	-	-	-
	1	72	21	2.9 ± 1.2	1.8 ± 1.1	29.6	-0.5	0.9	-0.5	0.9
	2	80	24	3.2 ± 1.2	1.8 ± 0.4	27.5	-1.0	0.3	-1.5	1.2
	3	102	25	2.5 ± 1.5	2.0 ± 0.0	26.8	-1.4	-0.7	-2.9	0.5
	4	100	16	3.7 ± 2.2	2.0 ± 0.0	23.6	-0.5	1.2	-3.4	1.7

	5	71	12	3.2 ± 2.0	2.0 ± 0.0	20.3	-1.7	-0.5	-5.0	1.2
	6	78	30	2.2 ± 1.3	1.1 ± 0.7	21.3	-1.2	-1.0	-6.2	0.3
	8	86	22	2.5 ± 1.1	1.2 ± 0.7	21.4	-1.0	0.3	-7.2	0.6
Disperser Replicate 1	0	121	18	2.0 ± 1.1	3.3 ± 0.6	121	-	-	-	-
	1	78	46	3.0 ± 1.4	3.6 ± 0.9	25.9	1.3	1.0	1.3	1.0
	2	79	17	3.1 ± 1.4	4.4 ± 0.7	22	0.7	0.1	1.9	1.1
	3	97	14	3.7 ± 1.8	5.6 ± 0.7	19.3	1.3	0.6	3.2	1.8
	4	78	12	5.0 ± 1.7	6.8 ± 0.8	17.2	1.9	1.2	5.2	3.0
	5	76	12	4.9 ± 2.2	7.3 ± 0.5	16	1.9	-0.1	7.0	2.9
	6	74	10	6.5 ± 1.6	8.6 ± 0.7	14.8	2.5	1.6	9.6	4.6
	8	77	14	6.1 ± 1.6	7.9 ± 0.6	14.7	2.0	-0.4	11.5	4.2
Disperser Replicate 2	0	121	13	2.0 ± 1.1	3.5 ± 1.0	121	-	-	-	-
	1	74	53	3.2 ± 1.3	3.7 ± 0.9	20.9	1.7	1.3	1.7	1.3
	2	81	15	3.4 ± 1.3	4.8 ± 0.8	18.5	0.5	0.1	2.2	1.4
	3	91	11	3.5 ± 2.0	5.6 ± 0.8	15.8	1.5	0.2	3.7	1.6
	4	83	15	5.0 ± 2.0	6.9 ± 1.0	15.6	2.1	1.5	5.8	3.0
	5	78	15	5.4 ± 1.9	7.4 ± 0.7	15.5	1.9	0.4	7.7	3.4
	6	72	15	6.4 ± 2.0	8.9 ± 1.2	15.4	2.0	1.1	9.7	4.5
	8	77	15	5.7 ± 2.0	7.9 ± 0.5	15.4	2.4	-0.7	12.1	3.7
Control	0	121	-	2.0 ± 1.1	-	-	-	-	-	-
	9	61	-	3.0 ± 1.1	-	-	-	1.1	-	0.77

Did artificial selection alter the dispersal behavior?

Two generations after the end of the selection experiment, we found that when dispersal was measured as the farthest dish in an array where the female laid the largest proportion of her eggs, was different among selection treatments (GLM with Conway-Maxwell Poisson distribution – Interaction between selection and density treatments: $\chi^2_2 = 5.4$, $p = 0.07$, Table S2). In all environments, the dispersal lines laid their farthest egg in the dispersal arrays farther than non-dispersal lines and all lines increased the distance in the array where they laid eggs as the conspecific density increased (Figure B1, Table B3 and B4).

When dispersal was measured as the location in a dispersal array after 24 h, there was no interaction between selection and environment treatments (Figure B1, Table B3 and B4).

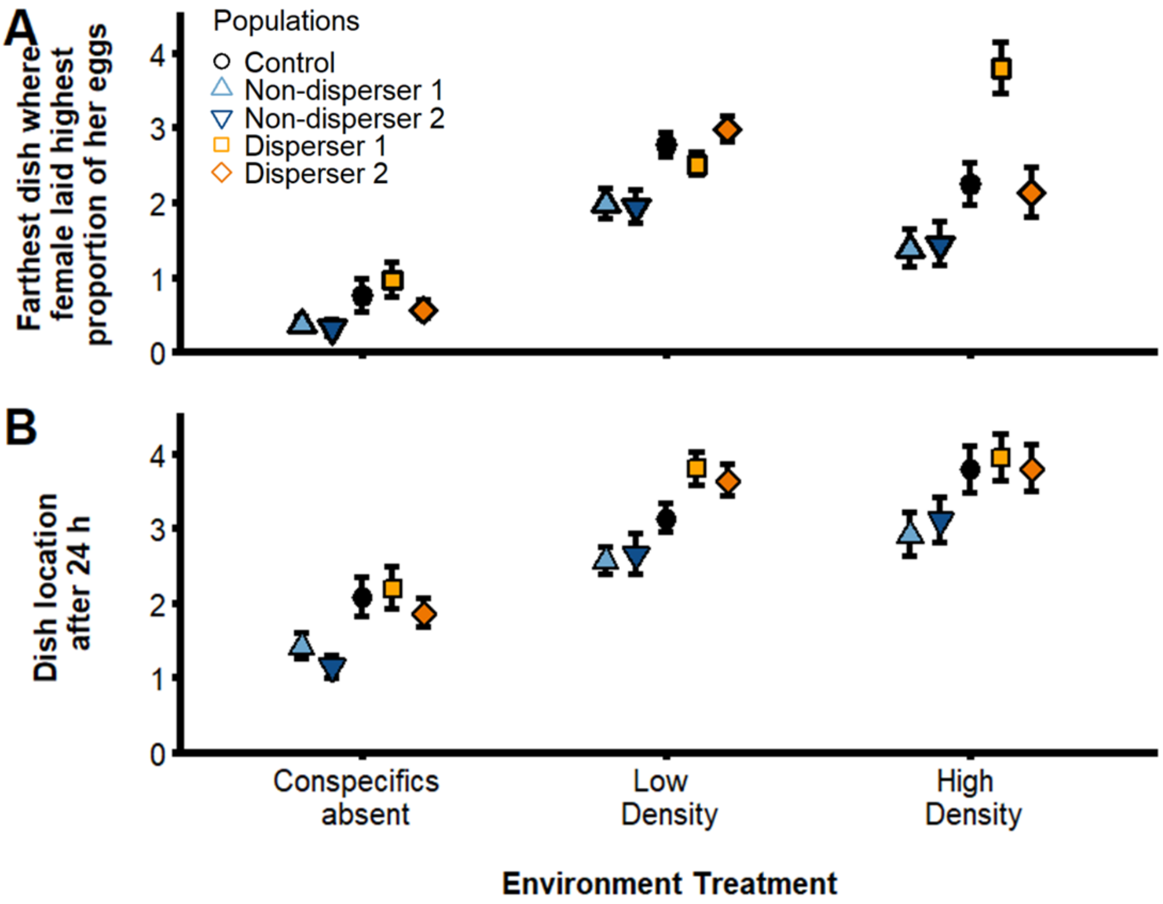

Figure B1. Mean dispersal distance (± SE) measured as the farthest dish where a female laid at least one egg and dish location after 24 h.

Table B3. ANOVA results for all models to evaluate directly selected dispersal traits (farthest dish with at least 1 egg laid, farthest dish where female laid at least 50% of her eggs, and location after 24 h) and indirectly selected dispersal traits (activity – total distance travelled, and dispersal tendency – number of location changes and time to leave the starting patch).

Response	Variable	$\chi2$	DF	P-value
Farthest dish with at least 1 egg	Selection Treatment	33.6	1	< 0.001
	Environment Treatment	239.5	2	< 0.001
	Block	3.5	1	0.06
	Selection: Environment	11.4	2	< 0.01
Farthest dish where female laid the highest proportion of her eggs	Selection Treatment	11.2	1	< 0.01
	Environment Treatment	88.3	2	< 0.001
	Block	0.0	1	0.99
	Selection: Environment	5.4	2	0.07
Location after 24 h	Selection Treatment	9.1	1	< 0.01
	Environment Treatment	70.0	2	< 0.001
	Block	0.0	1	0.95
	Selection: Environment	1.1	2	0.58
log[Total distance travelled (mm) +1]	Selection Treatment	3.2	1	0.07
	Block	0.1	1	0.7
Number of location changes	Selection Treatment	5.8	1	< 0.001

Table B4. Contrast results comparing dispersal selected lines vs non-dispersal selected lines for models to evaluate directly selected dispersal traits (farthest dish with at least 1 egg laid, farthest dish where female laid at least 50% of her eggs, dish location after 24 h in array) for three environmental treatments (conspecifics absent, conspecifics present at low density, and conspecifics present at high density). The contrast estimate is calculated on the log scale from the statistical model, whereas the mean ± SE presented for each group are calculated with the raw data.

Trait	Environment	Disperser mean ± SE	Non-Disperser mean ± SE	Estimate	SE	z - Ratio	p-value
Farthest dish where a female laid at least one egg	Conspecifics absent	2.4 ± 0.2	1.4 ± 0.1	0.6	0.1	5.6	< 0.001
	Low density	3.1 ± 0.2	2.1 ± 0.1	0.3	0.1	3.9	< 0.001
	High density	4.4 ± 0.3	3.2 ± 0.2	0.2	0.1	3.5	< 0.001
Farthest dish where a female laid the largest proportion of her eggs	Conspecifics absent	0.7 ± 0.1	0.3 ± 0.1	0.55	0.10	5.64	< 0.001
	Low density	1.5 ± 0.1	1.1 ± 0.1	0.27	0.07	3.94	< 0.001
	High density	2.2 ± 0.2	0.9 ± 0.1	0.18	0.05	3.48	< 0.001
Dish location at 24 h	Conspecifics absent	2.0 ± 0.2	1.3 ± 0.1	0.80	0.24	3.25	< 0.01
	Low density	2.8 ± 0.2	1.8 ± 0.1	0.34	0.13	2.54	0.01
	High density	3.0 ± 0.2	2.0 ± 0.2	0.75	0.14	5.25	< 0.001

Correlated responses of life-history traits to selection for dispersal

Table B5. ANOVA results for all life-history traits to evaluate phenotypic correlations between dispersal, represented by the dispersal- and non-dispersal-selected lines, across multiple environments (conspecifics absent, low conspecific density, and high conspecific density). Models for body mass and egg distribution report an F test statistic, all other models report egg a χ^2 test statistic.

Response	Variable	Test Statistic	DF	P-value
Body mass	Selection Treatment	73.67	1	< 0.001
24-hr Fecundity (sum of hatched & unhatched)	Selection Treatment	1.37	1	0.24
	Environment Treatment	107.47	2	< 0.001
	Body Mass	2.38	1	0.12
	Selection: Environment	13.74	2	< 0.01
Egg Distribution	Selection Treatment	0.01	1	0.94
	Environment Treatment	17.89	2	< 0.001
	Selection: Environment	1.70	2	0.18
Egg length (mm)	Selection Treatment	6.14	1	0.01
	Environment Treatment	4.56	2	0.10
	Selection: Environment	1.96	2	0.38
Egg width (mm)	Selection Treatment	1.04	1	0.31
	Environment Treatment	4.66	2	0.10
	Selection: Environment	3.78	2	0.15
Lifetime Fecundity (sum of hatched & unhatched)	Selection Treatment	0.03	1	0.87
	Environment Treatment	1.47	2	0.47
	Selection: Environment	3.84	2	0.15
Lifespan (days)	Selection Treatment	1.08	1	0.30
	Environment Treatment	0.13	2	0.93
	Selection: Environment	1.16	2	0.56
Time to Emerge (days)	Selection Treatment	0.01	1	0.92
	Environment Treatment	3.32	2	0.19
	Selection: Environment	0.42	2	0.81

APPENDIX C. SELECTION FOR HIGHER DISPERSAL IN FEMALES REVEALS CROSS-SEX GENETIC CORRELATIONS

Table C1. Sample sizes for all measures of dispersal and life-history traits of male and female seed beetles. Dispersal traits were measured in a single environment but repeated for each individual 3 times (Trial 1, Trial 2, and Trial 3). Larval development time and reproductive output were measured in multiple environments.

Activity

			Non-dispersal 1	**Non-dispersal 2**	**Control**	**Dispersal 1**	**Dispersal 2**
Females	Block 1	Trial 1	22	22	23	24	24
		Trial 2	23	24	23	23	24
		Trial 3	23	23	23	24	24
	Block 2	Trial 1	25	24	24	28	30
		Trial 2	26	24	24	27	30
		Trial 3	25	24	24	26	28
Males	Block 1	Trial 1	23	22	23	22	24
		Trial 2	23	22	22	23	24
		Trial 3	23	22	23	23	24
	Block 2	Trial 1	27	29	25	30	31
		Trial 2	27	29	25	29	29
		Trial 3	25	27	24	30	29

Dispersal Tendency

		Non-dispersal 1	**Non-dispersal 2**	**Control**	**Dispersal 1**	**Dispersal 2**
Females	Trial 1	40	38	41	39	39
	Trial 2	40	38	41	39	39
	Trial 3	40	38	41	39	39
Males	Trial 1	39	38	44	41	38
	Trial 2	39	38	44	41	38
	Trial 3	38	38	44	41	38

Body Mass

		Non-dispersal 1	**Non-dispersal 2**	**Control**	**Dispersal 1**	**Dispersal 2**
Females	Block 1	71	70	69	72	71
	Block 2	80	85	71	87	89
Males	Block 1	71	70	69	72	71

Block 2	80	85	71	87	89

Larval Development Time

	Non-dispersal 1	**Non-dispersal 2**	**Control**	**Dispersal 1**	**Dispersal 2**
Conspecifics Absent	27	27	25	26	32
Low Density	21	19	13	24	30
High Density	27	24	23	26	30

Reproductive Output

		Non-dispersal 1	**Non-dispersal 2**	**Control**	**Dispersal 1**	**Dispersal 2**
Females	Conspecifics Absent	43	48	40	46	50
	High Density	45	46	41	48	49
Males	Conspecifics Absent	35	51	38	48	61
	High Density	34	41	25	24	29

Table C2. ANOVA results for all models to evaluate dispersal traits (activity – total distance travelled, and dispersal tendency – number of location changes and time to leave the starting patch) and life-history traits (body mass, larval development time – number of days from egg laying to adult emergence, and reproductive output – total number of eggs laid in 24 h for females and spermatophore weight for males).

Response	**Variable**	**$\chi 2$**	**DF**	**P-value**
log[Total distance travelled (mm) +1]	Selection Treatment	3.26	1	0.07
	Sex	32.05	1	< 0.001
	Block	2.85	1	0.09
	Selection: Sex	0.97	1	0.32
Number of Location Changes in Array	Selection Treatment	15.72	1	< 0.001
	Sex	14.60	1	< 0.001
	Selection: Sex	4.61	1	0.03
Time to Leave Starting Dish of Array	Selection Treatment	10.84	1	< 0.001
	Sex	8.35	1	< 0.01
	Selection: Sex	0.76	1	0.38
Body Mass (mg)	Selection Treatment	40.50	1	< 0.001
	Sex	2210.48	1	< 0.001
	Block	0.99	1	0.32
	Selection: Sex	12.64	1	< 0.001

Larval Development Time (days)	Selection Treatment	0.01	1	0.91
	Sex	0.19	1	0.66
	Environment Treatment	3.32	2	0.19
	Selection: Sex	0.01	1	0.90
	Selection: Environment	0.42	2	0.81
	Sex: Environment	0.14	2	0.93
	Selection: Sex: Environment	0.001	2	0.98

Reproductive Output	Selection Treatment	3.17	1	0.08
	Environment Treatment	46.36	1	< 0.001
	Sex	10.71	1	< 0.01
	Mass	49.70	1	< 0.001
	Selection: Environment	5.27	1	0.02
	Selection: Sex	0.07	1	0.80
	Environment: Sex	16.64	1	< 0.001
	Selection: Environment: Sex	4.89	1	0.03

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Zwoinska, M.K., T. Larva, Z. Sekajova, H. Carlsson, S. Meurling, and A.A. Maklakov. 2020. Artificial selection for increased dispersal results in lower fitness. Journal of Evolutionary Biology 33:217-224.

VITA

EDUCATION AND CERTIFICATES

- University of Kentucky, Ph.D. Biology. In progress, Expected August 2023 (Lexington, KY)
  Qualifying Exam Completed December 2017 GPA: 3.86/4.0
- University of Arizona, M.Sc. Natural Resources - Wildlife Conservation and Management Emphasis, 2015. (Tucson, AZ) GPA: 4.0/4.0
- St. Lawrence University, B.S. Conservation Biology, cum laude and Honors in major, minor in Mathematics, 2010 (Canton, NY) GPA: 3.34/4.0
- Cornell University. Professional Certification – Bioacoustic Analysis. 2019. (Ithaca, NY)
- University of Kentucky. Professional Certification – Applied Statistics. 2017. (Lexington, KY)
- James Cook University, Study abroad, 2009 (Queensland, Australia)

PROFESSIONAL EXPERIENCE

USDA Pre-Doctoral Fellowship, UK: Jun 2020 - present

Graduate Teaching Assistant – *Evolution*, UK (Dr. Madhusudan Srinivasan): Jan 2018 - May 2020

Dept of Biology Graduate Merit Fellowship – UK, Aug - Dec 2017

Graduate Teaching Assistant – *Evolution,* UK (Dr. Madhusudan Srinivasan): Jan - May 2017

Graduate Teaching Assistant – *Ecology*, UK (Dr. Kausalya Shenoy): Jan - May 2016

Graduate Teaching Assistant – *Intro Biology*, UK (Dr. Lin Xiang): Aug - Dec 2015

Graduate Teaching Assistant – *Natural Resources Measurements*, UA (Dr. Robert Steidl): Jan-May 2014

Graduate Research Assistant, UA (Dr. John Koprowski): Aug 2012- Aug 2015

Research Assistant, Universitaet Regensburg (Dr. Peter Poschold, Regensburg, Germany): Apr - Jul 2012

Research Technician, Florida State University (Dr. Nora Underwood): Jun 2010 - Feb 2012

Research Technician, Florida State University (Dr. Thomas Miller): May - Aug 2011

Volunteer, US Forest Servcie: Red Cockaded Woodpecker Monitoring Program (Charles Hess, Apalachicola National Forest): Apr - Sep 2011

Intern, University of Washington (Dr. Charles Halpern): Jun - Aug 2009

Intern, Boston University (Dr. Pamela Templer): Jun - Aug 2008

PUBLICATIONS

Peer- Reviewed

Kilanowski, A.L., and J.L. Koprowski. 2017. Female-biased sexual dimorphism: Ontogeny, seasonality, and fecundity of a chipmunk (*Tamias dorsalis*). Journal of Mammalogy. 98: 204-210.

Kilanowski, A.L., and J.L. Koprowski. 2016. Communal denning of cliff chipmunks (*Tamias dorsalis*). Southwestern Naturalist. 61: 248-261

Jessen, T.J., **A. L. Kilanowski**, R. N. Gwinn, M. J. Merrick, and J. L. Koprowski. 2016. *Microsciurus flaviventer* (Rodentia: Sciuridae). Mammalian Species Account. 48:59-65.

Kim, T., B. Spiesman, A. Buchanan, A. S. Hakes, S. Halpern, B.D. Inouye, **A.L. Kilanowski**, N. Kortessis, D.W. McNutt, A.C. Merwin, and N. Underwood. 2015. Selective manipulation of a non-dominant plant and its herbivores affects an old-field plant community. Plant Ecology 216:1029-1045.

Halpern, C.B., R. D. Huago, J.A. Antos, S. S. Kaas, and **A. L. Kilanowski**. 2012. Grassland restoration without fire: evidence from a tree removal experiment. Ecological Applications 22: 425-441.

Non-Peer Reviewed

Kilanowski, A.L., H.M. Moore, and A.M. Veals. 2015. Cooperation between grads and undergrads for a better field season: Tips for working together to promote a successful and positive work environment. The Wildlife Society Newsletter. May Issue. PDF
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SCHOLASTIC AND PROFESSIONAL HONORS

- College of Arts and Sciences Outstanding TA Award (University of Kentucky, 2020)
- Dept. of Biology Morgan Fellowship (DECLINED, University of Kentucky, 2020)
- Scherr Opportunity Fellowship (University of Kentucky, 2019)
- Dept. of Biology Merit Fellowship (University of Kentucky, 2017)
- Ribble Mini Research Grant (University of Kentucky, 2017)
- Ecological Society of America Student Chapter Travel Grant (2016)
- Ribble Travel Grant (University of Kentucky, 2016)
- Daniel R. Reedy Quality Achievement Fellowship (University of Kentucky, 2015-2017)
- Graduate Student Council Travel Grant (University of Kentucky, 2015)
- Ribble Research Start-up Fellowship (University of Kentucky, 2015)
- Graduate Student Council Travel Grant (University of Arizona, 2015)
- Institute of the Environment Travel Grant (University of Arizona, 2015)
- C. P. Patrick Reid Leadership Scholarship (University of Arizona, 2015)
- Runner-up Earthweek Graduate Research Poster Competition (University of Arizona, 2015)
- Arrington Memorial Scholarship (University of Arizona, 2014-15)
- Graduate Student Council Travel Grant (University of Arizona, 2014)
- Institute of the Environment Travel Grant (University of Arizona, 2014)
- Outstanding Public Service and Outreach Award (University of Arizona, 2014)
- T&E Inc Research Grant (2013)
- American Society of Mammalogists Research Grant (2013)
- Soil and Water Conservation Society of New York State Scholarship (2010)

- Pi Mu Epsilon, Mathematics Honor Society (2010)
- Omicron Delta Kappa, National Leadership Society (2009-2010)
- Bradley R. Evers Outstanding First Year Student Award (St. Lawrence University, 2007)