The Effects of Food Availability on Body Condition and Dispersal in the Backswimmer, *Notonecta undulata*

by

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A thesis submitted in conformity with the requirements for the degree of Master of Science
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Abstract

Dispersal is the movement of organisms across space that has the potential to cause gene flow. It therefore has important implications for ecological and evolutionary processes. Previous studies have demonstrated that dispersal is influenced by body condition; however, the results of these studies have been inconsistent with respect to the direction of this relationship. I asked whether predation risk interacts with condition to cause variable effects on dispersal. I tested this by imposing diet treatments on backswimmers (*Notonecta undulata*) in the laboratory. I measured the effects of food availability on condition. I then measured the effects of condition and predators on dispersal in a field experiment. I found that dispersal was a positive function of both body condition and predation risk. However, their effects were additive, not interactive. Therefore, the interaction between condition and predation risk is likely not contributing to the inconsistency in the results of condition-dependent dispersal studies.
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Appendix 1: Carryover effects of juvenile diet on adult physiology and dispersal
General Introduction

Dispersal is the movement of organisms across space from a natal site or site of reproduction to a new site of reproduction (Howard 1960, Matthysen 2012). Dispersal therefore encompasses both the movement of individuals across physical space, as well as the potential for gene flow among populations. Both of these aspects of dispersal can have important implications for ecological and evolutionary processes (Clobert et al. 2001, Bowler and Benton 2005, Ronce 2007).

The movement of individuals across physical space has consequences for population and community dynamics. Dispersal influences the strength and variability of intraspecific competition across the landscape by altering the density of individuals within patches through emigration and immigration (Bowler and Benton 2005, Ronce 2007). The dispersal ability or propensity of a species can influence whether it is found in a given patch, and so influence local and regional species compositions (Brown 1950, Clobert et al. 2012a). Dispersal can also provide spatial refuge for prey or inferior competitors, and thereby stabilize antagonistic interactions, and enable coexistence (Sabelis and Diekmann 1988, Comins and Hassell 1996).

The movement of individuals is also a fundamental driver of metapopulation characteristics such as synchrony and persistence (Kuno 1981, Pulliam 1988, Ranta et al. 1995, Kendall et al. 2000). Theoretical studies have shown that dispersal among patches can influence metapopulation synchrony, but the direction of this effect depends on factors such as the rate of dispersal, the level of demographic stochasticity, and population size (Hauzy et al. 2010, Simonis 2012). Whether dispersal increases or decreases metapopulation synchrony may be an important question, as synchronous dynamics increase the risk of entire metapopulation extinction (Heino et al. 1997). However, when metapopulation dynamics are not synchronized, metapopulation theory suggests that dispersal should decrease the risk of extinction, because growing populations send emigrants to declining or empty patches (termed the “rescue effect”; Brown and Kodric-Brown 1977).

Dispersal is the mechanism by which gene flow occurs, and therefore it can have important consequences for the evolution of populations. Gene flow reduces the effects of drift and prevents inbreeding depression, and so can influence the genetic structure of the metapopulation and reduce population extinction rates (Tallmon et al. 2004). Gene flow also influences the rate
of local adaptation. High rates of gene flow may decrease the rate of local adaptation by flooding patches with locally maladaptive genotypes (Rasanen and Hendry 2008), or by uniting divergent haplotypes, producing maladaptive gene combinations that impede local adaptation (Wade and Goodnight 1998). However, gene flow may also increase the rate of local adaptation by bringing together novel allele combinations (Holt and Gomulkiewicz 1997), or by phenotype-habitat matching (whereby individuals preferentially settle in the environment that best matches their phenotype, causing assortative mating and faster rates of local adaptation; Edelaar et al. 2008).

In order to fully understand the implications of dispersal for populations and communities, we must characterize the drivers of dispersal. These drivers can be categorized as ultimate or proximate causes (Clobert et al. 2001, Bowler and Benton 2005). Ultimate causes include the evolutionary history and evolutionary forces underpinning the trait, while proximate causes include the ontogenetic, physiological, or behavioural mechanisms producing the trait (Tinbergen 1963).

The ultimate causes of dispersal fall into four general categories. Dispersal can evolve in order to avoid inbreeding, to avoid competing with kin, as a spatio-temporal bet hedging strategy, or to allow individuals to colonize empty or under-utilized habitats in heterogeneous environments (for reviews see Bowler and Benton 2005, Matthysen 2012). Since kin are generally clustered in the natal site, dispersal is theorized to have evolved to avoid the negative consequences of inbreeding (Greenwood 1980). Similarly, dispersal may also evolve to move individuals away from kin at the natal site in order to avoid kin competition and the reduction in inclusive fitness that results from kin competition (Hamilton and May 1977). In an environment with high spatial and temporal variation, devoting resources to producing dispersive offspring may be beneficial as a bet-hedging strategy; by spreading offspring across the landscape, dispersal may decrease the risk that locally poor conditions pose to the fitness of the parent (den Boer 1968). Finally, individuals that colonize under-utilized patches benefit from low competition and may have a selective advantage over non-dispersive individuals (Comins et al. 1980, McPeek and Holt 1992).

Ultimately, dispersal evolves when the benefits of dispersal described above are greater than the inherent costs of dispersal (Bowler and Benton 2005). The costs of dispersal include an energetic cost of moving across the landscape, an opportunity cost of spending time moving instead of
foraging or reproducing, and the potential cost of immigrating into a more stressful patch (Bonte et al. 2012).

The proximate causes of dispersal are more varied, and include many aspects of the environment, social structure, and individual phenotype. Abiotic environmental factors that influence dispersal include temperature and humidity. For example, juvenile common lizards (*Lacerta vivipara*) disperse more out of dry habitats than humid habitats, and the magnitude of this effect depends on temperature (Massot et al. 2002). Biotic factors that influence dispersal include habitat structure, predation risk, and population density. For example, Remy et al. (2011) showed that artificially degrading vegetation cover leads to earlier dispersal in root voles (*Microtus oeconomus*). The presence of predators increases dispersal in many taxa. For example, larval salamanders (*Ambystoma barbouri*) increase nocturnal drift in the presence of fish predators (Sih et al. 1992), and planthoppers (*Prokelisia crocea*) are more likely to emigrate out of patches containing spider predators (Cronin et al. 2004). As predicted by theory, dispersal rates generally exhibit positive density dependence (Bowler and Benton 2005). For example, aphids (*Aphis craccivora*) produce greater numbers of dispersive offspring when they are on crowded plants (Johnson 1965). However, some studies have found negative density-dependent dispersal, or no relationship between density and dispersal. For example, Kuussaari et al. (1996) showed that butterflies (*Melitaea cinxia*) were less likely to disperse away from high-density populations.

The structure of the social environment can also influence dispersal. For example, De Meester and Bonte (2010) showed that female agrobiont spiders (*Erigone atra*) increase dispersal rates in response to high densities of other female spiders, whereas male spiders respond to the ratio of males to females. The presence of kin can also be an important aspect of the social environment. In Townsend’s voles (*Microtus townsendii*), female dispersal depended on the density of females in the population, while male dispersal was induced by the presence of female kin (Lambin 1994).

Finally, many phenotypic characters produce variation in dispersal rates. Dispersal is often biased towards one sex, although the sex that is more dispersive is not consistent across studies. For example, in an experiment on soil mites (*Sancassania berlesei*), males were the more dispersive sex (Bowler and Benton 2009), while in shrews (*Crocidura russula*), females were found to have greater dispersal rates (Favre et al. 1997). Dispersal can also be influenced by
levels of hormones such as corticosterone and testosterone, although the relationship between hormone levels and dispersal can vary among species and contexts (Dufty and Belthoff 2001, Meylan et al. 2002).

As the above examples illustrate, the observed effects of proximate factors on dispersal have been variable. One hypothesis for this inconsistency is that different studies have investigated different parts of the dispersal process. Functionally, dispersal can be divided into three stages: emigration, transfer, and immigration (Lidicker and Stenseth 1992, Clobert et al. 2001). During emigration, the organism leaves the original habitat patch. Transfer involves locomotion across inhospitable matrix habitat. Finally, immigration involves settlement into a new habitat patch. There is some evidence that proximate causes of dispersal may have different effects on each part of the dispersal process (Ims and Hjermann 2001, Matthysen 2012). Since most studies have investigated only one dispersal stage (but see Kuussaari et al. 1996, Bowler and Benton 2009, Remy et al. 2011 for exceptions), comparing studies without considering the stage of dispersal they investigated may cause the appearance of inconsistency. However, this hypothesis has not been formally tested.

An alternative hypothesis for the inconsistency in the observed effects of proximate factors on dispersal is that there are unrecognized interactions among proximate factors that produce variation among studies (Ims and Hjermann 2001, Bowler and Benton 2005, Matthysen 2012). With some exceptions (e.g. Bowler and Benton 2009, Remy et al. 2011), most studies of dispersal have investigated the effects of a single factor, and therefore do not consider the effects of interactions between factors. This is surprising given the probability that organisms in natural settings are exposed to cues from multiple factors simultaneously, and that organisms are capable of using cues from multiple sources to make dispersal decisions. If proximate factors have interactive, rather than additive effects, then ignoring the possibility of interactions in dispersal studies will cause inconsistency in their results. For example, McCauley and Rowe (2010) demonstrated that notonectids (Notonecta undulata) exhibit predator-induced dispersal. However, in a subsequent study (Baines et al. 2014) showed that predators increase notonectid dispersal rates only at medium notonectid densities. Therefore, whether or not a researcher observes an effect of predation risk on notonectid dispersal depends on the level of competition
experienced by prey. If interactions like these are not recognized by researchers, they could produce variation in the observed effects of proximate factors on dispersal.

A common explanation for why interactions have been ignored is simply that dispersal is difficult to study (Clobert et al. 2012b). Many experimental studies can only feasibly manipulate one factor, and many observational studies lack the power needed to differentiate the effects of different causal factors. There are, however, notable exceptions where researchers have investigated interactions between proximate factors. For example, Massot et al. (2002) demonstrated that dispersal in juvenile common lizards (\textit{Lacerta vivipara}) depends on the interaction between humidity and the temperature experienced during gestation, and Cote et al. (2013) showed that the role that personality plays in dispersal depends on the level of predation risk. The few dispersal studies that have considered interactive effects have generally suggested that they are important for dispersal. This thesis will focus on one proximate factor, physiological condition, that has been shown to have inconsistent effects on dispersal. Here, I test the hypothesis that unrecognized interactions between proximate factors contribute to the variability in the results of studies investigating the link between condition and dispersal.

Condition-dependent dispersal has been investigated in many empirical studies, however, like many proximate factors influencing dispersal, condition does not have consistent effects on dispersal. Some studies demonstrate a negative relationship between condition and dispersal. For example, dispersing red-cockaded woodpeckers (\textit{Picoides borealis}) had lower body mass than philopatric individuals (Pasinelli and Walters 2002). However, more studies demonstrate a positive relationship between condition and dispersal. For example, O’Riain et al. (1996) demonstrated that in naked mole rats (\textit{Heterocephalus glaber}), dispersers are heavier and have a higher fat content than philopatric individuals. Similarly, heavier roe deer (\textit{Capreolus capreolus}) are more likely to disperse and travel further than light individuals (Debeffe et al. 2012), and dispersing ants (\textit{Formica truncorum}) are larger and have greater fat and glycogen content than philopatric ones (Sundstrom 1995).

Recently, several authors have developed hypotheses to attempt to explain the observed relationships between condition and dispersal in the empirical literature. Cases in which low-condition individuals are more dispersive are seemingly easy to understand (Bonte and De La Pena 2009, Gyllenberg et al. 2011). Organisms may use condition as an indicator that, in
combination with other cues, provides information on aspects of habitat quality such as resource availability and local population density (Bonte and De La Pena 2009, Matthysen 2012). Therefore, low-condition individuals are likely to perceive themselves to be in poor-quality habitats, and so have a greater motivation to disperse from their current patch (Matthysen 2012). Individuals in low condition are also more likely to be subordinate and weak competitors, and may be forced to disperse by stronger, dominant individuals (the ideal despotic distribution hypothesis; Fretwell 1972).

The cases in which individuals in high condition are more likely to disperse are harder to understand. Individuals in high condition likely have higher dispersal capacity (Cockbain 1961, Stamps 2006). However, even high-condition individuals likely suffer large costs when dispersing (e.g. energetic costs, opportunity costs, and the potential costs of immigrating into a patch of poorer quality than the one they left; Bonte et al. 2012). Moreover, we expect that individuals in high condition are likely to be strong competitors who have high fitness when they are philopatric. It is therefore unclear why individuals in high condition would choose to disperse (Bonte and De La Pena 2009, Gyllenberg et al. 2011). One possibility is that higher observed dispersal rates in high condition individuals are a by-product of routine movements. Routine movements are movements associated with resource acquisition in the current patch (e.g. movement for foraging or mate-searching), and are distinguished from ‘special’ movements, which are undertaken for the purpose of dispersal (Van Dyck and Baguette 2005). High condition individuals may simply displace themselves further during routine movements, for example, by moving faster or for longer periods (Beck and Congdon 2000), or because they are more exploratory or more aggressive and so more likely to move past the boundaries of their home ranges to exploit resources in neighbouring ranges (Myers and Krebs 1971, Dingemanse et al. 2003, Cote et al. 2010). Routine movements may account for higher dispersal rates in high condition individuals in some cases, but cannot account for situations in which low-condition individuals are more dispersive. Moreover, this hypothesis cannot explain the relationship between condition and dispersal in cases where organisms use different modes of locomotion for routine and special movements. For example, agrobiont spiders (Erigone atra) perform routine movement by walking, but disperse by “rappelling” or “ballooning” (using silk threads to bridge long distances or float through the air, respectively; Bonte et al. 2011). In this species, high-quality individuals are more likely to disperse (Bonte et al. 2011), but this cannot be explained
by the routine movement hypothesis, because “rappelling” and “ballooning” behaviours are undertaken only for dispersal.

Recently, Gyllenberg et al. (2008, 2011) have put forth an alternative hypothesis for why high condition individuals disperse more in some cases, which extends the theory of Hamilton and May (1977) for dispersal under kin competition. Gyllenberg et al. (2008, 2011) showed that within families, high-condition individuals evolve to be more dispersive when they experience lower dispersal costs than their low condition kin. Under this hypothesis, high-condition individuals gain inclusive fitness benefits by reducing kin competition, even while accruing dispersal costs (Gyllenberg et al. 2011). Gyllenberg et al. (2008, 2011) also seek to explain why the direction of the relationship between condition and dispersal is inconsistent in empirical studies. They further demonstrated that when individuals in low condition experience lower dispersal costs, then they evolve to be more dispersive than their high condition kin. However, there is little evidence of dispersal costs being lower for low-condition individuals. In a rare example, Bowler and Benton (2009) found that female soil mites (Sancassania berlesei) in a low food availability treatment had lower dispersal mortality than females in a high food availability treatment. In general, however, the evidence from the empirical literature suggests that high-condition individuals have higher dispersal capacity (Cockbain 1961, Stamps 2006) and experience lower costs, especially during immigration (Clarke et al. 2008, Bonte et al. 2011).

A final hypothesis to explain the results of empirical studies of condition-dependent dispersal is that there are unrecognized interactions between condition and other proximate factors (Cote and Clobert 2012). Several authors have suggested that internal state may mediate the perception of, or response to, cues from proximate factors that influence dispersal (Bowler and Benton 2005, Clobert et al. 2012a). For example, the effect that food availability has on emigration propensity in the soil mite, Sancassania berlesei, depends on the sex of the mite (Bowler and Benton 2009). Similarly, body condition may mediate how organisms perceive or respond to other proximate factors influencing dispersal. One candidate for a factor that may interact with condition in this way is predation risk. Many studies have shown that condition and predation risk have interactive effects on other behaviours. For example, Kohler and McPeek (1989), demonstrated that satiated mayflies (Baetis tricaudatus) spend more time in refuge in the presence of predators.
than hungry mayflies. This type of interactive effect may provide a general explanation for the inconsistency in the results of condition-dependent dispersal studies.

The goal of this thesis was to test whether unrecognized interactions could contribute to the inconsistency in the results of condition-dependent dispersal studies. Specifically, I asked whether condition interacts with predation risk to influence dispersal in the semi-aquatic insect, *Notonecta undulata*. I manipulated condition artificially in the laboratory by imposing diet treatments varying in the quantity of food provided to wild-caught notonectids. In order to connect dispersal propensity to actual physiological mechanisms, I investigated the physiological differences of individuals from different diet treatments by analyzing the body composition (fat and protein content) of a sample of the notonectids on which the diet treatments were imposed. Finally, I measured the consequences of both condition and predation risk for dispersal in a mesocosm experiment in the field.

In addition to asking whether variation in adult condition influences dispersal, I also asked whether resource availability experienced during juvenile development has carryover effects on adult dispersal rates. Previous studies have demonstrated that environmental stressors experienced during juvenile development can have different effects on dispersal-related phenotypes than the same stressor experienced during adulthood (e.g. Johnson 1965). To test this, I imposed diet treatments varying in the quantity of food provided to juvenile notonectids. I analyzed the body condition of these notonectids once they reached adulthood, to test whether resource limitation during juvenile development and during adulthood had the same effects on body composition. I then measured the carryover effects of juvenile diet on adult dispersal rates in a mesocosm experiment in the field, and tested whether the interaction between condition and predation risk differed when condition variation was produced by variation in resources available during juvenile development, rather than resources available during adulthood. The results of this project are described in the appendix to this thesis.

**Study System**

*Notonecta spp.* (Heteroptera: Notonectidae) are semi-aquatic insects that live in freshwater ponds, streams, and lakes (Clark 1928). They complete their entire life-cycle in the aquatic environment, but can disperse by flight among ponds (Clark 1928).
Notonectids are good model organisms for dispersal studies because they use different modes of locomotion for routine (resource exploitation) and special (dispersal) movements (Van Dyck and Baguette 2005). Notonectids perform routine movements by swimming and disperse by flight. This means that routine and special movements cannot be conflated in this group. Any notonectid that flies out of a pond can be unambiguously classified as a disperser.

*Notonecta undulata* is generally associated with fishless ponds, but can co-occur with fish (Bendell 1986, Bennett and Streams 1986), including the pumpkinseed sunfish, *Lepomis gibbosus*, which was used as the predator in these experiments. *L. gibbosus* readily consumes *N. undulata* adults in the laboratory (Cook and Streams 1984). In a previous study, McCauley and Rowe (2010) demonstrated that dispersal in *N. undulata* is induced by perceived predation risk from caged *L. gibbosus*. It is not known how body condition influences dispersal in this species.
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Chapter 1
The effects of food availability during adulthood on dispersal-related physiological traits

1.1 Introduction

Body condition is a phenotype that has been demonstrated to influence dispersal in many taxa (Bowler and Benton 2005, Clobert et al. 2009). The term ‘body condition’ has been used generally to refer to the size, health, or energy reserves of an individual (Clobert et al. 2012). Here, I will restrict the terms ‘body condition’ or ‘condition’ to refer to the energy reserves of an individual, and specifically to protein and fat content.

Both protein and fat content influence dispersal capability. Protein content in the form of flight muscle has a direct effect on locomotory capability. Fats are the main fuel source used for flight in many insects, including twig wilters (Holopterna alata; Gade et al. 2006), crickets (Gryllus spp.; Zera et al. 1999), and backswimmers (Notonecta glauca; Gade et al. 2004), and therefore individuals with higher fat content are able to sustain longer periods of flight (e.g. Cockbain 1961).

In this chapter, I describe an experiment I conducted to test whether diet influences dispersal-related physiological traits, specifically, fat and protein content, in N. undulata. I maintained adult notonectids on different diet regimens varying in food quantity. I preserved a sample of the notonectids immediately after the diet manipulation to measure body composition. The remaining notonectids from the diet manipulation were used in an experiment conducted to measure dispersal in the field (described in Chapter 2). I preserved all of the notonectids that did not disperse or were recaptured after dispersal events. I predicted that fat and protein content would be positively related to the quantity of food received during the diet manipulation. Also, because fat is the fuel used for flight in these insects, I predicted that fat content would be lower in dispersers than in philopatric individuals.
1.2 Materials and Methods

1.2.1 Creating variance in adult notonectid condition

On July 30, 2013, I collected ~400 adult *N. undulata* individuals from a small fishless pond (~13,000 m²) at the Koffler Scientific Reserve (KSR) in Ontario, Canada (44°01’ N, 79°32’ W). On the same day as collection, the notonectids were transported to a laboratory at the University of Toronto, in buckets of pond water at densities of ~50 individuals per 5L. They were held in these buckets until they were processed in the subsequent 1-2 days.

Upon arrival at the laboratory, notonectids were randomly assigned to one of three diet treatments (low, medium, or high). All individuals were marked with a unique 3-digit ID number, and a symbol to denote their diet treatment (a red ‘V’, a blue ‘•’, or a green ‘|’), using Sharpie permanent markers. They were then placed in plastic drinking cups (diameter: 11 cm, height: 9 cm) filled with ~250 mL of aerated tap water. Each cup contained a strip of craft foam (8 cm × 2.5 cm x 0.2 cm) weighted with a stone, to provide habitat structure. Cups were then placed in a growth chamber set to 24°C, and a 15H day: 9H night cycle to mimic conditions experienced in June in the area where the source pond is located. Individuals of the three diet treatments were positioned randomly within the growth chamber.

Notonectids were fed daily with dead fruit flies (*Drosophila melanogaster*). Notonectids in the low, medium, and high diet treatments were fed 3, 6, and 12 fruit flies per day, respectively. In addition, each notonectid was fed ½ cricket twice per week. We recorded the ID and diet treatment of all notonectids that died in the laboratory. The diet manipulation began when the notonectids were placed in the growth chamber, and ended on August 19, 2013.

On August 19th, immediately after the diet manipulation ended, I selected a random sample of 11-12 notonectids from each diet treatment and preserved them individually in vials filled with 70% ethanol. These samples were collected so that I could estimate the effects of the diet manipulation on total body mass, fat mass and protein mass. The remaining notonectids from the diet manipulation were transported to KSR and used in a field experiment measuring dispersal rates in the field from August 19 – September 7, 2013.
1.2.2 Field experiment: measuring dispersal

In the field experiment, notonectids were placed in uncovered cattle tanks filled with water and zooplankton for food. They were allowed to disperse over the course of 19 days. Notonectids that left their original cattle tanks were classified as dispersers. Notonectids that remained in their original cattle tanks for the entire course of the field experiment were considered residents. Details of the field experiment are provided in Chapter 2 – Methods: Estimating dispersal rates in the field.

1.2.3 Body composition analysis

I performed body composition analysis on notonectids to test whether body composition was influenced by diet. I analyzed all of the notonectids that were preserved immediately after the diet manipulation. I also analyzed all of the notonectids that were classified as dispersers and a random sample of the notonectids that were classified as residents from the field experiment. The order in which the notonectids were analyzed was completely randomized. In total, 164 individuals were selected for body composition analysis, with a roughly equal number of individuals from each diet treatment.

First, I recorded the sex of each individual. I then removed the head, legs, and wings of each individual, leaving only the thorax and abdomen. I chose a random sample of notonectids and dissected their thoraces to determine whether they had developed flight muscles. Dissected individuals were classified as having or lacking developed flight muscles.

I then placed the notonectids in a drying oven at 60°C and dehydrated them to a constant weight (approximately 46-48 hours). When they were completely dry, I removed them from the drying oven, and measured their total dry mass to the nearest 0.01 mg with a Mettler Toledo XS105 scale.

I used chloroform redux to measure the fat mass of each notonectid. 10-11 individuals were placed in a fat-free thimble (Advantec; 33 mm D x 80 mm L), with the individuals divided by pieces of filter paper. Thimbles were then put in a Soxhlet extractor for 6 hours. This process submerges the specimens in cycles of warm, liquid chloroform to dissolve triglyceride fat and move it away from the specimens. After 6 hours, I removed the specimens from the Soxhlet
extractor, and allowed the chloroform to evaporate overnight in a fumehood. I then placed the specimens back into the drying oven set to 60°C, and dehydrated them to a constant weight. When they were completely dry, I measured the mass of the fatless samples. I estimated dry fat mass as the difference between the dry mass and the dry fatless mass (dry fat mass = dry mass – dry fatless mass).

To measure the protein mass of each notonectid, I submerged the dry, fatless notonectids in 0.2 mol/L potassium hydroxide (KOH) for 48 hours. The KOH solution dissolves protein, and leaves the exoskeleton intact. After 48 hours, I removed the specimens from the KOH solution and rinsed them in distilled water. I then placed them back into the drying oven set to 60°C, and dehydrated them to a constant weight. When they were completely dry, I measured their mass again. I estimated the dry protein mass as the difference between the dry, fatless mass, and the dry, fatless mass after the KOH treatment (dry protein mass = dry, fatless mass – dry, fatless mass after KOH treatment).

1.2.4 Statistical analysis

First, I tested the effects of diet and sex on body composition of individuals preserved immediately after the diet manipulation (pre) and individuals preserved after the field experiment (post). To compare the effects of the cattle tank environment to the diet manipulation, I excluded dispersers. I did this because dispersers did not spend the entire course of the field experiment in the cattle tanks, and they underwent dispersal, which is costly, so they are not representative of the effects of the cattle tanks on body composition. The effects of diet treatment and sex on total body mass of pre- and post-field samples were analyzed using analysis of variance. The effects of diet treatment and sex on fat and protein mass were analyzed using analysis of covariance, using total body mass as a covariate. The distribution of fat mass of post-field samples was not Normally distributed, therefore, this variable was square-root transformed before analysis of covariance.

Differences in body mass, fat mass, and protein mass between dispersers and residents from the field experiment were analyzed using analysis of variance. All analyses were performed in JMP v.11.0.0.
1.3 Results and Discussion

1.3.1 Body mass in the lab

Immediately after the diet manipulation, total dry body mass was positively associated with diet treatment, as expected (diet: $F_{2,28} = 14.8674$, $p < 0.0001$; Figure 1). Independent contrasts showed that individuals from the low diet treatment had the lowest body mass (Low diet – Medium diet: $t = -3.488$, $p = 0.0015$; Figure 1). Individuals from the high diet treatment had a higher body mass than individuals from the medium diet treatment, but this difference was not significant (Medium diet – High diet: $t = -1.52$, $p = 0.1386$).

1.3.2 Body mass after the field experiment

After the field experiment, notonectids were heavier on average than notonectids preserved immediately after the diet manipulation (type: $F_{1,148} = 62.7883$, $p < 0.0001$; Figure 1). This increase was most pronounced in the low diet treatment, so that after the field experiment, there was no longer a discernible effect of diet treatment on body mass (diet: $F_{2,115} = 0.2280$, $p = 0.7965$). This result suggests that the notonectids became heavier over the course of the field experiment, and that individuals from the low diet treatment gained mass at a higher rate than individuals in the medium and high diet treatments. It is therefore probable that the cattle tanks in which the notonectids were held during the field experiment contained a higher quantity or quality of food than was provided during the diet manipulation, especially compared to the low diet treatment.

1.3.3 Body mass of males and females

Immediately after the diet manipulation, there was no difference in dry body mass between males and females (sex: $F_{1,28} = 3.2112$, $p = 0.0839$; Figure 1). However, after the field experiment, females were larger than males (sex: $F_{1,115} = 5.6384$, $p = 0.0192$). The result that females were heavier than males is consistent with previous observations that females of this species are slightly larger (Hungerford 1934). A possible explanation for the fact that there was no difference in body mass between the sexes immediately after the diet manipulation is that, at that point, mean body mass was very low (Figure 1). Since there is a lower limit to how light an individual can be, there may have been less potential for a difference between the sexes to be
discernible immediately after the diet treatment. Moreover, the sample size of individuals preserved immediately after the diet manipulation was low, which means there was less statistical power to detect a difference between the sexes. Alternatively, these results could be due to differences in energy use or allocation between the sexes, which has been observed previously in other taxa (e.g. Dmitriew et al. 2009).
Figure 1. Mean body mass +/- s.e. of backswimmers of all three diet treatments. “pre” = backswimmers preserved immediately after the diet manipulation (n = 35). “post” = backswimmers preserved after field the experiment (n = 119).
1.3.4 Fat mass in the lab

Among notonectids preserved immediately after the diet manipulation, fat content depended on diet treatment (diet: $F_{2,28} = 10.3992$, $p = 0.0004$; Figure 2). Independent contrasts showed that individuals from the low diet treatment had the lowest fat content (Low diet – Medium diet: $t = -2.40$, $p = 0.0232$), and individuals from the high-diet treatment had the highest fat content (High diet – Medium diet: $t = 2.83$, $p = 0.0085$). This result is consistent with previous studies demonstrating that food availability is positively associated with fat content (Rolff et al. 2004, Dmitriew et al. 2009). Since fat is the fuel used for flight in many insects, including a member of the *Notonecta* genus (Gade et al. 2004), this result suggests that individuals from the low diet treatment have the lowest dispersal capacity, individuals from the medium diet treatment have intermediate dispersal capacity, and individuals from the high diet treatment have the highest dispersal capacity.

In addition to fat mass depending directly on diet treatment, the slope of the line when fat mass was regressed on body mass also depended on diet treatment (body mass × diet: $F_{2,28} = 5.7303$, $p = 0.0082$; Figure 2). The low-diet treatment had the shallowest slope (Low diet – Medium diet: $t = -3.37$, $p = 0.0022$), but there was no difference between the slopes of the medium and high diet treatments (High diet – Medium diet: $t = -1.94$, $p = 0.0630$). This suggests that diet treatment changed patterns of energy use and allocation. Individuals from the low diet treatment allocated extremely low levels of energy to fat, regardless of their structural body size (Figure 2). Conversely, individuals in the medium and high diet treatments had a high enough energy intake to be able to allocate energy to fat stores (Figure 2). These results indicate that individuals from the low diet treatment would incur the highest marginal costs of dispersal; the energetic costs of dispersal would be a very high proportion of their total energy stores, compared to individuals from the medium and high diet treatments.

1.3.5 Fat mass after the field experiment

After the field experiment, notonectids had greater fat mass, on average, than notonectids preserved immediately after the diet manipulation (type: $F_{1,141} = 7.1201$, $p = 0.0085$; Figure 2). This difference was again most pronounced in the low-diet treatment, so that after the field
experiment, there was no longer a discernible effect of diet treatment on fat mass (diet: $F_{2,109} = 0.4302$, $p = 0.6515$; Figure 2). Again, this was likely because the cattle tanks had a higher quantity or quality of food than was provided in the diet manipulation, especially compared to the low diet treatment. This is consistent with observations that fat content is positively associated with diet (Figure 2, Rolff et al. 2004). After the field experiment, fat mass depended strongly on body mass (body mass: $F_{1,109} = 17.2978$, $p<0.0001$; Figure 2), which is consistent with the observed relationship between fat mass and body mass among individuals from the medium and high diet treatments preserved immediately after the diet manipulation (Figure 2). This again suggests that individuals from the low diet treatment altered allocation to fat in the diet manipulation in response to food shortage.
Figure 2. Fat mass vs body mass +/- 95% confidence of fit bands of all three diet treatments. “pre” = backswimmers preserved immediately after the diet manipulation (n = 35). “post” = backswimmers preserved after field the experiment (n = 119).
1.3.6 Fat mass of males and females

Immediately after the diet manipulation, there was no difference in fat mass between males and females (sex: $F_{1,23} = 0.0356$, $p = 0.8520$; Figure 3). However, after the field experiment, females had slightly greater fat mass than males (sex: $F_{1,109} = 4.0514$, $p = 0.0466$). This suggests that females allocate more energy to fat than males. This may ultimately be driven by the greater energetic cost of reproduction for females, or it could be a by-product of higher activity rates in males (e.g. energy spent on aggressive interactions among males). Greater allocation to fat in females may also indicate that females have greater dispersal capacity than males in this species. Previous studies have demonstrated sex-biased dispersal in other taxa (e.g. lizards: Vignoli et al. 2012, and corixids: Boda and Csabai 2009); however, the association between sex and dispersal has not been investigated in *Notonecta.*
Figure 3. Fat mass vs body mass +/- 95% confidence of fit bands of males and females.

“pre” = backswimmers preserved immediately after the diet manipulation ended (n_{male} = 25, n_{female} = 10). “post” = backswimmers preserved after the field experiment (n_{male} = 71, n_{female} = 48).
1.3.7 Flight muscles and protein mass

All of the notonectids dissected had developed flight muscles, which suggests that flight muscle histolysis is probably not a strategy utilized by these insects under food stress. Protein mass did not depend on body mass, diet treatment, or their interaction, neither immediately after the diet manipulation (body mass: $F_{1,23} = 0.0153$, $p = 0.9025$, diet: $F_{1,23} = 1.5178$, $p = 0.2304$, body mass × diet: $F_{1,23} = 2.1662$, $p = 0.1546$; Figure 4), nor after the field experiment (body mass: $F_{1,109} = 0.2513$, $p = 0.6171$, diet: $F_{2,109} = 1.2613$, $p = 0.2874$, body mass × diet: $F_{2,109} = 0.0405$, $p = 0.9603$; Figure 4). This result indicates that diet treatment did not produce differences in dispersal capacity through effects on protein mass. After the field experiment, notonectids had greater protein mass, on average, than notonectids preserved immediately after the diet manipulation (type: $F_{1,152} = 104.2808$, $p < 0.0001$; Figure 4), again suggesting that the quality or quantity of food in the cattle tanks was higher than that provided in the diet manipulation. These results seem contradictory because protein content did not produce differences between individuals from the three different diet treatments immediately after the diet manipulation, but the high resource availability in the cattle tanks did produce a difference in protein mass between individuals immediately after the diet manipulation and after the field experiment. Altogether, this may indicate that the food received by all three treatments during the diet manipulation was low in protein, which caused either an increase in muscle catabolism, or a decrease in muscle production.

The result that protein mass was not a function of body mass was unexpected. Previous studies have demonstrated a positive association between body mass and protein mass (e.g. Dmitriew et al. 2009). The lack of a relationship in this experiment could be due to other factors producing noise that overwhelms any signal of a relationship between protein mass and body mass. There was especially high variation in protein mass among individuals preserved after the field experiment (Figure 4). This could have been the result of differences in foraging activity or prey selection among individuals. Some of this variation may also be the result of egg production in females. The method used to measure protein mass in this experiment cannot distinguish between muscle and egg proteins. Therefore variance in reproductive status or the number of eggs produced could contribute to the variance in protein mass.
Figure 4. Protein mass vs body mass +/- 95% confidence of fit bands of all three diet treatments. “pre” = backswimmers preserved immediately after the diet manipulation (n = 35). “post” = backswimmers preserved after the field experiment (n = 119).
1.3.8 Protein mass of males and females

There was no difference in protein mass between males and females immediately after the diet treatment (sex: $F_{1,33} = 1.6407, p = 0.2092$; Figure 5), but females had greater protein mass than males after the field experiment (sex: $F_{1,119} = 8.3138, p = 0.0047$; Figure 5). This may indicate that females allocate more energy to muscle mass than males; however, the more likely explanation is that the observed difference is a consequence of females producing eggs once they are put in the (relatively) high-quality cattle tank environments. The method that I used to measure protein mass cannot distinguish between muscle protein and protein in eggs. I therefore cannot determine whether the higher investment to protein in females is due to investment in muscle mass (for dispersal) or eggs (for reproduction).
Figure 5. Protein mass vs body mass +/- 95% confidence of fit bands of males and females.

"Pre" = backswimmers preserved immediately after the diet manipulation (n$_{\text{male}}$ = 25, n$_{\text{female}}$ = 10). "Post" = backswimmers preserved after the field experiment (n$_{\text{male}}$ = 71, n$_{\text{female}}$ = 48).
1.3.9 Body composition of recaptured dispersers

I recaptured eight dispersers from the cattle tank array. There were 4, 1, and 3 dispersers from the low, medium, and high condition groups, respectively. There was no discernible difference between dispersers and non-dispersers in mass ($F_{1,125} = 0.1759, p = 0.6757$; Figure 6A), fat content ($F_{1,125} = 0.1014, p = 0.7506$; Figure 6B), or protein content ($F_{1,125} = 0.0009, p = 0.9763$; Figure 6C). These results are far from conclusive given the sample sizes. Moreover, 6 of the 8 dispersers flew from one cattle tank to another within the array, and therefore flew a maximum of ~20m, while the other two dispersers were found in the original source pond in which these notonectids were collected, >1km away. These dispersers were therefore not a representative sample of dispersers as a whole; the sample was biased towards very short-distance dispersers who probably expended little energy moving those short distances, and are therefore likely to be more similar to residents than the average disperser.
Figure 6. A) Body mass, B) fat mass, and C) protein mass of dispersers and residents.

Dispersers are notonectids that left their original tanks and were recaptured (n = 8).

Residents are notonectids that remained in their original tanks over the entire course of the field experiment (n = 119).
1.4 References

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Chapter 2

The effects of predation risk and food availability during adulthood on dispersal

2.1 Introduction

Previous studies have shown that dispersal is influenced by body condition; however, the relationship between dispersal and condition is inconsistent in the empirical literature. For example, dispersing red-cockaded woodpeckers (*Picoides borealis*) had lower body mass than philopatric individuals (Pasinelli and Walters 2002), but dispersing naked mole rats (*Heterocephalus glaber*) had higher body mass and higher fat content than philopatric individuals (O’Riain et al. 1996). Moreover, the theoretical literature does not provide a straightforward prediction for how condition should be related to dispersal. Low condition individuals may perceive themselves to be in poor-quality habitats, and therefore have a greater motivation to disperse out of their current habitat patch (Matthysen 2012). However, high condition individuals likely have greater dispersal capacity (Cockbain 1961, Stamps 2006).

One hypothesis to explain the inconsistency in the results of empirical studies of condition-dependent dispersal is that body condition mediates how organisms perceive or respond to proximate factors influencing dispersal motivation and capacity. This would produce variation with respect to the relationship between condition and dispersal (Cote and Clobert 2012). One candidate for a proximate cause of dispersal that may interact with condition is predation risk. Previous studies have shown that condition and predation risk have interactive effects on other behaviours (e.g. Kohler and McPeek 1989). Here, I will test the hypothesis that predation risk interacts with body condition to influence dispersal.

In Chapter 1, I described an experiment I conducted in which I imposed diet treatments varying in the quantity of food provided to notonectids. I measured the body mass, fat content, and protein content of notonectids from the three diet treatments. I demonstrated that fat content was positively related to the amount of food provided during the diet manipulation. I argued that this
demonstrates that high condition notonectids have higher dispersal capacity than low condition notonectids, which may cause higher dispersal rates in high condition individuals. In this chapter, I describe an experiment I conducted to test whether body condition influences dispersal rates in *Notonecta undulata*. Since body condition may also mediate the perception of predation risk (Kohler and McPeek 1989), I asked whether the relationship between predation risk and dispersal depends on body condition. I tested this by placing notonectids from the diet manipulation in pond mesocosms in which I manipulated predation risk from non-lethal (caged) predators. I then measured emigration rates out of these pond mesocosms and asked whether emigration depended on notonectid condition and predation risk.

2.2 Materials and Methods

2.2.1 Creating variance in adult notonectid condition

The notonectids from the diet manipulation were the source of experimental animals for both the body composition analysis and the field experiment. I reproduce pertinent details of the diet manipulation here. For more details on how variance in notonectid condition was created, see Chapter 1: Methods: creating variance in backswimmer condition.

On July 20, 2013, I collected ~400 adult *N. undulata* individuals from a small fishless pond at KSR. They were transported to the University of Toronto and randomly assigned to one of three diet treatments (low, medium, or high). All individuals were marked with a unique 3-digit ID number, and a symbol to denote their diet treatment (a red ‘V’, a blue ‘•’, or a green ‘|’), using Sharpie permanent markers. Notonectids were placed in cups of water and fed with dead fruit flies (*Drosophila melanogaster*). Notonectids in the low, medium, and high diet treatments were fed 3, 6, and 12 fruit flies per day, respectively. In addition, each notonectid was fed ½ cricket twice per week. On August 19, 2013, the notonectids were transported to the Koffler Scientific Reserve (KSR). During transport, the notonectids remained in their cups, and the cups were placed in covered plastic trays to prevent them from escaping.

2.2.2 Estimating dispersal rates of adults in the field

In June 2013, I placed an array of 40 cattle tanks (tanks: 378 L; 1.35 m × 0.79 m × 0.64 m) in an open field at KSR. I also placed 24 smaller pools (diameter: 1.5 m × height: 0.28 m) in the field,
in four perpendicular transects moving away from the cattle tank array at increasing distances (Figure 7). I filled the tanks and pools with water and a standard number of rabbit chow pellets, and left them uncovered to aerate. On July 30th, 2013, I added an equal amount of zooplankton to each cattle tank to provide food for the notonectids.

I placed a fish cage in each cattle tank. Fish cages consisted of a 5L plastic basket with a Styrofoam lid, covered in 1mm mesh screening. In predator treatments, these cages allow notonectids to receive visual and olfactory cues signaling the presence of a predator without being consumed. In predator absent treatments, empty cages controlled for the presence of this structure. On August 15th, I caught eight pumpkinseed sunfish (*Lepomis gibbosus*; standard length of fish ± standard deviation = 17.5 ± 0.8 cm), and put them in the fish cages in five of the cattle tanks. I fed each fish one cube of frozen bloodworms plus four live notonectids per day.

On August 19th, notonectids were transported from the growth chamber at the University of Toronto to the field mesocosm experiment at KSR. They were divided into ten cattle tanks. Each tank received 12-13 individuals of all three diet treatments, with each tank receiving 36-37 notonectids in total. This notonectid density falls within the natural range for this species (Bennett and Streams 1986).

I placed strips of craft foam weighted with stones in all tanks to provide habitat structure. I also covered ~⅓ of each tank with a piece of 70% shade cloth. The shade cloth kept the water temperature of the tanks cool, but did not prevent the notonectids from dispersing.

The cattle tanks were left uncovered for 19 days to allow notonectids to disperse. I estimated emigration rates by recording the markings of each individual present in each tank every three days. When dead notonectids were found, I recorded their markings and discarded them away from the cattle tank array. Even notonectids which died as a result of cannibalism could be accounted for in this way, because notonectids consume the insides of their prey and leave the exoskeleton intact, so the ID markings of any cannibalised individuals could be recorded. All individuals that left their original tanks were considered dispersers. All individuals that remained in their original tanks over the entire course of the experiment were considered residents.
Recording the individuals present in all tanks was time-consuming, and could not be done in a single day. I therefore divided the tanks into two time blocks, and recorded the individuals present within each block every three days. Time blocks 1 and 2 contained 4 and 6 tanks, respectively. Both predator treatments were equally represented in both blocks.

I monitored the pool transects daily for any dispersing notonectids. Any colonists in these pools were preserved individually in vials filled with 70% ethanol. I also monitored the source pond from which all the notonectids were originally collected. All marked notonectids found in the source pond were preserved individually in 70% ethanol. On September 6-7, 2013, the markings of all of the notonectids remaining in the tanks were recorded, and the notonectids were preserved individually in vials filled with 70% ethanol.
Figure 7. Diagram of cattle tank array and pool transects used in field dispersal experiment. The cattle tank array consisted of 40 cattle tanks in an area 16 m x 14 m. Each diamond represents one pool. Numbers indicate the approximate distance of each pool, in metres, from the closest cattle tank. The transects fell roughly in line with the four cardinal directions (north, east, south, west).
2.2.3 Statistical analysis

The effects of diet treatment, predator treatment, and time on dispersal rates were analyzed using survival analysis as per Allison (2010). I used a generalized linear mixed model with a binomial error distribution and a logit link, using dispersal status (dispersed or resident) as the response. I allowed dispersal status to be right-censored, to account for individuals that died during the course of the experiment. The fixed effects were time, predator treatment, diet treatment, and all possible interactions. I included tank nested within block as a random effect. I evaluated significance of the fixed effects using type III sum of squares. This analysis was performed in R v.2.14.2.

2.3 Results and Discussion

Initially, high-condition individuals dispersed more than low-condition individuals (Figure 8A, B), but this difference decreased through time (Figure 8A, C). Consequently, there was a significant interaction between diet and time (diet × time: $\chi^2_2 = 11.114$, $p = 0.004$; Figure 8A) and the main effect of diet was only marginally significant (diet: $\chi^2_2 = 5.6388$, $p = 0.060$). Many previous studies have demonstrated positive condition-dependent dispersal, including studies on naked mole rats (O'Riain et al. 1996), and roe deer (Debeffe et al. 2012). The decrease in the magnitude of the effect of diet on emigration through time was likely due to the fact that individuals from all three diet treatments were in the same tanks, eating the same food over the course of the field experiment. There is evidence that differences between notonectids from the three diet treatments in body mass, fat mass, and protein mass decreased over the course of the field experiment (Figure 1, Figure 2, Figure 4). Therefore, the interaction between diet treatment and time is likely a by-product of the fact that the differences among the three diet treatments in body condition was decreasing through time.

More notonectids emigrated from fish tanks than fishless tanks, overall (predator: $\chi^2_1 = 23.443$, $p = 1.3 \times 10^{-6}$; Figure 8A), and this difference increased through time (predator × time: $\chi^2_1 = 3.997$, $p = 0.046$; Figure 8A, B, C). These results are consistent with previous studies of the effect of predation risk on dispersal (McIntosh et al. 2002, Cronin et al. 2004), including a study conducted on the same species demonstrating that \textit{N. undulata} exhibits predator-induced
dispersal (McCauley and Rowe 2010). However, this is the first study to show that the magnitude of the effect of predation risk can change through time. One possible explanation for the fact that the effect size of predation increased through time is that the concentration of kairomones in the cattle tanks increased though time. Kairomones are chemical signals released when a prey item is injured or digested by a predator. Previous studies have shown that prey respond to these cues (Schoepner and Relyea 2005). Kairomones were present in the tank water because notonectids were provided to the fish as food during the experiment. If the time lag between when the kairomones were released and when they deteriorated was long enough, then the concentration of kairomones in the tank water could have increased over the course of the experiment. Therefore, the level of predation risk perceived by the notonectids could have also increased over the course of the experiment, causing the effect of predators to increase over time as well.

An alternative explanation, not exclusive of the first, for the fact that the effect size of predation increased through time is that condition interacted with predation risk through time. Results from the body composition analysis indicate that notonectid body condition increased over the course of the experiment, especially for low-condition individuals (Figure 1, Figure 2, Figure 4). We also know that dispersal propensity was a positive function of body condition (Figure 8A, B). If notonectids delayed dispersal until condition improved, and were also more likely to disperse out of fish tanks, then this could be responsible for the increase in the effect size of predators through time. An indication of this is seen in the low-condition individuals. One possible explanation for the pattern of dispersal seen in this group is that initially, a large proportion of individuals did not surpass the condition threshold for dispersal. Through time, as they increased in condition, a greater number of individuals surpassed the threshold. These individuals, now capable of dispersal, were more likely to disperse out of fish tanks than fishless tanks (Figure 8A). If this explanation were true, we would expect to see a three-way interaction between predator treatment, diet treatment, and time. The observed interaction is not significant; however, a non-significant result does not rule out the possibility that changes in condition through time are contributing to the increasing effect size of predators through time.

I expected emigration rate to depend on the interaction between diet treatment and predator treatment, however, this interactive effect was not significant at any time point (predator × diet: \( \chi^2 = 2.6467, p = 0.266 \); predator × diet × time: \( \chi^2 = 3.1536, p = 0.2066 \); Figure 8A, B, C). The
relationship between condition and dispersal was similar in both predator treatments; individuals from the high diet treatment had the highest emigration rates, and individuals from the low diet treatment had the lowest emigration rates, regardless of predator treatment. This suggests that the interaction between condition and predation risk is not responsible for the inconsistency in the results of empirical studies of condition-dependent dispersal.
Figure 8. A) Kaplan-Meier curves for mean probability of philopatry of individuals for each fish x diet treatment in each round. Rounds are separated by three days.
Figure 8. B) Mean proportion of philopatric individuals for each fish × diet treatment in the first three days of the field experiment. C) Mean proportion of philopatric individuals for each fish × diet at the end of the experiment.
2.4 References


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General Discussion

In this thesis, I described a project I conducted in which I manipulated the diets of notonectids (*Notonecta undulata*) and measured the consequences of the diet manipulation for total body mass, fat content, and protein content. I then tested whether notonectid body condition influenced emigration out of pond mesocosms in the field, and whether condition mediated the relationship between predation risk and dispersal.

The results I presented in Chapter 1 demonstrated that the diet manipulation affected body mass. As expected, individuals from the low diet treatment were the lightest, individuals from the medium diet treatment had intermediate body mass, and individuals from the high diet treatment were the heaviest (Figure 1). Diet treatment also influenced fat mass, and changed the shape of the relationship between fat mass and total body mass. Among individuals preserved immediately after the diet manipulation, individuals from the low diet treatment had the lowest mean fat mass, and the shallowest relationship between fat mass and body mass. Individuals from the medium diet treatment had intermediate fat mass, and individuals from the high diet treatment had the highest fat mass (Figure 2). Since fat is the fuel used for flight in these insects (Gade et al. 2004), these data indicate that dispersal capacity is an increasing function of diet treatment, and that the magnitude of the marginal cost of dispersal is a decreasing function of diet treatment. Protein content was not related to body mass or diet treatment (Figure 4), and all notonectids tested had developed flight muscles, indicating that variation in observed dispersal capacity is probably not due to variation in flight muscle mass. I also presented results demonstrating that females have higher fat mass, protein mass, and total body mass than males (Figure 1, Figure 3, Figure 5).

In Chapter 2, I presented the results of the pond mesocosm experiment I conducted to measure emigration rates in the field. I demonstrated that notonectids emigrated at higher rates when a fish predator was present in the mesocosm (Figure 8A, C). I asked whether body condition mediated the response of prey to predation risk in a way that influenced dispersal decisions. I found that emigration was an increasing function of condition (Figure 8A, B); however, condition did not interact with predation risk to influence emigration rates.
Predator-induced dispersal has been demonstrated in a wide variety of taxa including planthoppers (Cronin et al. 2004), mayflies (McIntosh et al. 2002), and *N. undulata* (McCauley and Rowe 2010). This result is predicted by general theory stating that individuals should maximize their fitness by moving away from poor-quality or dangerous patches in favour of high-quality, safe patches, as long as the benefits of leaving outweigh the costs of dispersal (Bonte et al. 2012, Clobert et al. 2012). Poethke et al. (2010) specifically investigated the evolution of predator induced dispersal and their model demonstrated that prey should evolve higher dispersal rates in the presence of predators when temporal autocorrelation in predation risk is high, as it is in the *Notonecta* system. This dispersal response provides spatial refuge for prey, and can enable regional coexistence of predators and prey, even when temporal autocorrelation in predation risk is not perfect (Hanski 2001).

Positive condition-dependent dispersal has been demonstrated in a variety of taxa (mostly mammals: O'Riain et al. 1996, Debeffe et al. 2012, and other vertebrates: Pasinelli and Walters 2002). Positive condition dependence is more commonly observed than negative condition dependence; however, it is not clear why high condition individuals would be more dispersive, or why the relationship between condition and dispersal is inconsistent in the empirical literature. One hypothesis to explain positive condition-dependent dispersal proposes that high-condition individuals appear to be more dispersive because they travel longer distances to conduct routine movements, as a by-product of them being larger, faster, or more aggressive (Beck and Congdon 2000, Cote et al. 2010). However, this hypothesis cannot explain the results observed in this study, because condition was found to influence the proportion of notonectids that flew out of the pond mesocosms, a behaviour that is not part of the repertoire of routine movements.

Another hypothesis that has recently been put forth by Gyllenberg et al. (2008, 2011) suggests that kin competition drives condition-dependent dispersal. This hypothesis proposes that in the presence of kin, the individuals that experience the lowest dispersal costs (these could be low or high condition individuals) are more dispersive than kin that experience high dispersal costs. I argue that this is unlikely to be a general explanation for the inconsistency in the results of condition-dependent dispersal studies because evidence of low condition individuals experiencing lower dispersal costs than high condition individuals is rare. Moreover, in the *Notonecta* system, juvenile notonectids move away from their siblings through routine
movements. Therefore, kin competition is probably not contributing to condition-dependent dispersal in *Notonecta*.

The observed results are more consistent with the hypothesis that the relationship between condition and dispersal relies on the relative dispersal capacity and dispersal motivation of low and high condition individuals. Empirical evidence suggests that high condition individuals have higher dispersal capacity, and therefore incur lower dispersal costs (Cockbain, 1961; Stamps, 2006). However, body condition may indicate habitat quality or competitive ability, and therefore low condition individuals likely have higher dispersal motivation; in other words, low condition individuals accrue greater benefits from dispersal (Bonte & De La Pena, 2009; Matthysen, 2012). Whether dispersal is a positive or negative function of condition depends, then, on the relative cost to benefit ratio for high and low condition individuals. If low condition individuals have a lower cost to benefit ratio (e.g. because the probability of low-condition individuals successfully finding a new patch of higher quality is high), then low-condition individuals will tend to be more dispersive. If high condition individuals have a lower cost to benefit ratio (e.g. because they are better able to find and compete for access to high-quality patches), then high-condition individuals will tend to be more dispersive. Since these cost to benefit ratios necessarily rely on environmental context, the relationship between condition and dispersal would vary among environments, and therefore among studies. This general explanation can therefore account for the inconsistency in the results of condition-dependent dispersal studies.

In this project, I tested the hypothesis that environmental variation in predation risk was contributing to the inconsistency in condition-dependent dispersal studies. I found that the relationship between condition and dispersal did not depend on the level of predation risk; however, this does not rule out the possibility that there are other factors interacting with condition such as resource availability or population density. In fact Hanski et al. (1991) demonstrated that population density interacts with body size in shrews (*Sorex araneus*) such that at low densities, small, competitively inferior, individuals are more dispersive, and at high densities, large individuals are more dispersive.
There may be a bias toward positive relationships between condition and dispersal if condition thresholds for dispersal are common. If low-condition individuals are less likely to surpass the threshold (under which dispersal is impossible or extremely costly because of lack of dispersal structures, or because the marginal cost of dispersal is prohibitive), this could remove a portion of low condition individuals from the pool of potential dispersers. This would reduce the probability of finding negative relationships between condition and dispersal. This may account for the observation that positive condition-dependent dispersal is more common in empirical studies.

This study, among others, has demonstrated that dispersers tend to be in better condition than philopatric individuals. High condition dispersers travel further distances (Ferrer 1993, Debeffe et al. 2012), compete more successfully for entry into high-quality habitat (Clarke et al. 2008, Bonte et al. 2011), and have greater fecundity (Bonte et al. 2011) than low condition dispersers. Thus, dispersal that is non-random with respect to body condition has consequences for a variety of ecological and evolutionary processes, even when there are no genetic differences between low and high-condition individuals (Edelaar and Bolnick 2012). High condition dispersers will have a greater impact on the populations that receive them than expected given the number of emigrants and assuming dispersers are a random sample of the population (Benard and McCauley 2008). As a result, fewer dispersers will be needed to “rescue” declining populations and increase metapopulation viability. Similarly, the same volume of gene flow can be accomplished with a few high condition dispersers than with many dispersers of random condition. Therefore, fewer dispersers may be required to alter genetic structure and change rates of local adaptation. Non-random gene flow may also influence the risk of species extinction. If high condition individuals are able to survive long distance dispersal events and are also likely to be fecund, this may ameliorate the risk of extinction in species living in highly fragmented habitats.

In the project described in Chapters 1 and 2, I created variance in condition by manipulating the amount of food provided to adult notonectids. However, variation in condition can be created before adulthood through maternal effects and through variation in the quality of the natal environment (Benard and McCauley 2008, Clobert et al. 2012); these factors may have carryover effects on adult phenotype. I investigated this possibility in another project that I have described in the appendix to this thesis.
In the pond mesocosm experiment, I found that the magnitude of the effects of condition and predators on emigration rates depended on time. The effect of condition decreased through time, likely because notonectids from the three different diet treatments were in the same tanks eating the same food during the course of the experiment, and therefore the differences in condition among individuals from the three diet treatments decreased through time (as is evident in the results of the body composition analysis; Figure 1, Figure 2, Figure 4). This may have practical implications for researchers attempting to measure the consequences of condition on dispersal, since the observed effect size likely depends on the amount of time elapsed between when condition manipulations are imposed, and when dispersal is observed. This may explain some cases in which researchers found no association between condition and dispersal. For example, Remy et al. (2011) manipulated condition in root voles (*Microtus oeconomus*) by artificially altering litter size, and measured the effects of this condition manipulation on juvenile and adult dispersal. They found that although condition treatment influenced mortality and competitive ability, there was no association between condition and dispersal. The authors suggested one possible explanation of this result was that the effect of litter size on condition did not last into adulthood.

Interestingly, the effect of predators increased through time. This is possibly due to the fact that the caged fish were given notonectids as food during the experiment. Previous studies have shown that prey respond to cues from digested conspecifics (Schoepfner and Relyea 2005). It is possible that the concentration of these chemical cues in the water of the tanks may have increased over the course of the experiment. This may have important implications for researchers attempting to predict the effects of environmental changes such as the introduction of fish to previous fishless lakes. The consequences of these changes for dispersal dynamics may depend on the time scale at which they are measured. However, it is also possible that the increase in the effect size of predators through time was a by-product of the fact that notonectid condition was increasing through time.

In the field experiment I conducted to measure dispersal rates, I attempted to measure all three stages of the dispersal process: emigration, transfer, and immigration. However, I was only successful in measuring emigration rates. The pool transects I set up to recapture notonectids dispersing from the cattle tank array were not effective. I only recaptured 8 dispersers, which
corresponds to only ~4% of dispersers. Since proximate causes of dispersal can have different effects on different parts of the dispersal process (Ims and Hjermann 2001, Matthysen 2012), the effects of the treatments on emigration rates observed in the pond mesocosm experiment may not perfectly reflect the impact that these treatment factors have on the entire dispersal process. High condition individuals had higher emigration rates than low condition individuals in this study (Figure 8). High condition individuals are probably also better able to survive transfer between habitat patches and successfully compete for space in a new habitat patch (Stamps 2006). Therefore, the difference in realized dispersal rates (i.e. successful completion of all three dispersal stages) between high and low condition individuals may be larger than we estimate from knowledge of emigration rates alone. In order to make accurate estimations of the effect sizes of proximate factors on dispersal, future research should measure the effects of these proximate factors on the entire dispersal process.

In this thesis, I describe an experiment I conducted in which I manipulated two factors (condition and predation risk) and measured their effects on emigration rates. This two-factor experiment is more ecologically realistic than the majority of experiments on dispersal, which have manipulated a single factor (Clobert et al. 2001, Clobert et al. 2012). However, organisms in nature are likely exposed to more than two cues, which they must assess and integrate to make dispersal decisions. Some of these factors would have additive effects, however, others are likely to have non-additive effects. For example, in a previous experiment, Baines et al. (2014) demonstrated that density interacts with predation risk to influence emigration rates in N. undulata. Researchers investigating dispersal must therefore be cautious when interpreting the results of dispersal studies, because estimates of effect sizes could depend on a myriad of other, unrecognized factors.

**Conclusion**

In this thesis, I demonstrated that body mass and fat content were positively associated with food availability. Since fat is the fuel used for flight in these insects (Gade 2006), this indicates that food availability was positively associated with dispersal capacity. In a field mesocosm experiment, I found that emigration rate was a positive function of condition. The majority of previous studies have also observed a positive relationship between condition and dispersal (e.g.
(O'Riain et al. 1996, Debeffe et al. 2012). If high condition individuals tend to be more dispersive, then dispersal may have a larger impact on metapopulations than would be predicted assuming that dispersers were a random sample of the population. However, the results of condition-dependent dispersal studies have been inconsistent; some previous studies have observed negative relationships between condition and dispersal (Pasinelli and Walters 2002). This inconsistency may be caused by unrecognized interactions between condition and factors that are themselves drivers of dispersal. In this project, I investigated whether one proximate cause of dispersal, predation risk, was interacting with condition and contributing to the inconsistency in the results of condition-dependent dispersal studies. I found that emigration was induced by predation risk, which is consistent with previous studies (e.g. McCauley and Rowe 2010). However, I found that the effects of condition and predation risk were additive, not interactive, and therefore there is no evidence that variation in predation risk is contributing to variation in the results of condition-dependent dispersal studies. This does not rule out the possibility that condition interacts with other proximate factors to produce the patterns that we observe in the empirical literature. For instance, condition may interact with population density to produce variation in the relationship between condition and dispersal.

In this thesis, I have described a project I conducted to measure dispersal in a realistic ecological context. This work indicates that dispersal is a complex process with many causal factors. In order to fully understand the causes of dispersal, and therefore its consequences for ecological and evolutionary processes, we must conduct more multi-factor experiments to investigate dispersal dynamics in realistic ecological contexts and through the entire dispersal process.
References


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Appendix 1: Carryover effects of juvenile diet on adult physiology and dispersal

Appendix Introduction

Variation in physiological condition may be created by environmental variation experienced by the mother, or experienced during juvenile development or adulthood. These three sources of variation have all been demonstrated to influence dispersal (Clobert et al. 2012); however they may not influence dispersal in the same way. In this thesis, I demonstrated that dispersal was an increasing function of condition, when variation in condition was caused by variation in resources available during adulthood. The environment experienced before adulthood or by the mother may have carryover effects on adult phenotype that influence dispersal differently. For example, mothers in low-quality habitats may invest more in dispersive offspring to produce macropterous (i.e. winged) offspring (e.g. Johnson 1965). Conversely, mothers in low-quality habitats may produce low-condition offspring with lower dispersal rates (e.g. Massot and Clobert 1995). Similarly, exposure to low-quality habitat during development may induce macroptery (e.g. Johnson 1965), or may lower condition and therefore dispersal capacity (e.g. Holekamp and Sherman 1989). If the effects of environmental quality on dispersal capacity vary among developmental stages, this would add a layer of complexity to the relationships between environment, phenotype, and dispersal.

Here, I present the results of a study conducted to investigate the effect of condition on dispersal in adults, when variation in adult condition was produced by variation in food availability during juvenile development. I asked whether condition influenced by juvenile diet
influenced dispersal rates, and whether this effect interacted with predation risk in *Notonecta undulata*. I manipulated condition artificially in the lab by imposing diet treatments varying in the quantity of food provided to juvenile notonectids. I investigated the physiological consequences of the diet treatments by analyzing the body condition of a sample of the notonectids on which the diet treatments were imposed. I then measured the effects of condition and predation risk on adult dispersal rates out of pond mesocosms in the field.

References


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Chapter S1

The effects of food availability during juvenile development on dispersal-related physiological traits

S1.1 Introduction

In this chapter, I tested whether resource availability experienced during juvenile development influences dispersal-related physiological traits in adults. I tested this by imposing diet treatments varying in food quantity on wild-caught juvenile notonectids until they reached adulthood. I then measured body mass, fat mass, and protein mass of the adults, because these traits are expected to be associated with dispersal capacity in notonectids (Gade et al. 2004). I compared notonectids from the three diet treatments. I also compared notonectids that were preserved immediately after the diet manipulation to notonectids that had been used in a two-week-long experiment to measure dispersal rates in the field. I predicted that fat and protein content would be positively related to the quantity of food received during the diet manipulation. Also, because fat is used as the source of energy during flight (Gade et al. 2004), I predicted that fat content would be lower in dispersers than in philopatric individuals.

S1.2 Materials and Methods

S1.2.1 Creating variance in juvenile notonectid condition

On June 25th - July 10th, 2013, I collected 1219 juvenile notonectids of instars 3-5 from a small fishless pond (13,000 m2) at KSR. On the same day as collection, the notonectids were transported to a laboratory at the University of Toronto, Earth Sciences building.

The notonectids were transported and held at densities of ~50-100 notonectids per 5L in buckets filled with water from the source pond. They were kept in these buckets in the laboratory until they were processed. Processing occurred ~2 hours – 5 days after they were collected.

In the laboratory, I first sorted them by species and instar. Only individuals of the species *N. undulata* in the 3rd and 4th instars were used in this experiment. The 5th instar is the last instar before the adult form emerges. I did not use 5th instars because they may have been close to emergence when they were collected, and my aim was to manipulate resource availability during
development, not adulthood. 773 of the 1219 notonectids collected met the criteria for use in the experiment. All other individuals were discarded in a bucket and later returned to the source pond at KSR.

I then gave each notonectid a unique ID number and randomly assigned them to one of three diet treatments (low, medium, or high). I placed them individually in plastic drinking cups (11 cm D x 9 cm H). The cups were filled with ~250 ml of aerated tap water, and contained a strip of craft foam (8 cm x 2.5 cm) weighted with a stone, to provide horizontal and vertical surfaces for the notonectids to rest on or hide under. All cups were transported to a growth chamber were set to 24°C, and a 15H day : 9H night light cycle to mimic conditions experienced in June in the area where the source pond is located. Individuals of the three diet treatments were randomly distributed within the growth chamber.

Notonectids were fed daily with dead fruit flies (*Drosophila melanogaster*). 3rd and 4th instar notonectids in the low, medium, and high diet treatments were fed 2, 3, and 6 fruit flies per day, respectively. Once they reached the 5th instar, individuals in the low, medium, and high diet treatments were fed were fed 3, 6, and 12 fruit flies per day, respectively. On July 24th, 2013, I added dead crickets to their diet, because of high juvenile mortality rates (see Chapter S1: Results and Discussion). Starting July 24th, each notonectid was fed ½ cricket twice per week, in addition to their daily allotment of fruit flies.

I recorded the ID and diet treatment of all notonectids that died in the laboratory. I also recorded the days on which each juvenile notonectid moulted to the next developmental stage. When each juvenile notonectid moulted to the adult stage, I waited at least five days for their exoskeletons to harden, and then marked them with a unique ID, and a symbol to denote their diet treatment (a red ‘V’, a blue ‘•’, or a green ‘|’), using Sharpie permanent markers.

The diet manipulation began when the notonectids were placed in the growth chamber. For the majority of notonectids (184 or 80%), the diet manipulation was terminated on August 19th, 2013. For a small number of notonectids (45 or 20%), the diet manipulation was extended until August 26th, 2013 because several notonectids (mostly from the low diet treatment) had not developed into adults in time for the August 19th termination date. I therefore kept the delayed notonectids, plus a random sample of individuals from the high and medium diet treatments in
the growth chamber until August 26th to allow time for the delayed notonectids to become adults, and for their exoskeletons to harden enough to be marked.

S1.2.2 Body composition analysis

On August 19th, immediately after the diet manipulation was terminated for the first group, I selected a random sample of adult notonectids (~1/10 individuals from each diet treatment), and preserved them individually in vials filled with 70% ethanol. These samples were taken so that I could estimate the effects of the juvenile diet manipulation on adult body mass, fat mass, and protein mass.

The remaining notonectids from the diet manipulation were transported to KSR and used in a field experiment designed to measure dispersal rates. Notonectids were placed in uncovered cattle tanks filled with water, and were allowed to disperse over the course of 15 days. Notonectids that left their original cattle tanks were classified as dispersers. Notonectids that remained in their original cattle tanks for the entire course of the field experiment were considered residents. Details of the field experiment are provided in the next chapter (Chapter S2: Materials and Methods: Estimating dispersal rates of adults in the field). I performed body composition analysis on notonectids to test whether adult body composition was influenced by juvenile diet. I analyzed all of notonectids that were preserved immediately after the diet manipulation. I also analyzed all of the notonectids that were classified as dispersers and a random sample of the notonectids that were classified as residents. In total, 87 individuals were selected for body composition analysis. Details on how body composition was analyzed were provided in this thesis in Chapter 1: Materials and Methods: Body composition analysis.

The notonectids from this project were analyzed at the same time, using the same protocols as the notonectids from the experiment in which the diet manipulation was imposed on adult notonectids (described in the main text of this thesis), so that body composition results could be compared between the two experiments.

S1.2.3 Statistical analysis

First, I tested the effects of diet and sex on body composition of individuals preserved immediately after the diet manipulation (pre) and individuals preserved after the field experiment
(post). To compare the effects of the cattle tank environment to the diet manipulation, I excluded dispersers. I did this because dispersers did not spend the entire course of the field experiment in the cattle tanks, and because they underwent dispersal, which is costly, and therefore are not representative of the effects of the cattle tanks on body composition.

The effects of diet treatment and sex on total body mass of pre- and post-field samples were analyzed using analysis of variance followed by independent contrasts. The effects of diet treatment and sex on fat and protein mass were analyzed using analysis of covariance, using total body mass as a covariate. Differences between residents and dispersers in body mass, fat mass, and protein mass were analyzed using analysis of variance. The effect of timing of the diet manipulation (adult or juvenile) on total body mass was analyzed using analysis of variance, followed by independent contrasts, with timing of diet manipulation and timing of preservation (pre- or post-field experiment) as factors. The effect of timing of the diet manipulation (adult or juvenile) on fat and protein mass was analyzed using analysis of covariance, with timing of diet manipulation and timing of preservation as factors, and total body mass as a covariate. These analyses were performed in JMP v.11.0.0.

S1.3 Results and Discussion

S1.3.1 Juvenile survival in the laboratory

The proportion of notonectids that survived from the day of collection to the end of the diet manipulation was 20%, 42%, and 38%, for individuals from the low, medium, and high diet treatments, respectively. There are no estimates of juvenile survivorship to adulthood in the wild, so survivorship itself is not conclusive evidence that the diets provided were suboptimal; however, this result, together with the result showing that notonectids gained weight after moving from the growth chamber to the pond mesocosms (Figure S1) indicates that the food provided to the notonectids in the diet manipulation was inferior compared to the food available in the cattle tanks, and therefore that mortality was likely high in the laboratory compared to a more natural environment.
S1.3.2 Body mass in the lab and after the field experiment

Immediately after the diet manipulation, total dry body mass depended on diet treatment (diet: $F_{2,26} = 31.9846, p < 0.0001$; Figure S1). Independent contrasts showed that individuals from the low diet treatment had the lowest body mass (Low diet – Medium diet: $t = -3.23, p < 0.0001$; Figure S1), and individuals from the high diet treatment had the highest body mass (Medium diet – High diet: $t = -2.28, p = 0.0008$). After the field experiment, notonectids were larger, on average, than notonectids preserved immediately after the diet manipulation (type: $F_{1,40} = 54.1730, p < 0.0001$; Figure S1). This increase in mass was greatest in the low-diet treatment, so that after the field experiment, there was no longer a discernible effect of diet treatment on body mass (diet: $F_{2,11} = 1.2542, p = 0.3231$). This suggests that, like the notonectids from the adult diet manipulation group, the notonectids in this group were also gaining weight over the course of the field experiment (see Chapter 1: Results and Discussion). This is consistent with the hypothesis that the cattle tanks in which the notonectids were held during the field experiment contained a higher quantity or quality of food than was provided during the diet manipulation, especially compared to the low diet treatment.

S1.3.3 Body mass of males and females

There was no difference in the dry body mass of males and females immediately after the diet manipulation (sex: $F_{1,23} = 0.0386, p = 0.8460$; Figure S1), nor after the field experiment (sex: $F_{1,11} = 0.6924, p = 0.4230$). These data do not appear consistent with the results of the adult diet manipulation group (Figure 1) or Hungerford (1934), showing that females are slightly larger.
Figure S1. Mean body mass +/- s.e. of notonectids of all three diet treatments in the juvenile diet manipulation group. “pre” = notonectids preserved immediately after the diet manipulation (n = 29). “post” = notonectids preserved after the field experiment (n = 17).
S1.3.4 Fat mass in the lab

Immediately after the diet manipulation, fat content was positively associated with diet treatment, but this effect was driven by the association between diet treatment and body mass (Figure S2). Variation in fat content was best explained by a quadratic relationship with total body mass only \((\text{body mass}^2): F_{1,27} = 59.9058, p < 0.0001\); Figure S2). The fit of this model was not improved by adding diet treatment as a factor (diet: \( F_{1,17} = 0.2008, p = 0.8200 \)). Therefore, individuals from the high diet treatment have higher absolute fat mass, and may have greater fat mass as a proportion of body mass because of the curvature in the relationship between body mass and fat mass. This indicates that individuals from the high diet treatment may have greater dispersal capacity than individuals in the medium and low diet treatments.

S1.3.5 Fat mass after the lab experiment

After the field experiment, notonectids had greater fat mass, on average, than notonectids preserved immediately after the diet manipulation \((\text{type}: F_{1,44} = 15.1436, p = 0.0003); \) Figure S2). Again, this was likely because the cattle tanks had a higher quantity or quality of food than was provided in the diet manipulation. After the field experiment, fat content again depended on total body mass \((\text{body mass}: F_{1,11} = 6.0325, p = 0.0319)\), but not diet treatment \((\text{diet}: F_{1,11} = 0.3841, p = 0.6899)\).
Figure S2. Fat mass vs body mass +/- 95% confidence of fit bands of all three diet treatments in the juvenile diet manipulation group. “pre” = notonectids preserved immediately after the diet manipulation (n = 29). “post” = notonectids preserved after the field experiment (n = 17).
S1.3.6 Fat mass of males and females

Males and females did not differ in fat content immediately after the diet treatment (sex: $F_{1,17} = 0.0004, p = 0.9529$; Figure S3), nor after the field experiment (sex: $F_{1,6} = 0.0559, p = 0.8210$). This result is not consistent with the results from the adult diet manipulation group showing that females had greater fat mass than males after the field experiment; however, the difference between males and females in fat content was larger in the juvenile diet manipulation group than the adult diet manipulation group (the difference between males and females in least-squares mean fat mass was 0.2885 mg in the juvenile diet manipulation group, and 0.1959 mg in the adult manipulation group). The lack of significance in the juvenile manipulation group is therefore likely a consequence of low sample size in this group. Further experimentation is needed to test the hypothesis that juvenile diet has carryover effects on sex-specific allocation to fat stores.
Figure S3. Fat mass vs body mass +/- 95% confidence of fit bands of males and females in the juvenile diet manipulation group. “pre” = notonectids preserved immediately after the diet manipulation \((n_{\text{male}} = 14, n_{\text{female}} = 15)\). “post” = notonectids preserved after the field experiment \((n_{\text{male}} = 6, n_{\text{female}} = 11)\).
S1.3.7 Flight muscles and protein mass

All of the notonectids dissected had developed flight muscles. Immediately after the diet manipulation, protein mass depended on body mass (body mass: $F_{1,17} = 4.6906, p = 0.0448$; Figure S4), but not diet treatment (diet: $F_{1,17} = 2.0028, p = 0.1656$). After the field experiment, protein mass did not depend on body mass, or diet treatment (body mass: $F_{1,11} = 0.2881, p = 0.6021$; diet: $F_{1,11} = 0.1656, p = 0.8494$; Figure S4). This result indicates that differences in protein content are probably not producing differences in dispersal capacity. After the field experiment, notonectids had greater protein mass, on average, than notonectids preserved immediately after the diet manipulation (type: $F_{1,42} = 28.7593, p < 0.0001$), again suggesting that the quality or quantity of food in the cattle tanks was higher than that provided in the diet manipulation.
Figure S4. Protein mass vs body mass +/- 95% confidence of fit bands of all three diet treatments in the juvenile diet manipulation group. “pre” = notonectids preserved immediately after the diet manipulation (n=29). “post” = notonectids preserved after the field experiment (n = 17).
S1.3.8 Protein mass of males and females

There was no difference between males and females in protein mass immediately after the diet manipulation (sex: $F_{1,17} = 1.0797$, $p = 0.3133$; Figure S5), nor after the field experiment (sex: $F_{1,6} = 1.1233$, $p = 0.3300$). This likely indicates that females in the juvenile diet manipulation group did not begin to allocate energy to egg production in the cattle tanks, but it could also be a consequence of low sample sizes in this group.
Figure S5. Protein mass vs body mass +/- 95% confidence of fit bands of males and females in the juvenile diet manipulation group. "Pre" = notonectids preserved immediately after the diet manipulation (n_{male} = 14, n_{female} = 15). "Post" = notonectids preserved after the field experiment (n_{male} = 6, n_{female} = 11).
S1.3.9 Recaptured dispersers from the juvenile diet manipulation group

I recaptured four dispersers from the cattle tank array. There were 2, 0, and 2 dispersers from the low, medium, and high condition groups, respectively. I did not test for differences between dispersers and residents in body physiology because the sample size was insufficient. However, a visual assessment indicated that, except for one light disperser, dispersers were near the top of the range for body mass (Figure S6A) and fat mass (Figure S6B), and near the bottom of the range for protein mass (Figure S6C). This is consistent with evidence that dispersers tend to be heavier and have higher fat content (all of these dispersers moved between tanks in the cattle tank array, and therefore probably did not expend much energy during dispersal), and that dispersers postpone egg production in favour of dispersal (and therefore have lower protein content). However, the data provided here do not give strong support because of the very low sample size. Both of these hypotheses are interesting avenues for future research.
Figure S6. A) Body mass, B) fat mass, and C) protein mass of dispersers and residents. Each blue dot represents one individual. Dispersers are notonectids that left their original tanks and were recaptured (n = 4). Residents are notonectids that remained in their original tanks over the entire course of the field experiment (n = 17).
S1.3.10 Comparison of notonectids from adult and juvenile diet manipulations

Notonectids from the juvenile diet manipulation had lower adult body mass than notonectids from the adult diet manipulation ($F_{1,212} = 54.0565, p < 0.0001$; Figure S7). Independent contrasts show that this was true when measured both immediately after the diet manipulation ($t = 5.84, p = 1.9 \times 10^{-8}$), and after the field experiment ($t = 4.502, p = 1.1 \times 10^{-5}$). This suggests that notonectids that underwent juvenile development in the laboratory were in poor condition relative to the notonectids that underwent juvenile development in the wild.

Notonectids from the juvenile diet manipulation had higher adult fat mass than notonectids from the adult diet manipulation ($F_{1,207} = 9.812, p = 0.002$; Figure S8). Independent contrasts show that this was true when measured both immediately after the diet manipulation ($t = 2.322, p = 0.0212$), and after the field experiment ($t = 2.177, p = 0.0306$). This suggests that the notonectids that experienced the low-quality laboratory environment during juvenile development invested more energy in fat mass than individuals that underwent juvenile development in the wild. This indicates that low-quality natal environments induce investment in dispersal capacity in this species. This phenomenon has been demonstrated previously in other taxa (e.g. ladybird beetles Dmitriew et al. 2009).

There was no difference in protein mass between notonectids from the juvenile diet manipulation and the adult diet manipulation ($F_{1,208} = 0.7829, p = 0.3773$; Figure S9). This result is consistent with the findings that protein mass did not depend on diet treatment, in the juvenile diet manipulation (Figure S4) nor in the adult diet manipulation (Figure 4). Since protein mass for both diet groups did increase over the course of the field experiment this may indicate that the food provided during the diet manipulation was low in protein, and all of the notonectids had low protein mass in the laboratory. Another possibility, not exclusive of the first, is that notonectids more invest resources in maintaining flight muscles when food availability is low, in order to maintain the capacity to disperse out of low-quality environments.
Figure S7. Mean body mass +/- s.e. of notonectids from the juvenile and adult diet manipulation groups. "Pre" = notonectids preserved immediately after the diet manipulation ($n_{juvenile} = 29$, $n_{adult} = 35$). "Post" = notonectids preserved after the field experiment ($n_{juvenile} = 17$, $n_{adult} = 119$).
Figure S8. Mean fat mass vs body mass +/- 95% confidence of fit bands of notonectids from the juvenile and adult diet manipulation groups. "Pre" = notonectids preserved immediately after the diet manipulation ($n_{\text{juvenile}} = 29$, $n_{\text{adult}} = 35$). "Post" = notonectids preserved after the field experiment ($n_{\text{juvenile}} = 17$, $n_{\text{adult}} = 119$).
Figure S9. Mean protein mass vs body mass +/- 95% confidence of fit bands of notonectids from the juvenile and adult diet manipulation groups. "Pre" = notonectids preserved immediately after the diet manipulation (n_{juvenile} = 29, n_{adult} = 35). "Post" = notonectids preserved after the field experiment (n_{juvenile} = 17, n_{adult} = 119).
S1.4 References


Chapter S2

The effects of predation risk and food availability during juvenile development on dispersal

S2.1 Introduction

In this chapter, I describe the experiment I conducted to test whether condition influences dispersal in adults, when condition is determined by food availability during juvenile development. I also tested whether the effects of condition interacted with perceived predation risk, as we may expect individuals in low condition to have higher foraging activity (Kohler and McPeek 1989), and therefore perceive themselves to be at higher predation risk. I asked this by manipulating the food provided to juvenile notonectids in the lab, and then measuring adult dispersal rates out of pond mesocosms with and without fish predators.

S2.2 Materials and Methods

S2.2.1 Creating variance in juvenile notonectid condition

The notonectids from the juvenile diet manipulation were the source of experimental animals for both the body composition analysis and the field experiment. I reproduce pertinent details of the diet manipulation here. For more details on how variance in backswimmer condition was created, see Chapter S1: Materials and Methods: Creating variance in juvenile notonectid condition.

On June 25\textsuperscript{th} - July 10\textsuperscript{th}, 2013, I collected 773 juveniles of the species \textit{Notonecta undulata} from instars 3-4 from a small fishless pond at KSR. They were transported to the University of Toronto and randomly assigned to one of three diet treatments (low, medium, or high). Notonectids were placed in cups of water and fed with dead fruit flies (\textit{Drosophila melanogaster}). 3\textsuperscript{rd} and 4\textsuperscript{th} instar notonectids in the low, medium, and high diet treatments were fed 2, 3, and 6 fruit flies per day, respectively. Once they reached the 5\textsuperscript{th} instar, notonectids in the low, medium, and high diet treatments were fed 3, 6, and 12 fruit flies per day, respectively. On July 24\textsuperscript{th}, 2013, I added dead crickets to their diet, because of high juvenile mortality rates. Starting July 24\textsuperscript{th}, each notonectid was fed \(\frac{1}{2}\) cricket twice per week, in addition to their daily allotment of fruit flies.
On August 19\textsuperscript{th}, 2013, and August 26\textsuperscript{th}, 2013 the notonectids were transported to the Koffler Scientific Reserve (KSR). During transport, the notonectids remained in their cups, and the cups were placed in covered plastic trays to prevent them from escaping.

S2.2.2 Estimating dispersal rates of adults in the field

The notonectids from this experiment were placed in the same cattle tank array at the same time as the notonectids from the experiment in which the diet manipulation was imposed on adult notonectids (described in the main text of this thesis). Here, I reproduce pertinent details of how the field mesocosm experiment was prepared. For more details on the field mesocosms experiment see Chapter 2: Materials and Methods: Estimating dispersal rates of adults in the field.

In June 2013, I placed an array of 40 cattle tanks in an open field. The cattle tanks acted as experimental source ponds; notonectids were placed in these at the beginning of the experiment, and their emigration rates was estimated over the course of 15 days. I also placed smaller pools in the field, in four perpendicular transects moving away from the cattle tank array at increasing distances (Figure 7). These pools were monitored for dispersing notonectids.

I placed a fish cage in each cattle tank, and placed one fish \textit{(Lepomis gibbosus)} in half of these cages. I fed each fish one cube of frozen bloodworms plus four live notonectids per day.

On August 19\textsuperscript{th}, marked, adult notonectids from both experiments were transported from the growth chamber at the University of Toronto to the field mesocosm experiment at KSR. This first notonectid transport consisted of 184 of the 229 (80\%) individuals placed in the cattle tanks from the juvenile diet manipulation experiment. Notonectids from the juvenile diet manipulation experiment were divided into six cattle tanks. Each tank received 7-8 individuals from the low diet treatment, 12-13 individuals from the medium diet treatment, and 11 individuals from the high diet treatment, with each tank receiving 30-31 notonectids in total. This notonectid density falls within the natural range for this species (Bennett and Streams 1986).

On August 26\textsuperscript{th}, the notonectids in the second transport to KSR were added to the field mesocosm experiment. This transport consisted of the remaining 45 of the 229 (20\%) individuals placed in the cattle tanks from the juvenile diet manipulation experiment. These individuals were
equally divided among the six cattle tanks used in the juvenile manipulation field experiment. Each tank received another 0-1 individuals from the low diet treatment, 3-4 individuals from the medium diet treatment, and 3-4 individuals from the high diet treatment. In total, each tank eventually received 38-39 notonectids, which falls within the natural range for this species (Bennett and Streams 1986).

Experimental tanks were left uncovered for 15 days to allow notonectids to disperse. I estimated emigration rates by recording the markings of each individual present in each tank every three days. Recording the individuals present in all tanks was time-consuming, and could not be done in a single day. I therefore divided the tanks into three time blocks, and recorded the individuals present within each block every three days. Time blocks 1 and 2 contained two and four tanks, respectively. Both predator treatments were equally represented in both blocks.

When dead notonectids were found, I recorded their markings and discarded them away from the cattle tank array. Even notonectids which died as a result of cannibalism could be accounted for in this way, because notonectids consume the insides of their prey and leave the exoskeleton intact, so the ID markings of any cannibalized individuals could be recorded. All individuals that left their original tanks were considered dispersers. All individuals that remained in their original tanks over the entire course of the experiment were considered residents.

I monitored the pool transects daily for any dispersing notonectids. Any colonists in these pools were preserved individually in vials filled with 70% ethanol. I also monitored the source pond from which all the notonectids were originally collected. All marked notonectids found in the source pond were preserved individually in 70% ethanol. On September 2-3, 2013, the markings of all of the notonectids remaining in the tanks were recorded, and the notonectids were preserved individually in vials filled with 70% ethanol.

S2.2.3 Statistical analysis

The effects of diet treatment, predator treatment, and time on dispersal rates were analyzed using survival analysis as per Allison (2010). I used a generalized linear mixed model with a binomial error distribution and a logit link, using dispersal status (dispersed or resident) as the response. I allowed dispersal status to be right-censored, to account for individuals that died during the
course of the experiment. The fixed effects were time, predator treatment, diet treatment, and all possible interactions. I included tank nested within block as a random effect. I evaluated significance of the fixed effects using type III sum of squares. This analysis was performed in R v.2.14.2.

S2.3 Results and Discussion

There was no difference in the number of notonectids that emigrated from fish and fishless tanks, overall (predator: $\chi^2_1 = 0.1035, p = 0.748$; Figure S10); however, there was a significant interaction between predator treatment and time (predator × time: $\chi^2_1 = 7.1479, p = 0.008$). This interaction was due to the fact that at the beginning of the experiment, more notonectids emigrated from fishless tanks than fish tanks; however, this effect was small and had mostly disappeared by the end of the experiment. The result that notonectids dispersed more out of fishless tanks is not consistent with previous studies demonstrating that predators induced dispersal (McCauley and Rowe 2010), as well as the results described Chapter 2 when food availability was manipulated in adults. It is possible that fish predators increased refuge use and decreased dispersal propensity in these notonectids; however, it is more likely that this result is spurious. Further experimentation is needed to determine whether predation risk can suppress dispersal propensity when physiological condition is low (as it seemingly was for individuals from all juvenile diet treatments).

The number of notonectids that emigrated did not depend on diet treatment at any time point (diet: $\chi^2_2 = 3.9066, p = 0.1418$; diet × time: $\chi^2_2 = 0.8972, p = 0.639$; Figure S10). The interaction between diet treatment and predator treatment did not have a significant effect on dispersal status at any time point (predator × diet: $\chi^2_2 = 1.0767, p = 0.584$; predator × diet × time: $\chi^2_2 = 1.8764, p = 0.3913$).
Figure S10. Kaplan-Meier curves for mean probability of philopatry of individuals in juvenile manipulation group for each fish × diet treatment in each round. Rounds are separated by three days.

S2.4 References


Appendix Discussion

In this appendix, I described a project I conducted to test how resource availability experienced during juvenile development influences dispersal-related physiological traits. I then tested whether these differences in resource availability had carryover effects on dispersal in adults, and how the relationship between condition and dispersal depended on predation risk. I found that variation in resource availability during development did not have a strong influence on dispersal-related physiological traits (fat mass and protein mass; Figure S2, Figure S4). However, I did find that individuals from the juvenile diet manipulation had lower total body mass (Figure S7), and lower protein mass (Figure S9) than individuals from the adult diet manipulation, indicating that the laboratory environment was suboptimal for juvenile development. I also found that the diet manipulation imposed on juveniles did not have carryover effects on adult dispersal rates; dispersal rates overall were low, and did not depend on diet treatment (Figure S10). Together, these results suggest that there is a condition threshold for dispersal in this species, and that a high proportion of individuals from the juvenile diet manipulation did not reach this threshold.

Interestingly, notonectids that experienced the low-quality laboratory environment during juvenile development had greater fat mass than notonectids that underwent development in the wild (Figure S8). This may indicate that notonectids invest more energy in dispersal capacity in response to low-quality natal environments, as has been shown in previous studies in other taxa (e.g. Dmitriew et al. 2009). In this study, the differences in fat mass did not translate to differences in emigration rates (Figure S10); however, this suggests the possibility that the direction of the relationship between condition and dispersal may depend on the life stage at which variation in condition is produced. Variation in condition created during juvenile development may cause negative condition-dependent dispersal, which would contrast with the result of this thesis demonstrating that variation in condition created during adulthood causes positive condition-dependent dispersal. Testing this question would be an interesting avenue of further study.

In this project, I asked whether resource availability experienced during development had carryover effects on adult dispersal. I found no relationship between resource availability and
dispersal; however, body composition analysis suggests that the notonectids reared in the laboratory were in poor condition, and that the laboratory environment was suboptimal for juvenile development. Because of this methodological problem, the results of this study are inconclusive. However, these results indicated that resource availability experienced during juvenile development might have different effects on dispersal capacity than resource availability experienced during adulthood. Future studies of condition-dependent dispersal should explicitly consider the source of the condition variation.

References