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THE EVOLUTION OF DISPERSAL CONDITIONED ON MIGRATION STATUS

(Spine Title: Dispersal Conditioned on Migration Status)

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by

SM Asaduzzaman

Graduate Program
in
Applied Mathematics

A thesis submitted in partial fulfillment
of the requirements for the degree of
Master of Science

The School of Graduate and Postdoctoral Studies
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Abstract

We build on the work of El Mouden and Gardner (2008) and consider the evolution of natal dispersal conditioned upon an individual's 'migration status'. In particular, we look to compare the evolution of this kind of conditional dispersal with the evolution of its unconditional counterpart. Our goal is to determine the extent to which dispersal conditional upon migration status changes predictions about population-wide levels of dispersal. Simply we ask: what weight should the possibility of this kind of conditional dispersal be given by an evolutionary biologist? We find the stable dispersal rates of natives and non-natives, respectively, are predicted to vary with changing parameter values, and the stable dispersal rates of natives and non-natives are predicted to differ from one another in a way consistent with inclusive-fitness theory. We also find differencs between Taylor's (1988) unconditional dispersal rate, and the population-average dispersal rate predicted by our model.

Keywords. Conditional dispersal, Dispersal conditioned on migration status, Stable dispersal, Conditional and unconditional dispersal.

Statement of Co-Authorship

The work presented in Chapter 2 has been submitted in the journal of Ecology and Evolution entitled with ' The Evolution of Dispersal Conditioned on Migration Status' for publication. The original draft was prepared under the supervision of Dr. Geoff Wild. Subsequent revisions, developing MATLAB codes for numerical analysis as well simulation were also performed under the supervision of Dr. Geoff Wild.

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Contents

List of Figures

Chapter 1

Introduction

1.1 Dispersal and its importance

Dispersal of an individual is the movement from its point of origin to the place where it reproduces or would have reproduced if it had survived and found a mate (Greenwood, 1980). Dispersal can also be defined as any movement of individuals or propagules with potential consequences for gene flow across space (Ronce, 2007). Dispersal involves three successive behavioral stages- called (a) departure (or emigration), (b) a vagrant stage (transience), and (c) settling (or immigration). The entire process should be referred to as dispersal. Dispersal is, generally, of two kinds: natal dispersal and breeding dispersal.

Natal dispersal is defined as active or passive movement by which an individual leaves its birth place to engage in mating or reproduction somewhere else (Greenwood, 1980; Ronce, 2007; Clobert el al., 2009), and breeding dispersal is the movement of an individual between successive breeding sites (Greenwood, 1980). Natal dispersal, both in plants and animals, is a widespread phenomenon (Taylor, 1988).

Usually, the terms migration and dispersal are used interchangeably but there are authors (e.g. Clobert el al., 2009) that make a distinction between them. Dispersal implies relocation of the natal breeding site, and can occur at any life stage, at any spatial scale above the individual range, and within more or less heterogeneous landscapes (Clobert el al., 2009).

There are different forms of dispersal such as (a) habitat selection, (b) condition dependence, (c) phenotype dependence, and (d) informed dispersal. *Habitat selection* is a type of dispersal behavioral process that results in a biased utilization of habitats, and influences the survival and reproduction of individuals. This form of dispersal is becoming increasingly apparent as more populations face the major threats posed by global climate change and the fragmentation of their habitat. For example, habitat quality and population density determine settlement differentially in small and large adult Great Tits (*Parus major*, Garant et al., 2005). The form of dispersal of individuals that depends on external factors (e.g. inbreeding risk, kin competition, intraspecific competition, and outbreeding risk) is termed *condition-dependent* dispersal. For example, kin competition among Fig Wasps (*Agaonidae*), influences the body size of male dispersers depending on levels of mate and resource competition (Moore et al., 2006). *Phenotype-dependent* dispersal depends on internal states of individuals. Phenotypic differences have been found for a variety of physiological, morphological, behavioral and life-history traits. Any dispersal decision based on social or non-social cues is termed *informed dispersal* because the individuals can gather and exchange information at the different stages of dispersal.

Dispersal may allow the exploitation of ephemeral resources, and is essential for most species to persist in their ever changing natural environment (Ronce, 2007). The importance of dispersal behavior for the ecology, and genetics of wild populations is becoming increasingly apparent as populations face global climate change and the destruction of their habitat (Thomas et al., 1998; Hill et al., 1999). Dispersal could also be influenced by habitat, intraspecific and interspecific interactions, and resource quality.

Dispersal is considered to be costly as the dispersing individual might not find a better or an emptier patch for mating or reproduction, and if they find one, the competition may be no less than what they would face in their natal patch (Taylor, 1988). Mortality may be increased during the transient stage of dispersal by the use of non-optimal habitat, and increased predation risk (Ims and Andreassen, 2000). For plants, a large fraction of wind-dispersed pollen never ends up on the stigma of a receptive flower of same species. One might reasonably ask: why do individuals of most species, then, tend to disperse? Among many reasons, individuals of most species tend to disperse for (a) inbreeding depression avoidance, (b) kin competition avoidance, and (c) colonization of new habitat.

The possibility of future encounters with each other decreases by the dispersal of individuals, and reduces kin competition. Competitive interactions, thus, among relatives can favor non-zero dispersal rates between patches, even in a temporally, and spatially constant environment (Hamilton and May, 1977; Motro 1982, 1983; Frank, 1986; Taylor, 1988). Therefore, natal dispersal serves to reduce kin competition, and to avoid inbreeding. Dispersal, thus, presents an evolutionary problem, since it imposes a personal cost on the disperser, and the benefits are shared by all siblings, and relatives that are not dispersing. As the cost of dispersal increased, compared with possible damage resulting from kin competition (Hamilton and May, 1977; Motro, 1983; Frank, 1986; Taylor 1988) or from inbreeding (Bengtsson 1978; Greenwood 1980), the evolutionary stable dispersal rate decreases. Population genetic models of selection, in multipatch environment indicate that if allelic fitnesses are temporally constant but different alleles are favoured in different patches, alleles for reduced dispersal can always invade (Balkau and Feldman, 1973). Ecological models also suggest that individuals should not disperse in spatially varying but temporally constant environment (Hastings, 1983; Holt, 1985), but these studies neglect kin effects.

The evolutionary stable dispersal strategy is, generally, a decreasing function of cost of dispersal (the cost associated with any dispersal event), and an increasing function of relatedness. Motro (1991), presented a simple population-genetic model that considered both the effects of sibling competition, and inbreeding avoidance to find the evolutionary stable strategies of dispersal. The evolutionary stable strategy of dispersal is also affected by environment, and the life history traits of the species (Gandon and Michalakis, 1999). In extant metapopulation models individuals with both a very large number of sites and very large number of individuals per site, escape from overcrowding is the cause of dispersal evolution (Gyllenberg et al., 2002).

Inbreeding depression is defined as the probability of two alleles, on complementary chromosomes, being identical by descent. If an individual has two identical copies of a deleterious recessive allele (recessive allele - an allele that produces its characteristic phenotype only when its paired allele is identical), the individual will express, then, a trait of lower fitness, or in the worst case, will cause death. Most empirical evidence to date suggests that the majority of inbreeding depression is caused by deleterious recessive or partially recessive alleles that are manifest in the homozygous state in inbreed individuals (Charlesworth and Charlesworth, 1987; Crnokrak and Roff, 1999; Charlesworth and Willis, 2009). Only a small proportion of these recessive alleles appear to be lethal in the homozygous state but a significant proportion appear to be nonlethal deleterious alleles, and partially recessive (Cheptou and Donohue, 2010). However, deleterious mutations could play a major role in causing inbreeding depression (Charlesworth and Charlesworth, 1999).

Individuals, thus, reduce the risk of inbreeding depression by dispersing from their natal site (Greenwood, 1980). Great Tits, for example, which mate with close relatives have a lower than expected nesting success (Greenwood et al., 1978). The viability of offspring sired by a male olive baboon (*Papio anubis*) which mated with probable female relatives was substantially less than that of outbred young (Packer, 1979). Elisabeth et al. (2010) considered full-sib mating to investigate the effects of inbreeding on viability, attractiveness, morphology and potentially secondary sexual traits in male and female zebra finches, *Taeniopygia guttata*. Though inbreeding depression has a great importance, we are neglecting the effect of inbreeding depression in Chapter 2.

Dominance relations among individuals can promote dispersal in temporally constant but spatially varying environment (Pulliam, 1988). The low frequency of dispersal of the butterfly (*Euphydrias editha*), from its colonies could be explained this way (Ehrlich, 1961). Dispersal is not, always, a willful event. Individuals, sometimes, are forced to disperse from their natal patch (Archer, 1970). Individuals forced to disperse are, frequently, the socially subordinate, younger and weaker member of the population. Increasing population density may be associated with high level of dispersal.

Animals and plants exhibit a broad spectrum of dispersal strategies (e.g. unconditional dispersal, and conditional dispersal). The simplest dispersal strategy, for individuals, is the unconditional strategy which is to disperse at constant per capita rates regardless of the environment. On the other hand, an individual could have a highly flexible dispersal strategy sensitive to habitat type, local population size, migration status on a patch, body-condition, and other predictors of local fitness. This type of dispersal strategy is termed conditional dispersal. McPeek and Holt (1992) considered both unconditional and conditional dispersal strategies of individuals in spatially, and temporally varying environments, and found, if individuals express conditional dispersal strategies, dispersal can be favored in a spatially varying but temporally constant environment.

In the next sections, we will discuss inclusive fitness theory, and branching processes to analyze a population model presented in section 1.4.

1.2 Inclusive fitness theory

Inclusive fitness theory, in evolutionary biology, provides an adaptive explanation for the existence of social behaviours. Inclusive fitness includes the reproductive success (how many of its own offspring it produces, and supports) and survival of an individual as well as the reproductive success and survival of that individual's relatives. Reproductive success of an individual, from a gene's point of view, depends on leaving behind the maximum number of copies of itself in the population. Until 1964, it was believed that reproductive success of an individual can only be achieved by leaving its maximum number of viable offspring. However, Hamilton (1964) argued that, because close relatives of an individual share some identical genes, fitness can also be increased by promoting the reproduction, and survival of these related individuals. Inclusive fitness theory, thus, offers a mechanism for the evolution of altruism (Hamilton, 1964).

Natural selection, in Hamilton's (1964) model, favours the gene(s) for altruism whenever $rb > c$ where c is the reproductive cost to altruist, b is the reproductive benefit to the recipient of the altruistic behaviour, and r is the probability, above the population average, of the individuals sharing an altruistic gene (relatedness between altruist and recipient). Hamilton's (1964) rule can be explained as follows: if a gene for altruism is to evolve, then the cost of altruism must, somehow, be balanced by compensating benefits to the altruist. The cost of altruism c is balanced by benefits b accrued by close relatives of the altruist, because the gene for altruism may be carried by close relatives. However, the close relatives have only the probability, r, of carrying the gene for altruism, and the benefits, thus, received must be weighted by the probability.

1.3 Branching processes

Branching processes were introduced by Galton and Watson in studying the survival of family names in the 1870s. Suppose N adult males in a population each have different surnames. Suppose in each generation, a_0 percent of the adult males have no male children who survive to adulthood; a_1 percent have one such child; a_2 percent have two, and so on upto a_5, who have five. Galton and Watson, then, were supposed to find the proportion of the surnames which become extinct after r generations. This process is known as a

Galton-Watson branching process. Mathematically, a branching process is described as follows.

Let X_0 denote the total size of population at the zeroth generation, and X_n the size of population at the nth generation. The process, then, $\{X_n\}_{n=0}^{\infty}$ has state space $\{0, 1, 2, \cdots\}$. Assume that in the nth generation, each individual gives birth to $Y \in \mathbb{N}$ offspring in the next generation with offspring distribution $\{p_k\}_{k=0}^{\infty}$,

$$\text{Prob}\,\{Y = k\} = p_k, \quad k = 0, 1, 2, \cdots$$

The process $\{X_n\}_{n=0}^{\infty}$ is refered to as a branching process.

1.4 The population model

In this section, we will propose a simple population model where the dispersal of individuals is not conditioned on their migration status. In this model, first, we will find the evolutionary stable dispersal rate of individuals using (a) inclusive fitness theory (Taylor, 1988), and (b) a branching process (Wild, 2011). In chapter two, we will extend this model to find the evolutionary stable dispersal rate if the dispersal of individuals is conditioned on migration status i.e. we will find the evolutionary stable dispersal rate when native and non-native individuals have different dispersal strategies to disperse offspring onto the other patch.

We consider a haploid asexual population undergoing discrete, non-overlapping generations. The population consists of a very large number of habitat patches (M) of identical quality, and each patch supports exactly N individuals (i.e. N breeding sites per patch). The model of the life cycle of an individual consists of a series of discrete stages- (a) birth of offspring, (b) dispersal of offspring, (c) death of parents, and (d) competition for breeding sites. In stage (a), each breeding adult produces a large number of offspring (K). In stage (b), a fraction of offspring disperses from its natal patch incurring a cost of dispersal c. In stage (c), all parents are assumed to die immediately after the dispersal stage of offspring, leaving N breeding sites vacant per patch for the next generation. In stage (d), a successful disperser will compete on a patch chosen uniformly at random from the population as a whole.

1.5 ESS dispersal using inclusive fitness theory

In this section, we will briefly review the inclusive fitness approach to unconditional dispersal presented by Taylor (1988). We want to find the evolutionary stable dispersal rate of individuals for the population model presented in section 1.4.

Taylor's (1988) approach works for diploid sexual and haploid asexual populations alike. We consider an adult mutant breeding on a focal patch, and the dispersal of offspring under parental control. The mutant female disperses its offspring with probability $d^* + \epsilon$, and each non-mutant female disperses its offspring with probability d^*. After the dispersal phase, the offspring (natives and immigrants) on each patch compete for the N mating spots, and every breeding site in the population is assumed to be occupied during every generation.

Denoting by p, the probability that each of these (natives or immigrants) offspring will be a winner on the patch, by c the cost of dispersal and by k the probability that each offspring is native to the patch, then according to Taylor (1988),

$$\begin{aligned} k &= \frac{(1-d^*)}{(1-d^*)+(1-c)d^*} \\ &= \frac{1-d^*}{1-cd^*}. \end{aligned} \tag{1.1}$$

The mutant breeder has the fitness through her dispersing offspring $(1-c)p$ instead of fitness p if the offspring would not disperse. Thus, the change in fitness due to her mutant behavior is $-\epsilon cp$. Since the mutant breeder sends out an extra ϵ proportion of her offspring elsewhere, thus an extra ϵp proportion of offspring would be able to breed on the focal patch. Thus, the fitness increment of the mutant adult through relatives is ϵpRk where R is the relatedness between the focal adult and average offspring born on the patch.

Therefore, the focal individual's inclusive fitness increment is $\Delta W = \epsilon p(-c + Rk)$. Natural selection should favour a change in dispersal behaviour from d^* to $d^* + \epsilon$ only if the inclusive fitness increment ΔW is positive. The condition, thus, for selection to favour an increased d^* is $Rk > c$ obtained by Taylor (1988). Since the population is haploid asexual, the relatedness R between the focal adult and average offspring born on the patch is found as the solution to the following recursive equation.

$$R = \frac{1}{N} + (1 - \frac{1}{N})k^2R. \tag{1.2}$$

Solving for R, the relatedness $R = \frac{1}{N-(N-1)k^2}$, and ESS dispersal rate is obtained by solving $Rk = c$ for d^*, which is then

$$d^* = \frac{1 + 2Nc - \sqrt{1 + 4N^2c^2 - 4Nc^2}}{2Nc(1 + c)}. \tag{1.3}$$

For $N = 1$, the ESS dispersal rate $d^* = \frac{1}{1+c}$ was found by Hamilton and May (1977) and Motro (1982, 1983) which is a special case of Taylor's result.

1.6 ESS dispersal using branching process

Wild (2011) considered a model similar to the model described in section 1.4 to study the evolution of altruism in a large population using multitype branching process. In this section, we will follow the procedure described by Wild (2011) to find the ESS dispersal rate of individuals of the model in section 1.4. So, our analysis very much resembles that of Wild (2011).

1.6.1 Patch updating procedure

Let us consider that the individuals are carrying two forms of gene either the mutant type (A), or wild-type (a). Let $i = 0, 1, 2, \cdots, N$ denote the number of mutants on a patch, and $(N - i)$ gives the number of wild-type individuals on the patch. On state-i patch, we mean there are i-mutants and $(N - i)$ wild-type individuals. We observe the population at discrete points in time $n = 0, 1, 2, \cdots\cdots$. Let $X_i(n)$ denote the number of state-i patches observed at time n, and $X(n) = \big(X_0(n), X_1(n), X_2(n), \cdots, X_N(n)\big)$.

Now, we fix our attention on a state-i patch. Denote the dispersal rate of mutant, and wild-type offspring by d^A and d^a respectively. Recall that we assumed, in our model, each individual (mutant or wild-type) is producing a large number (K) of offspring. Thus, there is no benefit over reproductive success for mutant allele-A. The exact proportion of competitive ability of mutant offspring, $(1 - d^A)$ is assigned for local competition. On the other hand, wild-type offspring assigns $(1 - d^a)$ proportion for local competition. The remaining fraction d^A and d^a, respectively, of mutant and wild-type offspring is devoted to non-local competition.

The total local competitive effort on state-i patch is give by

$$(1 - d^A)i + (1 - d^a)(N - i), \tag{1.4}$$

and since an individual can compete non-locally on its native patch, the total non-local competitive effort is given by

$$\frac{1-c}{M}\sum_{k=0}^{N}(X_k(n)(N - k)d^a + X_k(n)kd^A). \tag{1.5}$$

In order to update, the occupancy of a site on state-i patch, we let

$$p_{i,L} = \frac{(1-d^A)i + (1-d^a)(N-i)}{(1-d^A)i + (1-d^a)(N-i) + \frac{1-c}{M}\sum_{k=0}^{N}\left(X_k(n)(N-k)d^a + X_k(n)kd^A\right)} \tag{1.6}$$

be the probability of putting a locally produced offspring on a site on a state-i patch, and let $p_{i,NL} = 1 - p_{i,L}$ be the probability of putting a non-locally produced offspring on a site on a state-i patch.

Let us now focus on a mutant allele-A, let

$$q_{i,A|L} = \frac{(1-d^A)i}{(1-d^A)i + (1-d^a)(N-i)} \tag{1.7}$$

be the probability that a site on a state-i patch will be occupied by an individual bearing a mutant allele-A, given that it is colonized by local offspring and a non-locally produced offspring, bearing mutant allele-A, will occupy the site on state-i patch with probability,

$$q_{i,A|NL} = \frac{\sum_{j=0}^{N} X_j(n)jd^A}{\sum_{j=0}^{N}(X_j(n)(N-j)d^a + X_j(n)jd^A)}. \tag{1.8}$$

To update the entire state-i patch, we will simply repeat the above process for each of N sites on the patch, and express the probability that a state-i patch at time n becomes a state-j patch at time $n+1$ as,

$$P_{ij} = \binom{N}{j}\left(p_{i,L}q_{i,A|L} + (1-p_{i,L})q_{i,A|NL}\right)^j\left(1 - p_{i,L}q_{i,A|L} - (1-p_{i,L})q_{i,A|NL}\right)^{N-j}. \tag{1.9}$$

The process, $\{\mathbf{X} : n \geq 0\}$ can be thought of as a Markov chain with one-step transition probabilities determined by P_{ij}.

1.6.2 Branching process approximation

We will use an approximation to study $\{\mathbf{X} : n \geq 0\}$ as a branching process. Since the mutant is globally very rare, and $X_i(n) \ll X_0(n)$ for $i \geq 1$, so $X_0 \approx M$. Consider a patch that was most recently occupied by individuals bearing mutant allele-A, and to find the probability that any given site on this patch becomes occupied by mutant allele-A in next time step, we find the total external competitive effort on this patch

$$\begin{aligned}
&\frac{1-c}{M}\sum_{k=0}^{N}\left(X_k(n)(N-k)d^a + X_k(n)kd^A\right)\\
&\qquad = \frac{1-c}{M}\left(\sum_{k=0}^{N-1} X_k(n)(N-k)d^a + \sum_{k=1}^{N} X_k(n)kd^A\right)\\
&\qquad = N(1-c)\left(\sum_{k=0}^{N-1}\frac{X_k(n)}{M}\frac{(N-k)}{N}d^a + \sum_{k=1}^{N}\frac{X_k(n)}{M}\frac{k}{N}d^A\right)\\
&\qquad = N(1-c)\left(d^a p^a(n) + d^A p^A(n)\right),
\end{aligned}$$

where $p^a(n)$ and $p^A(n)$ denote, respectively, the global frequencies of the wild-type allele-a and mutant allele-A at time n. On a state-i patch the total internal competitive effort is

$$(1-d^a)(N-i) + (1-d^A)i.$$

We use P_i^A to denote the probability that any given site on a state-i patch will be occupied by a mutant in next time step, then

$$P_i^A = \frac{(1-d^A)i + d^A(1-c)Np^A(n)}{(1-d^a)(N-i) + (1-d^A)i + N(1-c)\left(d^a p^a(n) + d^A p^A(n)\right)}.$$

Applying the large-X_0 approximation, we find that

$$p_{i,L}q_{i,A|L} + (1-p_{i,L})q_{i,A|NL} \approx \frac{(1-d^A)i}{(1-d^a)(N-i) + (1-d^A)i + N(1-c)d^a}.$$

Use $\tilde{P}_i$ to denote this approximation i.e.

$$\tilde{P}_i = \frac{(1-d^A)i}{(1-d^a)(N-i)+(1-d^A)i+N(1-c)d^a}. \tag{1.10}$$

The previous transition probability (1.9), thus, can be written as

$$\tilde{P}_{ij} = \binom{N}{j}(\tilde{P}_i)^j(1-\tilde{P}_i)^{N-j}. \tag{1.11}$$

At time n, the state-i patch can be denoted by a set of new random variables, $\{A_{ij}^L, A_{ij}^{NL}\}_{j=1}^N$ where the random variable A_{ij}^L denotes the number of state-j patches produced by a state-i patch through local competitive effort, and the random variable A_{ij}^{NL} denotes the number of state-j patches produced by a state-i patch through non-local competitive effort of its inhabitants.

The probability generating function (pgf) for the joint distribution of $\{A_{ij}^L\}_{j=1}^N$ is

$$f_i^L(z_0, z_1, \cdots, z_N) = \left(1 - \sum_{j=0}^{N} \tilde{P}_{ij}\right) + \sum_{j=0}^{N} \tilde{P}_{ij} z_j. \tag{1.12}$$

On the other hand, the state-i patch sends out $i(1-c)d^A$ units of competitive effort, and this competitive effort is divided evenly over the M patches to compete against $(1-d^a)N + N(1-c)d^a$ units of competitive effort. The competitive effort given by state-i patch, therefore, will succeed with probability $\frac{\frac{1}{M}d^A(1-c)i}{(1-d^a)N+N(1-c)d^a}$. Since the probability of success is very small compared to number of trials NM, the distribution of random variable $\{A_{ij}^{NL}\}_{j=1}^N$, can be approximated by Poisson distribution with mean $NM\frac{\frac{1}{M}d^A(1-c)i}{(1-d^a)N+N(1-c)d^a}$, i.e. A_{i1}^{NL} follows the distribution $A_{i1}^{NL} \sim \text{Poisson}\big(i\frac{d^A}{d^a}m\big)$ approximately, where $m = \frac{(1-c)d^a}{1-cd^a}$ is the wild-type backward migration rate. Thus, the probability generating function (pgf) of distribution $\{A_{ij}^{NL}\}_{j=1}^{N}$ is

$$f_i^{NL}(z_1) = \exp\left\{ i\frac{d^A}{d^a} m(z_1 - 1) \right\}. \tag{1.13}$$

The probability generating function for the joint distribution of descendent patches is $f_i(z_1, ..., z_N) = f_i^{NL}(z_1) f_i^L(z_1, ..., z_N)$ because the probability generation functions of $\{A_{ij}^{L}\}_{j=1}^{N}$ and $\{A_{ij}^{NL}\}_{j=1}^{N}$, respectively, are independent of each other. The extinction probability of mutant can be found by finding the fixed point of the probability generating function

$$F(z_1, ..., z_N) = [f_1(z_1, ..., z_N), ..., f_N(z_1, ..., z_N)]. \tag{1.14}$$

We will use the equation (1.14) to find extinction probability of mutants (see MATLAB codes in appendix G) for different combination of dispersal strategy of wild-types (d^a) and mutants (d^A), respectively. We recorded the combination of d^a and d^A for which the extinction probability of mutants is always less than one (Figure 1.1). The regions where the mutant invasion is successful have been marked with small squares (Figure 1.1, marked regions). The ESS dispersal strategy has been reported as the dispersal strategy of wild-types that can not be invaded by any other mutant strategy.

1.7 Conclusion and preview of later chapters

In this chapter, we presented two important tools- inclusive fitness theory, and branching processes to find the evolutionary stable dispersal rate of individuals. In chapter two, we will extend the model presented in this chapter where we will consider that the individual's dispersal rate is conditioned on its migration status. To find the population-average dispersal rate of individuals in that situation, we will use a version of inclusive fitness theory

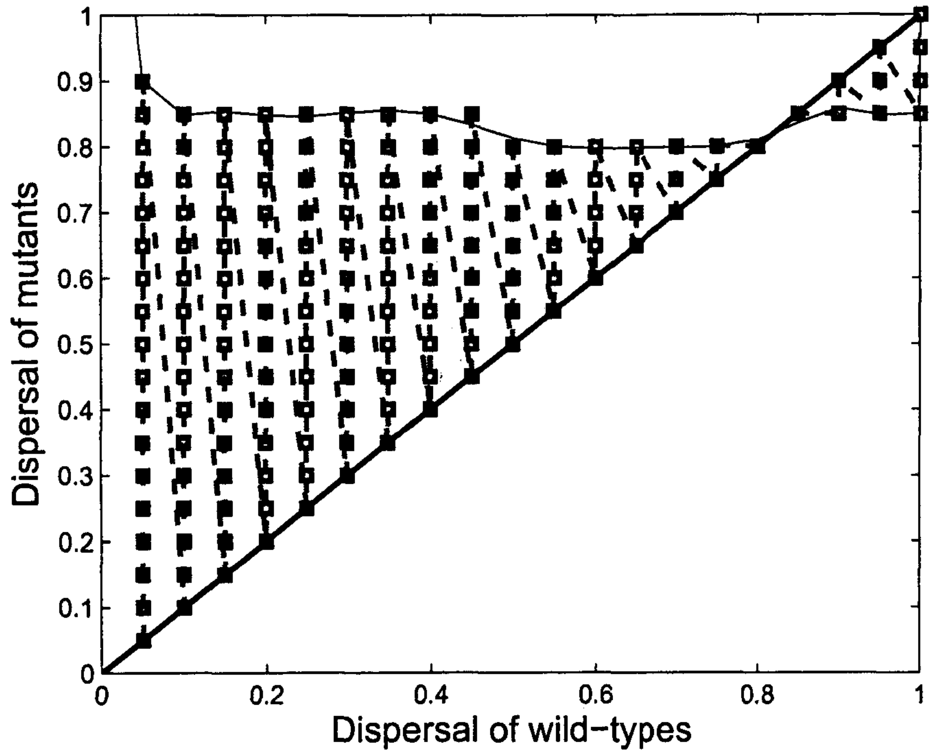

Figure 1.1: The pairwise invasibility plot shows that mutant invasion is successful on the marked regions.

given by Taylor and Frank (1996). Our goal, in chapter two, will be to determine the extent to which dispersal conditioned on individual's migration status, changes our predictions about population-levels of dispersal. In chapter three, we indicate a few possibilities for improving our work in chapter two.

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Chapter 2

The evolution of dispersal conditioned on migration status

2.1 Introduction

Adaptive social behaviour balances the selfish interest of an actor against those of genetically related neighbours (Hamilton, 1964; Frank, 1998). Information about the degree of relatedness between an actor and its neighbours can tip this balance, and sets the stage for the evolution of social behavoiur with conditional expression.

Conditional expression of social behaviour is ubiquitous in nature. Greenbeards, for example, are altruistic or cooperative behaviours that avoid exploitation by cheaters by interacting only with those individuals that exhibit a conspicuous phenotype (a 'green beard') that is linked to the gene(s) responsible for the tendency toward altruism or cooperation (West and Gardner, 2010). Though originally proposed as a hypothetical example by Dawkins (1976), the concept remained a theoretical possibility until 1998, when a green-beard gene was first found in the red imported fire ant, *Solenopsis invicta* (Grafen, 1998; Keller and Ross, 1998). Greenbeard behaviours have also been identified in a number of taxa, ranging from the slime mold, *Dictyostelium discoideum* (Queller et al., 2003) to side-blotched lizards, *Uta stansburiana* (Sinervo et al., 2006).

Conditional expression of social behaviour can have tremendous practical implications. For example, the 'imprinting' of genes expressed in the placenta and brains of mammals is considered to be a kind of allelic social behaviour that is conditioned on its parent-of-origin (Haig, 2000). Conditional expression, here, is maintained because parents are related by differing amounts to the social partners of their offspring. Imprinting, or rather the break-down of imprinting, has been implicated in certain genetic disorders of humans (Angelman's syndrome, Prader-Willi syndrome; Ùbeda, 2008) and may contribute to abnormal psychosocial development (Badcock and Crespi, 2008).

Theoretical work on conditional expression of social behaviour is varied, and the basic conclusions drawn are, in a sense, mixed. In some cases, theoretical investigations carried out under the assumption of conditional expression of behaviour have led to predictions that differ markedly from those obtained by investigations carried out under the assumption of unconditional expression. El Mouden and Gardner (2008) have shown that costly expression of helpful behaviours can be advantageous when expression is conditional on 'migration status' (i.e. on whether one has dispersed or not from one's natal site), a result that is not only quite different from that obtained in the absence of such conditioning (Taylor, 1992; Wilson et al., 1992), but also a result that matches more closely with the observation that altruism and cooperation are widespread in nature (Nowak, 2006).

In contrast to the theoretical work on helping, Wild and West (2009) have shown that imprinting of genes responsible for sex allocation behaviour changes corresponding unconditional predictions about the sex ratio only very slightly (for certain mating systems). In cases like these, giving consideration to conditional expression of social behaviour does not appear to sharpen our understanding of nature at all. It seems reasonable, then, to question the general significance of conditional expression: should we readily expect that conditional expression of social behaviour results in an improved match between theory and observations? We will address this question, in part, here by comparing the prediction of theories based on certain conditional and unconditional expression of natal dispersal behaviour.

Natal dispersal is defined as active or passive movement by which an individual leaves its birth place to engage in mating or reproduction somewhere else (Ronce, 2007; Clobert el al., 2009). Unconditional expression of natal dispersal has been studied extensively (Hamilton and May, 1977; Comins et al., 1980; Motro, 1982, 1983; Frank, 1986; Taylor, 1988; Gandon and Michalakis, 1999; Gandon and Rousset, 1999; Rousset and Billiard, 2000; Rousset and Gandon, 2002). One common theoretical observation is that highly fecund parents can disperse many of their offspring to reduce kin competition.

Although some theoretical work has focused on conditional dispersal (e.g. Crespi and Taylor, 1990; Ronce et al., 1998, 2000; Travis et al., 1999; Kisdi, 2004; Bonte and Pena, 2009), dispersal conditioned upon migration status has been neglected. It, therefore, remains unclear if this kind of conditional dispersal would alter predictions significantly (e.g. as with helping, El Mouden and Gardner, 2008) or relatively insignificantly (e.g. as with sex ratio, Wild and West, 2007).

In this chapter we build on the work of El Mouden and Gardner (2008) and consider the evolution of natal dispersal, expressed conditioned upon an individual's 'migration status'. In particular, we look to compare the evolution of this kind of conditional dispersal with the evolution of its unconditional counterpart. Overall, our goal is to determine the extent to which dispersal conditional upon migration status changes predictions about population-wide levels of dispersal. Simply put, we ask: what weight should the possibility of this kind of conditional dispersal be given by an evolutionary biologist? We calculate the population-average dispersal rate conditioned on its migration status. We find that the stable dispersal rates of natives and non-natives, respectively, are predicted to vary with changing parameter values in a way that is consistent with inclusive-fitness theory. Furthermore, the stable dispersal rates of natives and non-natives are predicted to differ from one another in a way that is consistent with inclusive-fitness theory. We also find a difference between Taylor's (1988) unconditional dispersal rate, and the population-average dispersal rate predicted by our model.

2.2 Inclusive fitness effect of unconditional dispersal

In this section, we will briefly review the inclusive fitness approach to unconditional dispersal in a population undergoing discrete, non-overlapping generations presented by Taylor (1988). Although Taylor (1988) considers sexual diploid and haplodiploid systems, we restrict ourselves to a haploid asexual one. The population, itself, is assumed to consist of a very large number of habitat patches of identical quality, and each patch supports exactly N breeding adults (i.e. N breeding sites per patch).

We now consider an adult breeding on a focal patch. The focal adult achieves fitness gains through two sources: (i) offspring that compete for breeding opportunities on the focal patch, and (ii) offspring that compete for breeding opportunities on a patch chosen uniformly at random from the population as a whole. We consider the dispersal of offspring under parental control, and a wild-type (i.e. non-mutant) breeding adult disperses d^* fraction of its offspring to compete elsewhere. Suppose the focal adult is a mutant that deviates from wild-type behaviour (d^*) by a small amount, call it ϵ. In other words, the focal mutant adult disperses $d = d^* + \epsilon$ fraction of its offspring to compete elsewhere.

Thus, if the behavioural deviation $\epsilon > 0$, the change represents a decrease in competition because the focal adult has dispersed more offspring than that of wild-type adult. If $\epsilon < 0$, the change represents an increase in competition because the focal adult has dispersed fewer offspring than that of wild-type adult. Since every breeding site in the population is assumed to be occupied during every generation, the change in the amount of local competition means that the fitness of offspring competition on the focal patch is improved (if $\epsilon > 0$) or reduced (if $\epsilon < 0$). Thus, the focal adult's inclusive fitness changes as result of its own deviant behaviour by an amount

$$\epsilon k R \tag{2.1}$$

where k is the probability that the change in competition affects an offspring born on the focal patch, and R is the relatedness between the focal adult and the average offspring born on its patch.

Deviant behaviour also affects fitness gains through competition on a patch other than the focal patch. If the dispersal of offspring is costly relative to their non-dispersal, then the deviant behaviour of the focal adult means that its offspring pay the cost of dispersal more (if $\epsilon > 0$) or less (if $\epsilon < 0$) frequently than that of wild-type adult. If c denotes the cost of dispersal, and r denotes the relatedness between the focal adult and its offspring, then

$$-\epsilon c r \tag{2.2}$$

expresses a further change in the inclusive fitness of the focal adult. Summing (2.1) and (2.2) we can express the overall change in the inclusive fitness of focal adult as

$$\epsilon(kR - cr)$$

As noted by Taylor (1988), $k = \frac{1-d^*}{1-cd^*}$ to zeroth order in ϵ. In a haploid asexual population $r = 1$, and a recursive argument gives $R = \frac{1}{N-(N-1)k^2}$ to zeroth order in ϵ. Selection is indifferent to changes in the wild-type level of dispersal when the net inclusive fitness gains of deviant behaviour is zero i.e. when $Rk = cr$. Solving the equation, we see that at evolutionary equilibrium,

$$d^* = \frac{1 + 2Nc - \sqrt{1 + 4N^2c^2 - 4Nc^2}}{2Nc(1+c)} \tag{2.3}$$

The equation (2.3) provides us with a benchmark against which we can compare the effect of conditional dispersal.

2.3 A Model for the evolution of dispersal conditioned on migration status

In this section we set out most of the basic assumptions used in the mathematical model. For the reader's convenience a brief description of all notation introduced in the main text is given in table 2.1 and table 2.2.

2.3.1 Preliminary details

Like Taylor (1988) we consider a population with discrete, non-overlapping generations that consists of a very large number of habitat patches (M) of identical quality where each patch supports exactly N individuals (i.e. N breeding sites per patch). Unlike Taylor (1988), we pay attention to the migration status of each breeder (i.e. whether the breeder is native or non-native on the patch).

A patch is classified according to the number of natives (individuals born on that patch) it supports, and we use $j = 0, 1, \cdots, N$ to indicate the number of natives breeding on that patch. Thus, on a type-j patch, there are j natives, and $(N - j)$ non-natives. The frequency of a type-j patch, denoted by π_j, is expected to fluctuate over time. To indicate that these frequencies have reached a demographic equilibrium (but not necessarily evolutionary equilibrium), we furnish π_j with a hat and write the distribution of patch types as

Table 2.1: Summary of notation used in the main text.

Symbol	Explanation
α_{ij}	The expected native component of the i-fitness of a native mutant breeding on a type-j patch
β_{ij}	The expected native component of the i-fitness of a non-native mutant breeding on a type-j patch
γ_{ij}	The expected non-native component of the i-fitness of a native mutant breeding on a type-j patch
δ_{ij}	The expected non-native component of the i-fitness of a non-native mutant breeding on a type-j patch
c	The cost of dispersal
ϵ	The little phenotypic difference between mutant and wild-type individual
K	Brood size of an individual breeding on a patch
N	The number of breeding individuals per patch (size of patch)
d_N^*	Dispersal probability of native population at equilibrium
d_{NN}^*	Dispersal probability of non-native population at equilibrium
d_N	Dispersal probability of native mutant ($d_N = d_N^* + \epsilon$)
d_{NN}	Dispersal probability of non-native mutant ($d_{NN} = d_{NN}^* + \epsilon$)
$\bar{d}_N$	Dispersal probability of average natives
$\bar{d}_{NN}$	Dispersal probability of average non-natives
p_j	The probability that a site is won by local natives given that the patch supported j- natives during parental generation
P_{ij}	Transition probability from type-j patch to type-i i.e. a patch supports i- natives given that it supported j- natives during parental generation
$\mathbf{n}_j$	The density of mutant individuals breeding on a type-j patch during parental generation
$\mathbf{n}_i'$	The density of mutant individuals breeding on a type-i patch during offspring generation
$\hat{\pi}_j$	The frequency of patches at demographic equilibrium, supporting j- natives

$$\left[\hat{\pi_0}, \hat{\pi_1}, \cdots, \hat{\pi_j}, \cdots, \hat{\pi_N}\right].$$

2.3.2 Phenotypes

Here, the phenotypes of interest relate to the fraction of offspring dispersed, i.e. the probability with which an individual's offspring disperses from its natal site. We consider two different phenotypes, both under parental control: (a) a phenotype that is expressed only by an individual breeding on its natal patch (native dispersal rate), and (b) a phenotype

Table 2.2: Summary of notation used in the main text (Continued).

Symbol	Explanation
R_j	The relatedness between focal individual and average natives breeding on type-j patch
$\tilde{R}_j$	The relatedness between focal individual and average non-natives breeding on type-j patch
$\mathbf{W}_{ij}$	A matrix-valued function that stores α_{ij}, β_{ij}, γ_{ij} and δ_{ij}, respectively
W	$= [\mathbf{W}_{ij}(d_N^*, d_N^*, d_{NN}^*, d_{NN}^*)]_{i,j}$
ΔW	A generalized version of Hamilton's (1964) inclusive fitness effect
$\mathbf{u}_j$	A vector whose elements give the frequency of a mutant breeding on a type-j patch as native and non-native, respectively
$\mathbf{u}$	$= [\mathbf{u}_j]_j$, the right eigenvector of W
$\mathbf{v}_i$	A vector whose elements give the reproductive value of a mutant breeding on a type-i patch as native and non-native, respectively
$\mathbf{v}$	$= [\mathbf{v}_i]_i$, the left eigenvector of W

that is expressed by an individual breeding away from its natal patch (non-native dispersal rate). Every individual possesses genes for both dispersal phenotypes, although only one phenotype is ever expressed (genes for the other phenotype are silent). Our immediate goal is to evaluate the success of a rare mutant form of one or the other conditional phenotypes in a wild-type (i.e. non-mutant) population at demographic equilibrium. Since mutations are assumed to be rare, we neglect the possibility of double mutants.

2.3.3 The Model life cycle

As a first step toward achieving our immediate goal, we must make certain assumptions about population dynamics. We will assume, then, that population dynamics are determined by a series of discrete life-cycle events that occur in the same order in every generation.

Birth

During the first event of the life-cycle, adults produce offspring. We use K to denote the very large number of offspring produced by each adult (natives and non-natives alike).

Dispersal

In the second phase, each adult disperses a certain fraction of its brood. We use d_N^* and d_{NN}^* to denote the fraction of offspring dispersed by wild-type native, and non-native parents, respectively. Thus, on a type-j patch that supports only wild-type individuals we expect to find

$$K\big(j(1-d_N^*)+(N-j)(1-d_{NN}^*)\big) \tag{2.4}$$

native offspring once dispersal is complete. We use $\bar{d}_N$ and $\bar{d}_{NN}$ to denote, respectively, the average native phenotype found on a patch that supports at least one native mutant, and the average non-native phenotype found on a patch that supports at least one non-native mutant. Recall that we neglect the possibility of double mutants on a patch. Thus, on a type-j patch that supports at least one native mutant we expect to find

$$K\big(j(1-\bar{d}_N)+(N-j)(1-d_{NN}^*)\big) \tag{2.5}$$

native offspring once dispersal is complete. Similarly, once dispersal is complete we expect to find

$$K\big(j(1-d_N^*)+(N-j)(1-\bar{d}_{NN})\big) \tag{2.6}$$

native offspring on a type-j patch that supports at least one non-native mutant.

Dispersal is often costly, and so we assume that a fraction (c) of dispersed offspring never find a new patch and perish as a result. The remaining fraction $(1-c)$, however, do find a new patch. If each patch receives an equal share of successful dispersers, then the number of non-native offspring found on any patch once dispersal is complete is given by $K\langle n_m^*\rangle$ where

$$\langle n_m^*\rangle = (1-c)\sum_{j=0}^{N}\hat{\pi}_j(jd_N^*+(N-j)d_{NN}^*). \tag{2.7}$$

Competition

We assume that, by the end of the previous life-cycle phase, all adults have perished, leaving N breeding sites per patch vacant. Competition for vacant breeding sites on a given patch then occurs among the native and non-native offspring found there. If we define

$$p_j(x,y) = \frac{j(1-x)+(N-j)(1-y)}{j(1-x)+(N-j)(1-y)+\langle n_m^*\rangle} \tag{2.8}$$

then $p_j(d_N^*, d_{NN}^*)$ gives the probability that a breeding site on a patch that had supported only wild-type individuals will be won by an offspring that is native to that patch. Thus, $p_j(\bar{d}_N, d_{NN}^*)$ and $p_j(d_N^*, \bar{d}_{NN})$ give, respectively, the probability that a breeding site on a patch that supported at least one native mutant will be won by an offspring that is native to that patch, and the probability that a breeding site on a patch that supported at least one non-native mutant will be won by an offspring that is native to that patch.

If we now define

$$P_{ij}(x,y) = \binom{N}{i} p_j(x,y)^i \left(1-p_j(x,y)\right)^{N-i} \tag{2.9}$$

then the transition probability from a type-j patch that supports only wild-type individuals to a type-i patch that supports only wild-type individuals will be denoted by

$$\begin{aligned} P_{ij}^* = P_{ij}(d_N^*, d_{NN}^*) = \binom{N}{i} \left(\frac{j(1-d_N^*)+(N-j)(1-d_{NN}^*)}{j(1-d_N^*)+(N-j)(1-d_{NN}^*)+\langle n_m^*\rangle}\right)^i \cdot \\ \left(1-\frac{j(1-d_N^*)+(N-j)(1-d_{NN}^*)}{j(1-d_N^*)+(N-j)(1-d_{NN}^*)+\langle n_m^*\rangle}\right)^{N-i}. \end{aligned}$$

Similarly, we use $P_{ij}(\bar{d}_N, d_{NN}^*)$ and $P_{ij}(d_N^*, \bar{d}_{NN})$ to denote, respectively, the transition probability from type-j patch that supports at least one native mutant to type-i patch, and the transition probability from type-j patch that supports at least one non-native mutant to type-i patch.

The transition probabilities indicate the probability that exactly i-natives secure breeding sites in the offspring generation when j-natives were breeding during the parent generation. Therefore, at demographic equilibrium the patch distribution satisfies

$$\hat{\pi}_i = \sum_{j=0}^{N} P^*_{ij}\hat{\pi}_j \qquad i = 0 \cdots N \tag{2.10}$$

$$\sum_{i=0}^{N} \hat{\pi}_i = 1 \tag{2.11}$$

while the mutant is absent. We can approximate the patch distribution with $\hat{\pi}_i$ when the mutant is rare.

2.3.4 Fitness

We define the i-fitness of a native or non-native individual breeding on a type-j patch as the number of offspring breeding on a type-i patch one generation in the future. An individual's i-fitness has both native and non-native components. The native component counts the number of offspring breeding as native on a type-i patch, and the non-native component counts the number of offspring breeding as non-native on a type-i patch. To state the expressions for various components of mutant fitness; first consider a native mutant using d_N to disperse its offspring. We will use

- $\alpha_{ij}(d_N, \bar{d}_N)$ to denote the expected native component of the i-fitness of a native mutant breeding on type-j patch;

- $\gamma_{ij}(d_N)$ to denote the expected non-native component of the i-fitness of a native mutant breeding on type-j patch, and we note that,

$$\alpha_{ij}(d_N,\bar{d}_N) = P_{ij}(\bar{d}_N, d^*_{NN})\frac{i(1-d_N)}{j(1-\bar{d}_N)+(N-j)(1-d^*_{NN})} \tag{2.12}$$

$$\begin{aligned}\gamma_{ij}(d_N) &= d_N(1-c)\sum_{k=0}^{N} P^*_{ik}\frac{\hat{\pi}_k(N-i)}{\langle n^*_m\rangle}\\ &= \frac{d_N(1-c)(N-i)}{(1-c)\sum_{j=0}^{N}\hat{\pi}_j(jd^*_N+(N-j)d^*_{NN})}\sum_{k=0}^{N} P^*_{ik}\hat{\pi}_k\\ &= \frac{d_N(N-i)\hat{\pi}_i}{\sum_{j=0}^{N}\hat{\pi}_j(jd^*_N+(N-j)d^*_{NN})}.\end{aligned} \tag{2.13}$$

Second, consider a non-native mutant using d_{NN} to disperse its offspring. We use

- $\beta_{ij}(d_{NN},\bar{d}_{NN})$ to denote the expected native component of the i-fitness of a non-native mutant breeding on type-j patch;
- $\delta_{ij}(d_{NN})$ to denote the expected non-native component of the i-fitness of a non-native mutant breeding on type-j patch,

where

$$\beta_{ij}(d_{NN},\bar{d}_{NN}) = P_{ij}(d^*_N,\bar{d}_{NN})\frac{i(1-d_{NN})}{j(1-d^*_N)+(N-j)(1-\bar{d}_{NN})} \tag{2.14}$$

$$\begin{aligned}\delta_{ij}(d_{NN}) &= d_{NN}(1-c)\sum_{k=0}^{N} P^*_{ik}\frac{\hat{\pi}_k(N-i)}{\langle n^*_m\rangle}\\ &= \frac{d_{NN}(1-c)(N-i)}{(1-c)\sum_{j=0}^{N}\hat{\pi}_j(jd^*_N+(N-j)d^*_{NN})}\sum_{k=0}^{N} P^*_{ik}\hat{\pi}_k\\ &= \frac{d_{NN}(N-i)\hat{\pi}_i}{\sum_{j=0}^{N}\hat{\pi}_j(jd^*_N+(N-j)d^*_{NN})}.\end{aligned} \tag{2.15}$$

In order to make sense of expressions (2.12)-(2.15), we note that on a type-j patch that supports at least one native mutant, the local competitive effort $K(1-d_N)$ units of a native mutant will compete against the native offsprings given by (2.5) to occupy a breeding site from i-breeding sites with probability of local success $\frac{(1-d_N)}{j(1-d_N)+(N-j)(1-d^*_{NN})}$.

Since $P_{ij}(\bar{d}_N, d^*_{NN})$ is the transition probability from type-j patch supported at least one native mutant to type-i patch, the equation in (2.12) correctly predicts the expected native component of a native mutant. Similarly, the equation in (2.14) correctly predicts the expected native component of a non-native mutant.

In addition, the native mutant will send out $Kd_N(1-c)$ units of non-local competitive effort to occupy a breeding site from $(N - i)$ breeding sites. Since each patch receives $K\langle n^*_m\rangle$ units of non-local pressure, the probability of non-local success of a native mutant is $\frac{d_N}{\sum_{j=0}^{N} \hat{\pi}_j (j d^*_N + (N-j) d^*_{NN})}$. Thus, the equation in (2.13) correctly predicts the expected non-native component of native mutant. Similarly, the equation in (2.15) correctly predicts the expected non-native component of non-native mutant.

We store α_{ij}, β_{ij}, γ_{ij} and δ_{ij} as matrix-valued function,

$$\mathbf{W}_{ij}(d_N, \bar{d}_N, d_{NN}, \bar{d}_{NN}) = \begin{bmatrix} \alpha_{ij}(d_N, \bar{d}_N) & \beta_{ij}(d_{NN}, \bar{d}_{NN}) \\ \gamma_{ij}(d_N) & \delta_{ij}(d_{NN}) \end{bmatrix} \tag{2.16}$$

If $\mathbf{n}_j$ is the column vector whose entries give the expected number of natives and non-natives respectively, breeding on type-j patch, then we have

$$\mathbf{n}'_i = \sum_{j=0}^{N} \mathbf{W}_{ij}(d_N, \bar{d}_N, d_{NN}, \bar{d}_{NN})\mathbf{n}_j$$

that describes the dynamics of the overall subpopulation of mutants while they are rare.

2.3.5 The effect of kin selection

The mutant will increase when the dominant eigenvalue of the matrix-valued function $\mathbf{W}_{ij}(d_N, \bar{d}_N, d_{NN}, \bar{d}_{NN})$ is greater than 1. Under the assumption of weak selection Taylor and Frank (1996) have shown that the size of the dominant eigenvalue of the matrix $[\mathbf{W}_{ij}(d_N, \bar{d}_N, d_{NN}, \bar{d}_{NN})]_{i,j}$ can be assessed in an indirect manner using the dominant left and right eigenvector of the nearby matrix $[\mathbf{W}_{ij}(d_N^*, d_N^*, d_{NN}^*, d_{NN}^*)]_{i,j}$ (call these $\mathbf{v} = [\mathbf{v}_i]_i$ and $\mathbf{u} = [\mathbf{u}_j]_j$, respectively) and marginal fitness expressed using partial derivatives of the elements of the matrix $[\mathbf{W}_{ij}(d_N, \bar{d}_N, d_{NN}, \bar{d}_{NN})]_{i,j}$. We will use their approach below.

The elements of $\mathbf{v}_i$ are interpreted as the reproductive value of mutant breeding as a native and non-native, respectively, on a type-i patch. The reproductive value is a measure of the evolutionary significance that can be attributed to a particular kind of reproductive success (Taylor, 1996; Frank, 1998). The elements of $\mathbf{u}_j$ are interpreted as the frequency of a mutant breeding as a native and non-native, respectively, on type-j patch. It is easy to show that $\mathbf{u}_j = [j\hat{\pi}_j, (N-j)\hat{\pi}_j]^T$. The vectors $\mathbf{v}$ and $\mathbf{u}$ weight various components of marginal fitness. As long as the phenotypic difference between mutant and wild-type individuals is small, the expressions

$$\Delta W^N = \sum_{i=0}^{N}\sum_{j=0}^{N} \mathbf{v}_i \left(\frac{\partial \mathbf{W}_{ij}}{\partial d_N}\Big|_* + \frac{\partial \mathbf{W}_{ij}}{\partial \bar{d}_N}\Big|_* R_j \right) \mathbf{u}_j \tag{2.17}$$

$$\Delta W^{NN} = \sum_{i=0}^{N}\sum_{j=0}^{N} \mathbf{v}_i \left(\frac{\partial \mathbf{W}_{ij}}{\partial d_{NN}}\Big|_* + \frac{\partial \mathbf{W}_{ij}}{\partial \bar{d}_{NN}}\Big|_* \tilde{R}_j \right) \mathbf{u}_j \tag{2.18}$$

correctly predict the fate of mutant allele natives and non-natives, respectively (Taylor and Frank, 1996) where $(.|_*)$ indicates that the derivatives are calculated at demographic equilibrium. The symbol R_j in (2.17) denotes the relatedness between focal individual and average natives (chosen with replacement) breeding on a type-j patch, and $\tilde{R}_j = \frac{1}{N-j} (j \leq N-1)$ in (2.18) denotes the relatedness between focal individual and average non-natives (chosen with replacement) breeding on a type-j patch.

When ΔW^N (resp. ΔW^{NN}) is greater than zero a native (resp. non-native) mutant that disperses slightly more offspring than the native (resp. non-native) wild-type will invade, in other words selection favours an increase in d_N^* (resp. d_{NN}^*). When ΔW^N (resp. ΔW^{NN}) is less than zero a native (resp. non-native) mutant that disperses slightly fewer offspring than native (resp. non-native) wild-type will invade, in other words selection favours a decrease in d_N^* (resp. d_{NN}^*). Conditional dispersal rates are at evolutionary equilibrium if ΔW^N and ΔW^{NN} are simultaneously zero. An evolutionary equilibrium will be considered stable when it is the long-term result of a selective process, and with this loose definition non-equilibrium wild-type dispersal rates (i.e. boundary rates, of zero or one) might also be stable.

2.3.6 Relatedness

It remains to calculate R_i from (2.17), the relatedness between the focal individual and average natives for the population that is at demographic equilibrium. We follow Taylor and Frank (1996) and calculate R_i under the assumption of weak selection.The calculation for R_i for $i \geq 1$ is as follow:

$$R_i = \frac{1}{i} + \frac{i-1}{i} \sum_{j=0}^{N} \frac{P_{ij}^* \hat{\pi}_j}{\hat{\pi}_i} \Bigg(\big(\frac{j(1-d_N^*)}{j(1-d_N^*) + (N-j)(1-d_{NN}^*)} \big)^2 R_j + \big(\frac{(N-j)(1-d_{NN}^*)}{j(1-d_N^*) + (N-j)(1-d_{NN}^*)} \big)^2 \tilde{R}_j \Bigg) \qquad (2.19)$$

2.4 Numerical procedure to find d_N^* and d_{NN}^*

Because our model is not analytically tractable we used it to simulate the evolution of d_N^* and d_{NN}^* numerically. The result of this numerical simulation is what we call a stable phenotype pair. Our numerical simulation started with an initial guess of stable values of d_N^* and d_{NN}^*. We then found the frequency of the patch distribution at equilibrium by solving (2.10), and (2.11) bearing in mind that $\hat{\pi}_j$ is initially unknown for $j = 0 \cdots N$.

The distribution of patch types allowed us to determine the elements of the matrix $[\mathbf{W}_{ij}(d_N^*, d_N^*, d_{NN}^*, d_{NN}^*)]_{i,j}$ for $i = 0 \cdots N$ and $j = 0 \cdots N$; the vectors $\mathbf{v}_i$ and $\mathbf{u}_i$ could then be calculated. The distribution of patch types also allowed us to determine the relatedness between two natives breeding on type-i patch from equation (2.19). With these various quantities in hand, the inclusive fitness increment of natives and non-natives were calculated from equation (2.17), and (2.18), respectively.

The initial guess was, then, improved depending on the sign of inclusive fitness increment of natives and non-natives, and the process repeated until a boundary was reached or until the size of the inclusive fitness effect fell below a predefined threshold. Since negative dispersal probability is biologically meaningless, we fixed the stable level of dispersal rate of non-natives at zero when it went below zero, and repeated the numerical procedure to find the stable level of dispersal rate of natives that satisfied the predefined accuracy. Once we found the stable level of dispersal rates of natives and non-natives, for a set of parameter values N and c, we used $\langle d^* \rangle = \frac{1}{N}\sum_{j=0}^{N}\hat{\pi}_j\left(jd_N^* + (N-j)d_{NN}^*\right)$ to calculate the population-average dispersal rate conditioned on its migration status. The MATLAB script of numerical procedure is presented in Appendix D.

2.5 Simulation experiment

To examine how robust our assumptions were, a finite population was simulated according to the events described in 'Model life cycle'. We fixed the number of patches in the environment, in our simulation at 200. Because simulations were computationally expensive, only a limited number of parameter combinations were investigated: we investigated for $N = 2, 4$ and 6, and $c = 0.1, 0.2, \cdots, 0.9$.

In our simulation we considered two random matrices of size N(patch size) by M(number of patches); one for native and the other for non-native dispersal phenotypes. Rather than simple mutants vs. wild-type dispersal, we considered the dispersal of individuals with greater flexibility. We also considered a binary matrix of size N by M where'one' indicated that the site is occupied by a native with dispersal phenotype corresponding to the native dispersal phenotype matrix, and 'zero' indicated that the site is occupied by non-native with dispersal phenotype corresponding to the non-native dispersal phenotype matrix. The binary matrix was updated, in each generation, according to the model life-cycle. The native and non-native dispersal phenotypes were, then, mutated by a small amount. The procedure of updating the binary matrix and mutating dispersal phenotypes continued generation after generation.

For each parameter combination we ran the simulation 50 times for 5000 generations (5000 generations appeared enough for stable dispersal behaviours to become established). After 50 runs, we calculated the average dispersal rate of natives and non-natives in each generation, and plotted average dispersal rate against time in generations.

We also calculated the 95% confidence interval from the simulated data. Stable levels of dispersal rates of natives and non-natives were, then, calculated over the last 2000 generations again because preliminary results suggested that evolutionary equilibrium were established well before this time. Each generation, the population-average dispersal rate was calculated by counting the expressed and unexpressed genetic contribution of natives and non-natives, and was averaged over the last 2000 generations.

The MATLAB script to simulate native and non-native stable dispersal rate simultaneously, is presented in Appendix E, and native dispersal rate when the dispersal rate of non-natives is at a stable level, is presented in Appendix F.

2.6 Results

2.6.1 Numerical results consistent with inclusive fitness theory

The analysis described above yields stable dispersal rates, conditioned on an individual's migration status. As expected we have observed consistent relationships between these stable dispersal rates (d_N^* and d_{NN}^*) and the parameters c and N, respectively. Specifically, we find that, all else being equal, the stable levels of conditional dispersal decrease with increasing c, and with increasing N (Figure 2.1).

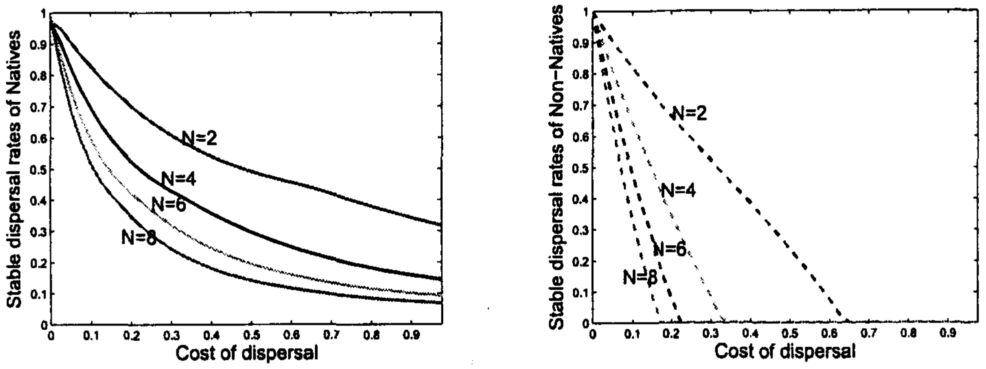

Figure 2.1: The left figure shows the stable dispersal rate of natives for $N = 2, 4, 6$ and 8, respectively and for $c = 0, \cdots, 0.975$. The right figure shows the stable dispersal rate of non-natives for $N = 2, 4, 6$ and 8, respectively and for $c = 0, \cdots, 0.975$. The figures exhibit that the stable dispersal rate of natives and non-natives decreases with increasing c, and with increasing N.

To understand the relationship between dispersal rates and c, recall that the stable level of dispersal represents a balance between the inclusive-fitness costs of the behavior and its inclusive-fitness benefits. The inclusive-fitness costs in this model are due in part to the uncertainty that surrounds a given dispersal event.

As c is increased so too is the risk associated with dispersal. Naturally, increased risk acts as a disincentive for dispersal. The reduced stable level of dispersal we observed, then, is simply a response to an increased inclusive-fitness disincentive.

As we have mentioned in our discussion of Taylor's (1988) work, the inclusive-fitness benefits of dispersal are associated with the decreased level of kin competition that it produces. By definition, increased N implies that the social group is larger, and so increased N effectively dilutes the benefit of dispersal. In other words, the stable level of dispersal decreases with increasing N simply as a response to a smaller inclusive-fitness dispersal incentive.

In addition to the consistent relationships between dispersal rates and model parameters, we have observed a consistent relationship between the dispersal rates themselves.

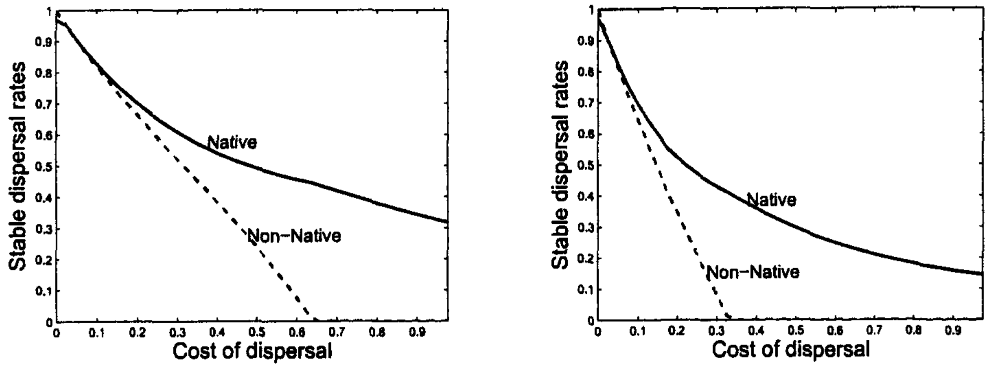

Figure 2.2: The left and right figure show the stable dispersal rate of natives and non-natives for $N = 2$ and $N = 4$, respectively. The figures exhibit that the stable dispersal rate of natives is always greater than that of non-natives.

Specifically, we found that the stable rate of dispersal by natives (d_N^*) is always greater than that by non-natives (d_{NN}^*) (Figure 2.2). Certainly natives have more relatives than non-natives in a given patch. The inclusive-fitness benefits of dispersal, therefore accrue at a higher rate for natives. A higher level of relatedness to patchmates acts as an incentive for dispersal to natives, and the stable level of dispersal we have found, is a response to this incentive.

2.6.2 The match between numerical and simulation results

The stable level of dispersal of natives and non-natives was also investigated with simulation. We have found a qualitative agreement between numerical and simulation results (Figure 2.3 and 2.4), but the level of quantitative agreement was mixed and depended on parameter combinations considered.

With smaller c and N respectively, the simulation tended to agree with the numerical results, in the sense that the 95% confidence interval over the last 2000 generations captures the numerical result (Figure 2.3 and 2.4). However, as either c or N increased, we observed a quantitative disagreement between numerical and simulation results in order of 10^{-2} (Figure 2.5). Specifically, for a set of parameter values, the simulation is either

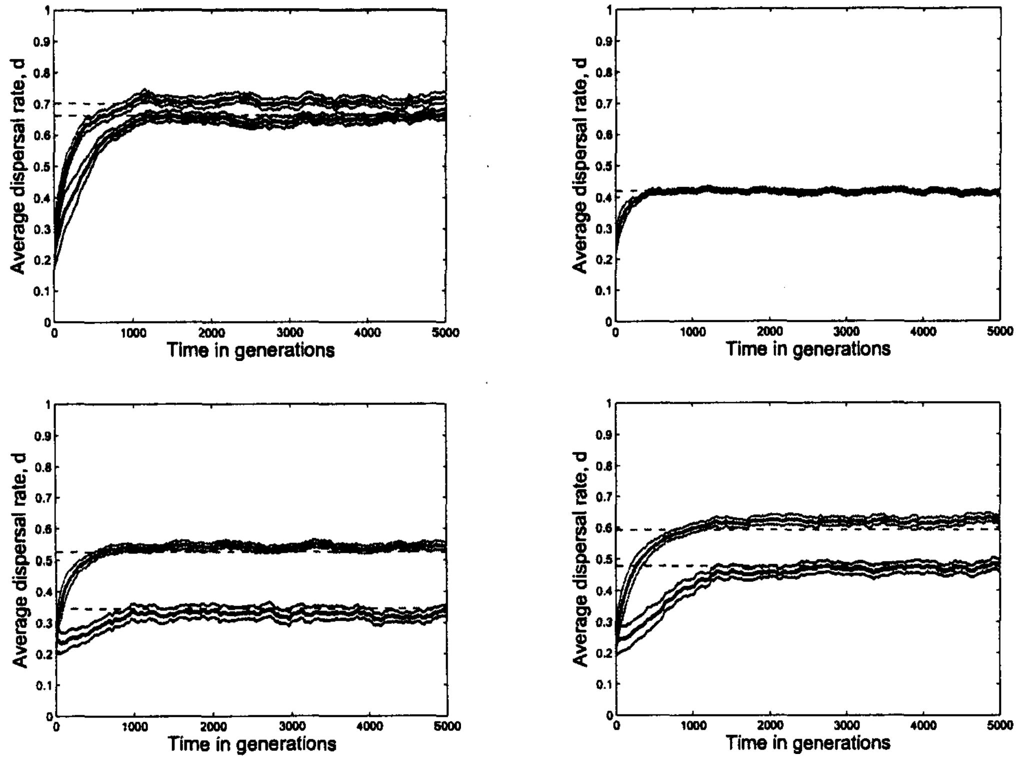

Figure 2.3: The top left, bottom left, and bottom right panel is the simulation of Natives and Non-natives for $N = 2$, $c = 0.2$; $N = 4$, $c = 0.2$, and $N = 6$, $c = 0.1$, respectively; Top right panel is simulation of Natives for $N = 2$, $c = 0.7$. The dotted lines are the numerical estimation of stable dispersal rate of natives and non-natives.

an over or under estimate of numerical results, but we cannot infer the parameter values for which the quantitative agreement begins to break down.

2.6.3 The effect of conditioning on population-average dispersal rate

Recall that we intended to find the population average dispersal rate $\langle d^* \rangle$ to compare with the unconditional result given by Taylor (1988). Because there is a disagreement between numerical and simulation results in general, we have calculated $\langle d^* \rangle$ in two ways. First, the population average dispersal rate $\langle d^* \rangle$ was computed using numerical analysis of the model. Second, $\langle d^* \rangle$ was computed from simulation data.

At the lowest cost of dispersal, Taylor's (1988) unconditional dispersal rate is higher than our model's population-average dispersal rate $\langle d^* \rangle$ computed numerically. At highest cost of dispersal, the $\langle d^* \rangle$ of our model is greater than Taylor's (1988) unconditional dispersal rate (Figure 2.6, 2.7 and 2.8; middle panel).

To understand this coarse-grained pattern, consider the fact that at lowest cost of dispersal, the frequency of non-natives is higher than that of natives (Figures 2.6, 2.7 and 2.8; bottom panel). The lower population-average dispersal we observed, then, is due to the fact that non-natives (who disperse less frequently) contribute more to $\langle d^* \rangle$.

At the highest cost of dispersal, the frequency of natives is more than that of non-natives (Figures 2.6, 2.7 and 2.8; bottom panel). The higher population-average dispersal, in that case, is due to the fact that natives (who disperse more frequently) contribute more to $\langle d^* \rangle$.

On a finer-grained scale, then, as we move from low to high cost of dispersal, the frequency of non-natives decreases (Figures 2.6, 2.7 and 2.8; bottom panels). The concomitant increased frequency of natives means that the higher conditional rate of dispersal (d^*_N) contributes more to $\langle d^* \rangle$; eventually, this pulls up the population-average dispersal rate to a level above Taylor's (1988) unconditional rate. The transition between the cases where the Taylor's (1988) unconditional rate is higher than our result, and the cases where this rate falls below our model's $\langle d^* \rangle$, naturally occurs at intermediate c.

As N is increased, the cost of dispersal where the aforementioned transition takes place, decreases (Figures 2.6, 2.7 and 2.8; middle panel), and for sufficiently large N, those cases where Taylor's (1988) result falls below our result would likely comprise the entire range of c.

The population average-dispersal rate $\langle d^* \rangle$ computed from simulation data, qualitatively supports (Figures 2.6, 2.7 and 2.8) the $\langle d^* \rangle$ computed numerically except for $N = 6$ where it reverses the numerical result. For $N = 6$, we observed, at high cost of dispersal the simulation is an under estimate of numerical results. The contribution of natives, as a result, to $\langle d^* \rangle$ is less than what it should be; therefore, the population average dispersal falls below Taylor's (1988) unconditional rate (Figure 2.8; right figure, middle panel).

Overall, we observed that the absolute difference between our model's $\langle d^* \rangle$ (computed either numerically or from simulation data) and Taylor's result is never greater than 0.1. In fact, using either numerical or simulation approach, the absolute difference between our result and Taylor's (1988) unconditional rate is often on the order of 10^{-2} (Figures 2.6, 2.7 and 2.8; middle panel). The effect of conditional dispersal (should it exist), then, is unlikely to be detected in an experiment; at least it is unlikely that such conditional behavior will confound the match between theory and data.

2.7 Discussion

Our analysis predicts that stable dispersal rates of natives and non-natives will vary with changing parameter values c and N in a way that is consistent with inclusive-fitness theory. Furthermore, the stable dispersal rates of natives and non-natives will be different from one another in a way that is consistent with inclusive-fitness theory.

We observed a qualitative agreement between numerical and simulation results, but the extent of quantitative agreement was dependent on parameter combinations considered. For smaller c, and N respectively, the simulation tended to capture the numerical result at the level of 95% confidence interval.

As either c or N increased, the quantitative disagreement between numerical and simulation results (when it existed) was most often observed on the order of 10^{-2}. We certainly observed a qualitative difference between Taylor's (1988) unconditional dispersal rate, and the population-average dispersal rate predicted by our model. The absolute difference between our result and Taylor's (1988) unconditional rate lies in the interval $[0.01, 0.06]$.

However, it is not uncommon to find a little difference between conditional and unconditional dispersal rates. Kisdi (2004), for example, considered density-dependent dispersal of individuals. If the fecundity is sufficiently small, Kisdi (2004) found a qualitative difference between conditional and unconditional dispersal rates with increasing c. In addition, if the dispersal rate is sex specific, Greenwood (1980) found the absolute difference between the dispersal rates of males and females of Scandinavian Flycatcher differs on the order of 10^{-2}.

One might reasonably ask, is the effect of conditional dispersal likely to confound an experiment? Suppose we are able to overcome the difficulties of determining the patch size N, and cost of dispersal c (e.g. Wolff, 1994), and have the data for c, and N, and Taylor's (1988) unconditional dispersal rate (d^*) at our disposal; the effect of conditional dispersal, then, a rough calculation suggested that a sample of size between $\left[10^2, 10^4\right]$ would be needed, with 95% confidence, to detect a difference between our result and Taylor's (1988) unconditional dispersal rate (sample size, Montgomery et al. 2011, pp 212).

A sample size on order of 10^2 is very common in designing field experiments. Greenwood et al. (1978), for example, worked on inbreeding depression of Great Tits (*Parus major*) based on the data collected from a sample of 885 nest boxes. Harvey et al. (1979) also worked on breeding dispersal of Great Tits (*Parus major*) taking data from 900 nest boxes. In addition, the natal dispersal, return rate, and age of first breeding of Pied Flycatchers (*Ficedula hypoleuca*) was measured by Potti and Montalvo (1990) based on the data from a sample of 240 nest boxes.

However, it is very hard to detect an absolute difference between theory and experimental data if the difference is very small. Density-dependent dispersal of black fly neonates, for example, was studied in slow and fast current speed by Fonseca and Hart, (1996). The absolute difference between the average dispersal rate for the fast and slow current speed treatment was recorded on the order of 10^{-2}. Since current speeds are extremely heterogeneous, and the experiment was carried out in a carefully designed laboratory condition, Fonseca and Hart (1996) mentioned it will be difficult to detect density-dependent dispersal from field studies unless streams and micro-currents are characterized on an appropriate scale.

So the effect of conditional dispersal could be detected in a carefully designed experiment but in field studies conducted in less than ideal conditions, microhabitat variation (like those observed by Fonesca and Hart, 1996) would overcome any difference between dispersal conditioned on migration status. Overall, it is unlikely that the effect of conditional dispersal (should it be detected) will confound the match between theory and data because the small difference could easily be regarded as experimental error.

The study of dispersal-dependent social behaviour in a viscous population by El Mouden and Gardner (2008), predicted that the level of harming by a non-native increases with the increase of population viscosity because they experience zero relatedness, and the level of helping by natives maximizes at intermediate population viscosity because of higher relatedness to social partners.

In contrast, we found that with high costs of dispersal the stable level of dispersal strategy (d^*_{NN}) of non-natives is to sustain all its offspring in the natal patch because of zero relatedness to patchmates, and the stable level of dispersal strategy (d^*_N) of natives is to mainly disperse offspring independent of the cost of dispersal because of the higher level of relatedness to patchmates. El Mouden and Gardner (2008) found substantial differences because inclusive fitness in helping is monotonic. Therefore, even a small change in inclusive fitness it can change the sign of the inclusive fitness increment (ΔW) and lead to a noticeable change in the outcome.

In addition, the evolution of sex differences in helping and harming behaviour by Johnstone and Cant (2008) showed that selection favours helping among the philopartric sex because they are closely related to the offspring they are helping, and harming behaviour should be more frequent among dispersing sex because of zero relatedness. For intermidate immigration rates the evolutionarily stable strategy sex ratio (Taylor and Crespi, 1994) of natives response with an increased female bias sex ratio because of higher relatedness to patchmates, and immigrants response with a male bias sex ratio.

Our analysis is conceptually related to the studies of dispersal-dependent social behaviour in a sense that if the frequency of non-natives is more than that of natives, the population exhibit higher unconditional dispersal rate than our model's population-average dispersal rate, conditioned upon migration status. On the other hand, if the frequency of natives is higher than that of non-natives, our model's population-average dispersal rate is higher than that of Taylor's (1988) unconditional dispersal rate.

2.7.1 Future work

Recall that in our model, we considered finite a number of patches, and each patch supports exactly N individuals. In our future work, we want to incorporate (a) spatially, and temporally heterogeneous environment, i.e. the carrying capacity of each patch varies with time, and (b) the conflict between parent and offspring for the control of dispersal decision. For both cases, we will consider the evolution of natal dispersal conditioned on an individual's migration status, and will pose the question, should the effect of conditional dispersal change predictions about population-wide levels of dispersal?

Our speculation, for the first case, is that the elastic patch size will reduce the level of kin competition, and act as a disincentive for natal dispersal, independent of c. Recall that in our present work, we considered a dispersal phenotype under parental control. In a patch, parents have more information (at least either native or non-native) than offspring, which helps to make the decision as to whether the parent will disperse or sustain its offspring. Therefore, for the second case if the dispersal is controlled by the offspring themselves we suspect the increasing cost of dispersal will act as a disincentive for natal dispersal.

For both cases, therefore, we will observe reduced levels of stable dispersal rates for both natives and non-natives. The frequency of natives, thus, will always be higher than that of non-natives. Consequently, the population average-dispersal $\langle d^* \rangle$ will be higher than Taylor's (1988) unconditional rate because of the fact that natives (who disperse more frequently) contribute more to $\langle d^* \rangle$.

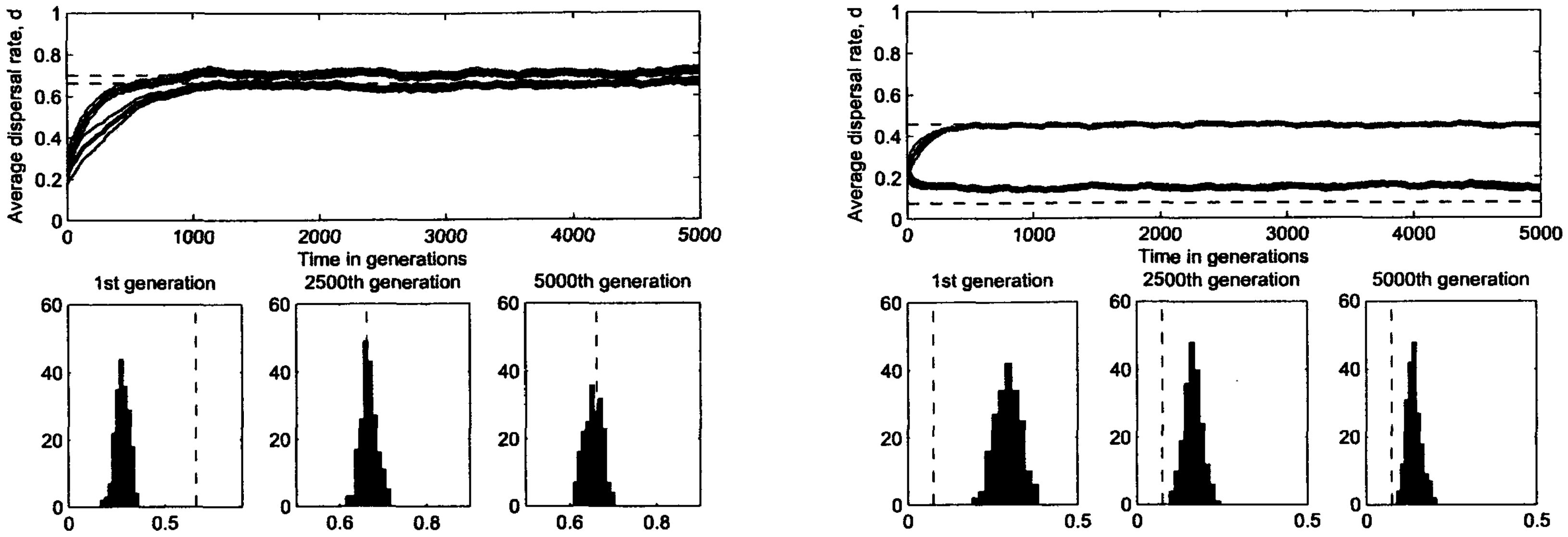

Figure 2.4: The top panel of left figure exhibits a qualitative agreement between numerical and simulation results for both natives and non-natives for the parameter $N = 2$ and $c = 0.2$. The bottom panel of left figure shows that the distribution of non-natives is symmetrical (when there is an agreement between numerical and simulation result) about the numerically predicted stable dispersal rate of non-natives. The top panel of right figure exhibits a disagreement between numerical and simulation results for non-natives for the parameter $N = 2$ and $c = 0.6$. The bottom panel of right figure shows that the distribution of non-natives is right skewed (when there is a disagreement between numerical and simulation result) about the numerically predicted stable dispersal rate of non-natives.

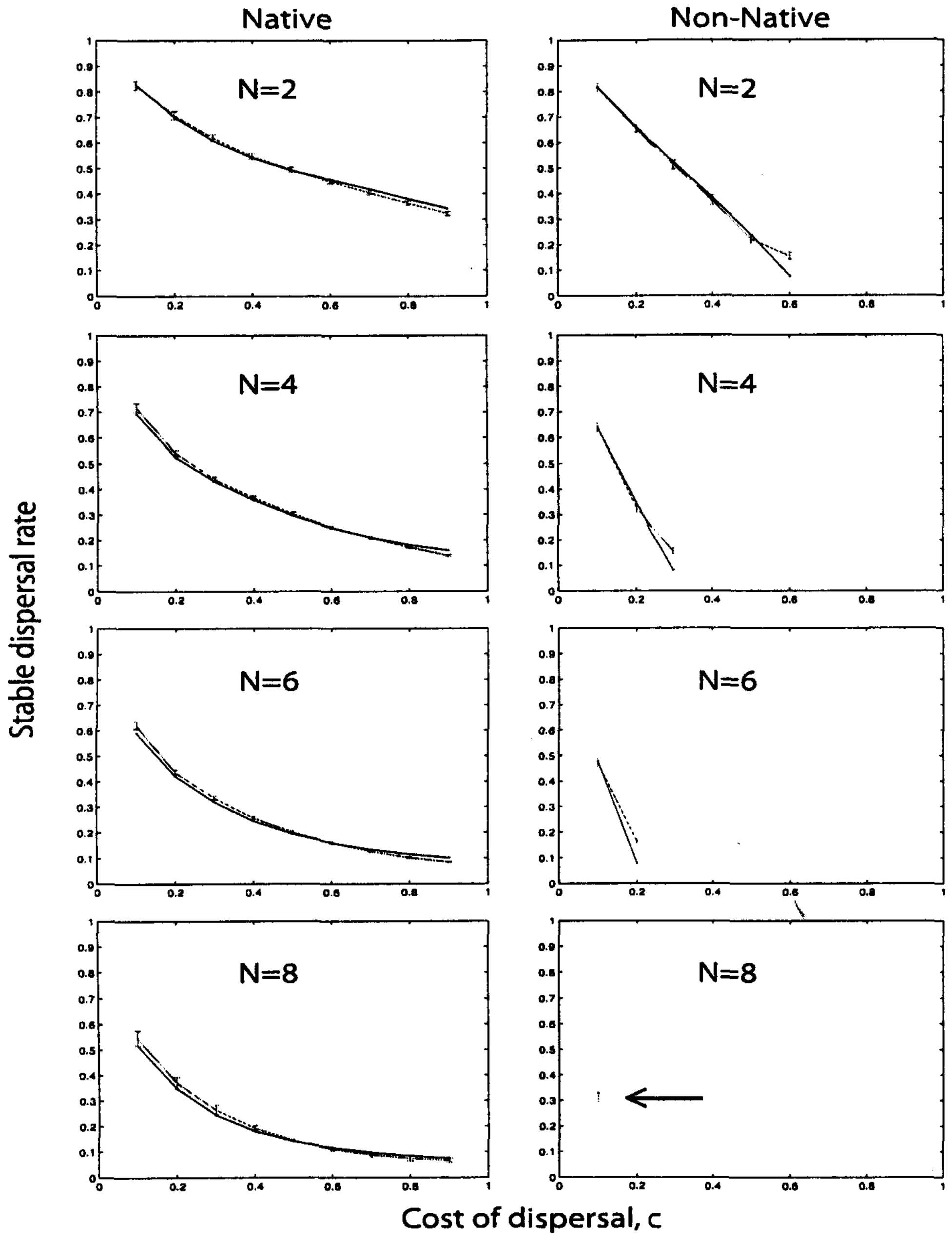

Figure 2.5: The level of agreement and disagreement between numerical and simulation results for natives (left column) and non-natives (right column). The incomplete figures for non-natives are due to fact that the stable dispersal rate either by numerical or simulation of non-natives is zero.

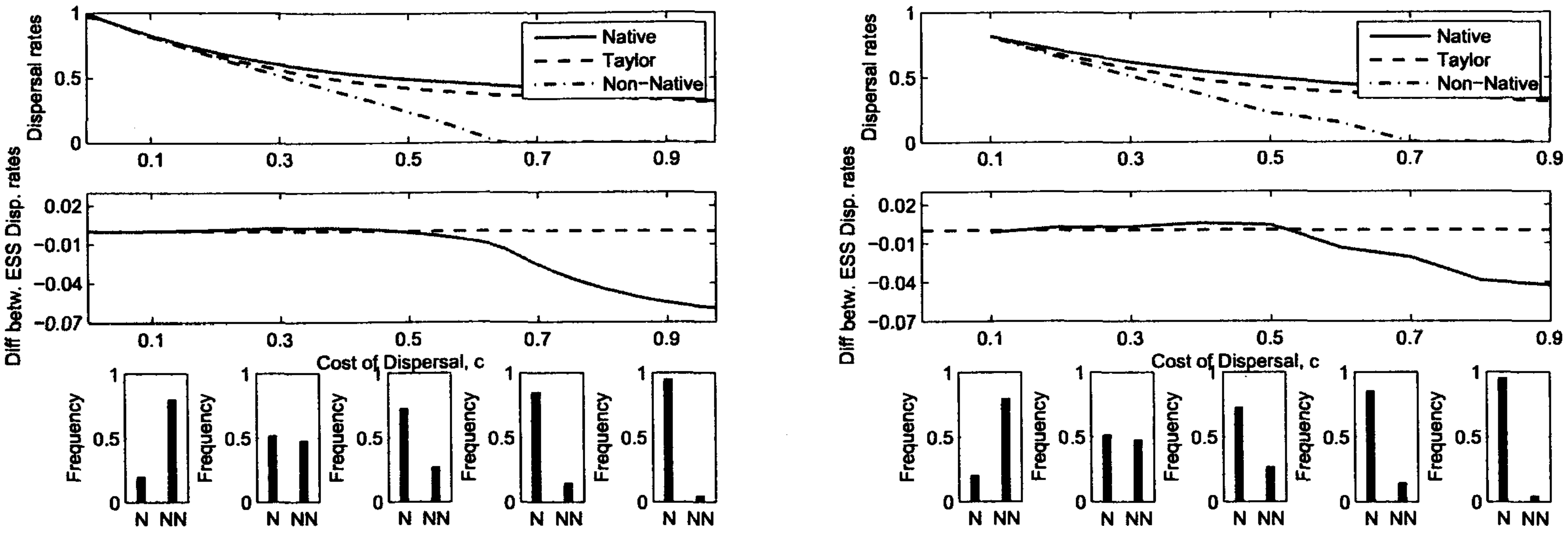

Figure 2.6: Population-average dispersal of individuals for $N = 2$. The left figure is from numerical data, and the right figure is from simulation data. The top panel of both figures shows the stable dispersal rate of natives, Taylor's (1988) unconditional dispersal rate, and stable dispersal rate of non-natives, respectively. The middle panel of both figures shows the difference between our result, and Taylor's (1988) unconditional dispersal rate. The bottom panel of both figures shows the frequency of natives and non-natives for $c = 0.1, 0.3, 0.5, 0.7$ and 0.9, respectively.

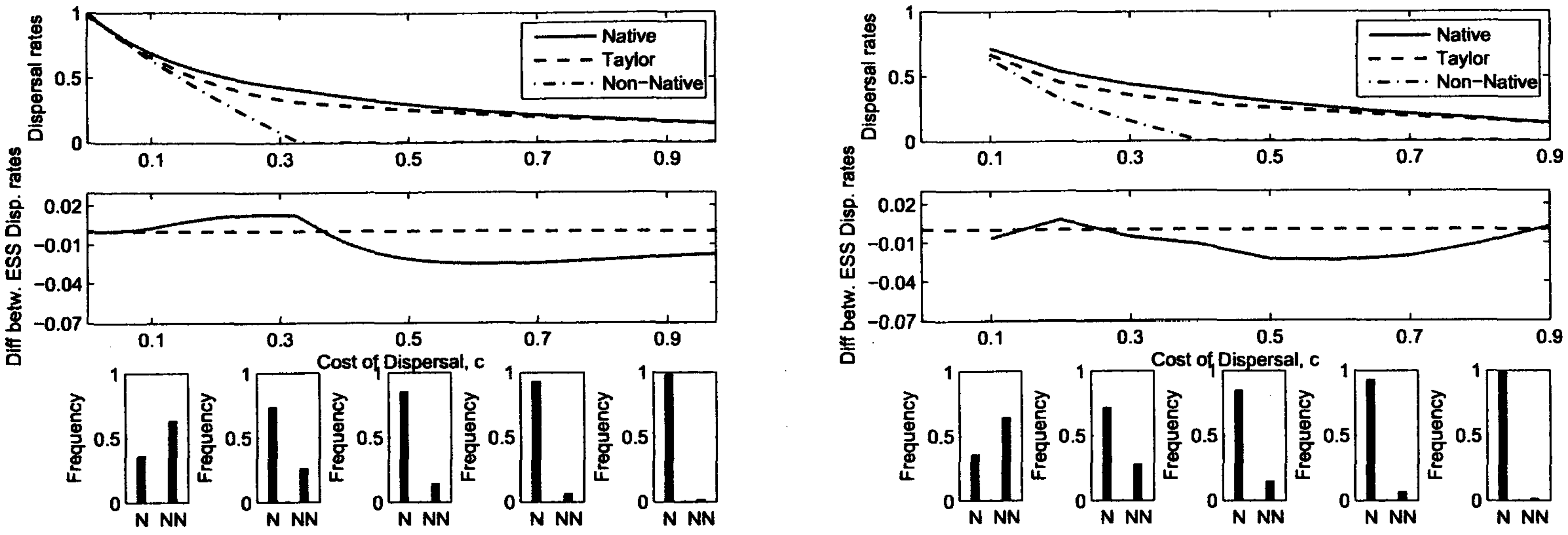

Figure 2.7: Population-average dispersal of individuals for $N = 4$. The left figure is from numerical data, and the right figure is from simulation data. The top panel of both figures shows the stable dispersal rate of natives, Taylor's (1988) unconditional dispersal rate, and stable dispersal rate of non-natives, respectively. The middle panel of both figures shows the difference between our result, and Taylor's (1988) unconditional dispersal rate. The bottom panel of both figures shows the frequency of natives and non-natives for $c = 0.1, 0.3, 0.5, 0.7$ and 0.9, respectively.

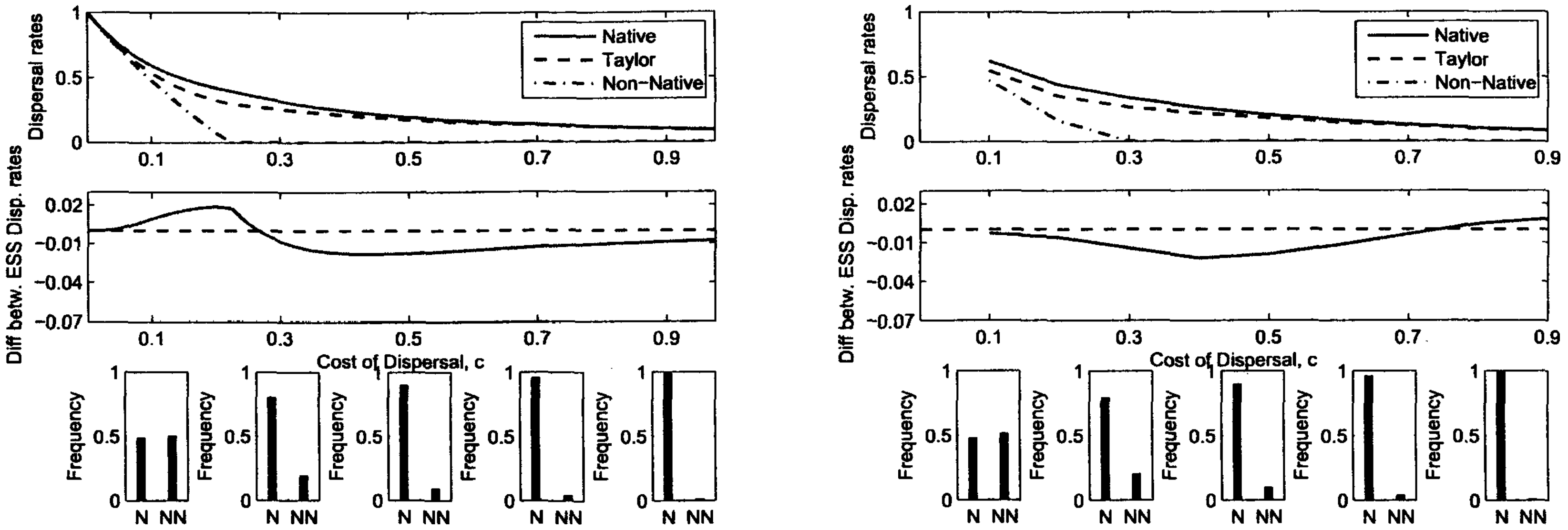

Figure 2.8: Population-average dispersal of individuals for $N = 6$. The left figure is from numerical data, and the right figure is from simulation data. The top panel of both figures shows the stable dispersal rate of natives, Taylor's (1988) unconditional dispersal rate, and stable dispersal rate of non-natives, respectively. The middle panel of both figures shows the difference between our result, and Taylor's (1988) unconditional dispersal rate. The bottom panel of both figures shows the frequency of natives and non-natives for $c = 0.1, 0.3, 0.5, 0.7$ and 0.9, respectively.

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Chapter 3

Summary and Future Work

3.1 Summary of thesis

Natal dispersal (a kind of social behaviour) is defined as active or passive movement by which an individual leaves its birth place to engage in mating or reproduction somewhere else (Greenwood, 1980). Though natal dispersal is often costly as the dispersing individual might not find a better or an emptier patch for mating or reproduction, and if they find one, the competition may be no less than what they would face in their natal patch (Taylor, 1988), natal dispersal is a common phenomenon in both plants and animals. Individuals of most species tend to disperse to colonize a new habitat, and to avoid inbreeding and kin competition.

Conditional expression of social behaviour is very common in nature. Greenbeards, for example, are linked to gene(s) responsible for the tendency toward altruism or co-operation (West and Gardner, 2010), 'imprinting' of gene(s) expressed in the placenta and brains of mammals is considered to be a kind of allelic social behaviour (Haig, 2000). The aim of this thesis was to develop a model to investigate the conditional expression of a particular kind of social behaviour namely dispersal. In particular, we aimed to find the population-average dispersal rate of individuals conditioned on migration status.

Our findings include results that show the stable dispersal rates of natives and non-natives will vary with changing parameter values in a way that is consistent with inclusive-fitness theory. Furthermore, the stable dispersal rates of natives and non-natives will be different from one another in a way that is consistent with inclusive-fitness theory. We calculate the population-average dispersal rate conditioned on migration status, and find a qualitative difference between Taylor's (1988) unconditional dispersal rate, and the population-average dispersal rate predicted by our model.

To obtain these results, we present two important tools- inclusive fitness theory, and branching processes in chapter one, and show how to use these tools in population models. We extend the population model introduced in chapter one to incorporate the conditional behaviour of the individual. We suppose the populations are at demographic equilibrium, and there are two kinds of individuals: natives and non-natives; dispersing their offspring at the demographic equilibrium rate. In that situation if mutation (though very rare) happens, we would observe a behavioural deviation to disperse offspring elsewhere. We want to evaluate the success of a rare mutant form over the wild-type dispersal phenotype. Therefore, in chapter two we build a simple probabilistic model to count the expected number of native and non-native mutants in an offspring generation. Since in the parental generation, individuals are of two kinds: natives and non-natives, we have four probabilistic equations to analyze the model. The analysis was carried out based on the methodology (inclusive fitness theory) introduced by Taylor and Frank (1996).

Since we observed an absolute difference between the population-average dispersal rate conditioned on migration status and Taylor's (1988) unconditional dispersal rate, we provided a rough calculation of the sample size to detect the effect of conditional dispersal in an experiment. We concluded that the effect of conditional dispersal could be detected in a carefully designed experiment but that in fields studies conducted in less than ideal conditions, microhabitat variation would overcome any difference between dispersal conditioned on migration status. Overall, it is unlikely that the effect of conditional dispersal (should it be detected) will confound the match between theory and data because the small difference could easily be regarded as experimental error.

3.2 Future work

3.2.1 Parasite virulence conditioned on migration status

Parasites include viruses, bacteria, protozoans, helminth and arthropod parasites. Parasite virulence is defined as the increased mortality or reduction in fertility of host due to infection. Several mathematical models have been developed to explore theoretical aspects of the evolution of virulence (May and Anderson, 1979; Levin and Pimentel, 1981; Frank 1992). Essentially, parasites compete and evolve in two different levels: within a host and between hosts. Coinfection and superinfection are, respectively, examples of within host and between host competition. Levin and Pimentel (1981) analyzed two-strain models with superinfection where the more virulent strain can take over a host infected by a less virulent strain, and found the condition for coexistence between the two strains. Stewart and Levin (1984) and Nowak (1991) worked with vertical transmission of parasites, and showed vertically transmitted parasites should be less virulent. Nowak and May (1994) generalized the two-strain model of Levin and Pimentel (1981) to an n-strain model with superinfection. May and Nowak (1995) considered the coinfection of different parasites in the same host. We want to build a model to investigate the virulence of parasites conditioned on migration status that has not been studied yet i.e. the virulence of a parasite depends on whether it is a native or non-native in the host. Our prediction is that, in a host, the infectivity (transmission rate) of native parasites will be less than that of non-natives. Overall, we want to find the population-average level of virulence for the parasite population.

3.2.2 Informed dispersal together with conditional migration

We could improve our present model by incorporating the ability of individuals to acquire and process social information. Individuals may acquire information about their environment through different cues (Danchin et al., 2004; Doligez et al., 2004). Nocturnal snakes, for example, choose thermally suitable habitats through the physical structure and temperature of rocks (Webb et al., 2004). In addition, social information is often considered to be cost free, and can provide effective means of deciding when to disperse (Dall et al., 2005). Common lizards, for example, are able to distinguish between natives and non-natives and can acquire information about the density of surrounding populations through some unknown traits of immigrant lizards (Cote et al., 2008). This social information derived from the presence of immigrants helps common lizards in their decision to disperse (Cote and Clobert, 2007). Therefore, if we take into account the concept of informed dispersal with dispersal condition on migration status, it may give us a better understanding of dispersal patterns of different species.

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Appendix A

Calculation of elements of the matrices in (2.17) and (2.18)

In this section, we will present the calculation of the elements of matrices $\frac{\partial \mathbf{W}_{ij}}{\partial d_N}\big|_*$ and $\frac{\partial \mathbf{W}_{ij}}{\partial \bar{d}_N}\big|_*$ in (2.17), and $\frac{\partial \mathbf{W}_{ij}}{\partial d_{NN}}\big|_*$ and $\frac{\partial \mathbf{W}_{ij}}{\partial \bar{d}_{NN}}\big|_*$ in (2.18). The matrices are as follows:

$$\frac{\partial \mathbf{W}_{ij}}{\partial d_N}\Big|_* = \begin{bmatrix} \frac{\partial \alpha_{ij}}{\partial d_N}\big|_* & 0 \\ \frac{\partial \gamma_{ij}}{\partial d_N}\big|_* & 0 \end{bmatrix} \tag{A.1}$$

$$\frac{\partial \mathbf{W}_{ij}}{\partial \bar{d}_N}\Big|_* = \begin{bmatrix} \frac{\partial \alpha_{ij}}{\partial d_N}\big|_* & 0 \\ \frac{\partial \gamma_{ij}}{\partial \bar{d}_N}\big|_* & 0 \end{bmatrix} \tag{A.2}$$

$$\frac{\partial \mathbf{W}_{ij}}{\partial d_{NN}}\Big|_* = \begin{bmatrix} 0 & \frac{\partial \beta_{ij}}{\partial d_{NN}}\big|_* \\ 0 & \frac{\partial \delta_{ij}}{\partial d_{NN}}\big|_* \end{bmatrix} \tag{A.3}$$

$$\frac{\partial \mathbf{W}_{ij}}{\partial \bar{d}_{NN}}|_* = \begin{bmatrix} 0 & \frac{\partial \beta_{ij}}{\partial d_{NN}}|_* \\ 0 & \frac{\partial \delta_{ij}}{\partial d_{NN}}|_* \end{bmatrix} \tag{A.4}$$

Using (A.1) and (A.2), the inclusive fitness increment (ΔW^N) of native mutant in (2.17) can be written as

$$\Delta W^N = \sum_{i=0}^{N}\sum_{j=0}^{N} \mathbf{v}_i \begin{bmatrix} \frac{\partial \alpha_{ij}}{\partial d_N}|_* + \frac{\partial \alpha_{ij}}{\partial \bar{d}_N}|_* R_j & 0 \\ \frac{\partial \gamma_{ij}}{\partial d_N}|_* + \frac{\partial \gamma_{ij}}{\partial \bar{d}_N}|_* R_j & 0 \end{bmatrix} \mathbf{u}_j \tag{A.5}$$

and the inclusive fitness increment (ΔW^{NN}) of non-native mutant in (2.18) can be written as

$$\Delta W^{NN} = \sum_{i=0}^{N}\sum_{j=0}^{N} \mathbf{v}_i \begin{bmatrix} 0 & \frac{\partial \beta_{ij}}{\partial d_{NN}}|_* + \frac{\partial \beta_{ij}}{\partial \bar{d}_{NN}}|_* \tilde{R}_j \\ 0 & \frac{\partial \delta_{ij}}{\partial d_{NN}}|_* + \frac{\partial \delta_{ij}}{\partial \bar{d}_{NN}}|_* \tilde{R}_j \end{bmatrix} \mathbf{u}_j \tag{A.6}$$

We will use the following derivative formula

$$\begin{aligned} &\frac{d}{dx}\left(\binom{n}{k}p(x)^k(1-p(x))^{n-k}\right) \\ &= \binom{n}{k}(p'(x)kp(x)^{k-1}(1-p(x))^{n-k} - p'(x)(n-k)p(x)^k(1-p(x))^{n-k-1} \\ &= \binom{n}{k}p(x)^k(1-p(x))^{n-k}p'(x)(\frac{k}{p(x)} - \frac{n-k}{1-p(x)}) \end{aligned} \tag{A.7}$$

to calculate $\frac{\partial p_j}{\partial \bar{d}_N}\big|_*$ and $\frac{\partial p_j}{\partial \bar{d}_{NN}}\big|_*$.

$$\begin{aligned}
\frac{\partial p_j}{\partial \bar{d}_N}\Big|_* &= \frac{-j\big(j(1-d_N^*)+(N-j)(1-d_{NN}^*)+\langle n_m^*\rangle\big)}{\big(j(1-d_N^*)+(N-j)(1-d_{NN}^*)+\langle n_m^*\rangle\big)^2}+\\
&\quad \frac{j\big(j(1-d_N^*)+(N-j)(1-d_{NN}^*)\big)}{\big(j(1-d_N^*)+(N-j)(1-d_{NN}^*)+\langle n_m^*\rangle\big)^2}\\
&= \frac{-j\langle n_m^*\rangle}{\big(j(1-d_N^*)+(N-j)(1-d_{NN}^*)+\langle n_m^*\rangle\big)^2}\\
&= \frac{-j}{\big(j(1-d_N^*)+(N-j)(1-d_{NN}^*)+\langle n_m^*\rangle\big)}(1-p_j^*)\\
&= \frac{-j}{j(1-d_N^*)+(N-j)(1-d_{NN}^*)}p_j^*(1-p_j^*) \qquad \text{(A.8)}
\end{aligned}$$

$$\begin{aligned}
&\frac{\partial p_j}{\partial \bar{d}_{NN}}\Big|_*\\
&= \frac{-(N-j)\big(j(1-d_N^*)+(N-j)(1-d_{NN}^*)+\langle n_m^*\rangle\big)}{\big(j(1-d_N^*)+(N-j)(1-d_{NN}^*)+\langle n_m^*\rangle\big)^2}+\\
&\quad \frac{(N-j)\big(j(1-d_N^*)+(N-j)(1-d_{NN}^*)\big)}{\big(j(1-d_N^*)+(N-j)(1-d_{NN}^*)+\langle n_m^*\rangle\big)^2}\\
&= \frac{-(N-j)\langle n_m^*\rangle}{\big(j(1-d_N^*)+(N-j)(1-d_{NN}^*)+\langle n_m^*\rangle\big)^2}\\
&= \frac{-(N-j)}{\big(j(1-d_N^*)+(N-j)(1-d_{NN}^*)+\langle n_m^*\rangle\big)}(1-p_j^*)\\
&= \frac{-(N-j)}{j(1-d_N^*)+(N-j)(1-d_{NN}^*)}p_j^*(1-p_j^*) \qquad \text{(A.9)}
\end{aligned}$$

At equilibrium, using the equations (A.7), (A.8) and (A.9), the derivative of transition probabilities: $P_{ij}(\bar{d}_N, d_{NN}^*)$ with respect to $\bar{d}_N$ and $P_{ij}(d_N^*, \bar{d}_{NN})$ with respect to $\bar{d}_{NN}$ is obatined as follows:

$$\begin{aligned}
\frac{\partial P_{ij}}{\partial \bar{d}_N}\Big|_* &= P_{ij}^*\frac{-j}{j(1-d_N^*)+(N-j)(1-d_{NN}^*)}p_j^*(1-p_j^*)\left(\frac{i}{p_j^*}-\frac{(N-i)}{1-p_j^*}\right)\\
\frac{\partial P_{ij}}{\partial \bar{d}_{NN}}\Big|_* &= P_{ij}^*\frac{-(N-j)}{j(1-d_N^*)+(N-j)(1-d_{NN}^*)}p_j^*(1-p_j^*)\left(\frac{i}{p_j^*}-\frac{(N-i)}{1-p_j^*}\right)
\end{aligned}$$

Using the above equations whenever necessary, we get the elements of the matrix in (A.5) as follows:

$$
\begin{aligned}
\frac{\partial \alpha_{ij}}{\partial d_N}\Big|_* &= -P^*_{ij}\frac{i}{j(1-d^*_N)+(N-j)(1-d^*_{NN})} \\
\frac{\partial \alpha_{ij}}{\partial \bar{d}_N}\Big|_* &= P^*_{ij}\frac{ij(1-d^*_N)}{\left(j(1-d^*_N)+(N-j)(1-d^*_{NN})\right)^2} \\
&\quad + \frac{i(1-d^*_N)}{j(1-d^*_N)+(N-j)(1-d^*_{NN}}P^*_{ij}. \\
&\quad \frac{-j}{j(1-d^*_N)+(N-j)(1-d^*_{NN}}p^*_j(1-p^*_j)\left(\frac{i}{p^*_j}-\frac{N-i}{1-p^*_j}\right) \\
&= P^*_{ij}\frac{ij(1-d^*_N)}{\left(j(1-d^*_N)+(N-j)(1-d^*_{NN})\right)^2}\left(1-p^*_j(1-p^*_j)\left(\frac{i}{p^*_j}-\frac{N-i}{1-p^*_j}\right)\right) \\
\frac{\partial \gamma_{ij}}{\partial d_N}\Big|_* &= (1-c)\frac{\hat{\pi}_i(N-i)}{\langle n^*_m\rangle} \\
\frac{\partial \gamma_{ij}}{\partial \bar{d}_N}\Big|_* &= 0
\end{aligned}
$$

and the elements of the matrix in (A.6) as follows:

$$
\begin{aligned}
\frac{\partial \beta_{ij}}{\partial d_{NN}}\Big|_* &= -P^*_{ij}\frac{i}{j(1-d^*_N)+(N-j)(1-d^*_{NN})} \\
\frac{\partial \beta_{ij}}{\partial \bar{d}_{NN}}\Big|_* &= P^*_{ij}\frac{i(N-j)(1-d^*_{NN})}{\left(j(1-d^*_N)+(N-j)(1-d^*_{NN})\right)^2} \\
&\quad + \frac{i(1-d^*_{NN})}{j(1-d^*_N)+(N-j)(1-d^*_{NN}}P^*_{ij}. \\
&\quad \frac{-(N-j)}{j(1-d^*_N)+(N-j)(1-d^*_{NN}}p^*_j(1-p^*_j)\left(\frac{i}{p^*_j}-\frac{N-i}{1-p^*_j}\right) \\
&= P^*_{ij}\frac{i(N-j)(1-d^*_{NN})}{\left(j(1-d^*_N)+(N-j)(1-d^*_{NN})\right)^2}\left(1-p^*_j(1-p^*_j)\left(\frac{i}{p^*_j}-\frac{N-i}{1-p^*_j}\right)\right) \\
\frac{\partial \delta_{ij}}{\partial d_{NN}}\Big|_* &= (1-c)\frac{\hat{\pi}_i(N-i)}{\langle n^*_m\rangle} \\
\frac{\partial \delta_{ij}}{\partial \bar{d}_{NN}}\Big|_* &= 0
\end{aligned}
$$

Thus, the inclusive fitness increment of native mutant in (2.17), and non-native mutant in (2.18) is obtained as follows:

$$\begin{aligned}
\Delta W^N &= \sum_{i=0}^{N}\sum_{j=1}^{N}\left[-v_i^N P_{ij}^* \frac{i}{j(1-d_N^*)+(N-j)(1-d_{NN}^*)}\right] j\hat{\pi}_j \\
&+\sum_{i=0}^{N}\sum_{j=1}^{N}\left[v_i^N P_{ij}^* \frac{ij(1-d_N^*)}{\left[j(1-d_N^*)+(N-j)(1-d_{NN}^*)\right]^2}\cdot \right. \\
&\left.\left(1-p_j^*(1-p_j^*)\left(\frac{i}{p_j^*}-\frac{N-i}{1-p_j^*}\right)\right)R_j\right] j\hat{\pi}_j \\
&+\sum_{i=0}^{N}\sum_{j=1}^{N}\left[v_i^{NN}(1-c)\frac{\hat{\pi}_i(N-i)}{\langle n_m^*\rangle}\right] j\hat{\pi}_j
\end{aligned} \tag{A.10}$$

$$\begin{aligned}
\Delta W^{NN} &= \sum_{i=0}^{N}\sum_{j=0}^{N-1}\left[-v_i^N P_{ij}^* \frac{i}{j(1-d_N^*)+(N-j)(1-d_{NN}^*)}\right] (N-j)\hat{\pi}_j \\
&+\sum_{i=0}^{N}\sum_{j=0}^{N-1}\left[v_i^N P_{ij}^* \frac{i(N-j)(1-d_{NN}^*)}{\left[j(1-d_N^*)+(N-j)(1-d_{NN}^*)\right]^2}\cdot \right. \\
&\left.\left(1-p_j^*(1-p_j^*)\left(\frac{i}{p_j^*}-\frac{N-i}{1-p_j^*}\right)\right)\tilde{R}_j\right] (N-j)\hat{\pi}_j \\
&+\sum_{i=0}^{N}\sum_{j=0}^{N-1}\left[v_i^{NN}(1-c)\frac{\hat{\pi}_i(N-i)}{\langle n_m^*\rangle}\right] (N-j)\hat{\pi}_j
\end{aligned} \tag{A.11}$$

Appendix B

Taylor's result as a special case of the model

In this section, we will show that if the dispersal phenotype of individuals, does not conditioned on its migration status, our model gives Taylor's (1988) unconditional result. Since the individual do not conditioned on its migration status, the dispersal rate of natives and non-native at equilibrium is same i.e. $d_N^* = d_{NN}^* = d^* = d$. Then, at the end of dispersal stage each patch will receive the migration pressure

$$\begin{aligned}\langle n_m^* \rangle &= (1-c)\sum_{j=0}^{N} \hat{\pi}_j \big(jd + (N-j)d\big) \\ &= (1-c)Nd\sum_{j=0}^{N} \hat{\pi}_j \\ &= (1-c)Nd\end{aligned}$$

and the probability to win a breeding site in type-j patch is

$$\begin{aligned} p_j^* &= \frac{(1-d)N}{N(1-d)+(1-c)Nd} \\ &= \frac{1-d}{1-cd} \\ &= k \end{aligned}$$

which is, actually, the probability that a breeding female is native on the patch (Taylor, 1988). The transition probability, thus, from type-j patch to type-i patch is a binomial distribution with mean Nk

$$P_{ij}^* = \binom{N}{i} k^i (1-k)^{N-i} \tag{B.1}$$

Using (2.11) and (B.1), it is easy to show that

$$\begin{aligned} \hat{\pi}_i &= \sum_{j=0}^{N} \hat{\pi}_j P_{ij}^* \\ &= P_{ij}^* \end{aligned} \tag{B.2}$$

and using (B.2), and the mean of binomial distribution, we have

$$\sum_{i=0}^{N} i\hat{\pi}_i = \sum_{i=0}^{N} iP_{ij}^* = Nk \tag{B.3}$$

With proper scaling, the individual's reproductive success can be taken as $\mathrm{v} = [1, 1]$ for all i. Thus, the inclusive fitness increment of native mutant and non-native mutant from

(A.10) and (A.11), respectively, can be written as

$$\begin{aligned}
\Delta W^N &= \sum_i \sum_j \left[\left(P^*_{ij} \frac{-i}{N(1-d)} + P^*_{ij} \frac{ij}{N^2(1-d)} (Nk - i + 1) \right) R_j \right. \\
&\quad \left. + \frac{\hat{\pi}_i (N-i)}{Nd} \right] j \hat{\pi}_j \\
\Delta W^{NN} &= \sum_i \sum_j \left[\left(P^*_{ij} \frac{-i}{N(1-d)} + P^*_{ij} \frac{i(N-j)}{N^2(1-d)} (Nk - i + 1) \right) \tilde{R}_j \right. \\
&\quad \left. + \frac{\hat{\pi}_i (N-i)}{Nd} \right] (N-j) \hat{\pi}_j
\end{aligned}$$

Splitting the summation and using $k = \frac{1-d}{1-cd}$, and (B.3) we get

$$\begin{aligned}
\sum_i \sum_j P^*_{ij} j \hat{\pi}_j \frac{-i}{N(1-d)} &= \frac{-1}{N(1-d)} \sum_i i P^*_{ij} \cdot \sum_j j \hat{\pi}_j \\
&= \frac{-Nk}{N(1-d)} \sum_j j \hat{\pi}_j \\
&= \frac{-1}{1-cd} \sum_j j \hat{\pi}_j
\end{aligned}$$

$$\begin{aligned}
&\sum_i \sum_j P^*_{ij} . j \hat{\pi}_j \frac{ij}{N^2(1-d)} (Nk - i + 1) R_j \\
&\qquad = \sum_j j^2 \hat{\pi}_j R_j \frac{Nk+1}{N^2(1-d)} . \sum_i i P^*_{ij} - \sum_j j^2 \hat{\pi}_j R_j \frac{1}{N^2(1-d)} \sum_i i^2 P^*_{ij} \\
&\qquad = \sum_j j^2 \hat{\pi}_j R_j \frac{Nk+1}{N^2(1-d)} . Nk + \sum_j j^2 \hat{\pi}_j R_j \frac{1}{N^2(1-d)} . Nk(Nk - k + 1) \\
&\qquad = \sum_j j \hat{\pi}_j R_j \frac{1}{N^2(1-d)} Nk^2 \\
&\qquad = \frac{1}{1-cd} \sum_j j \hat{\pi}_j \left(j \frac{R_j}{N} \right) k
\end{aligned}$$

Using the above equations whenever necessary, the inclusive fitness increment (ΔW^N) of native mutant

$$\begin{aligned}
\Delta W^N &= \frac{-1}{1-cd}\sum_j j\hat{\pi}_j + \sum_j j\hat{\pi}_j\left(\frac{1}{Nd}\sum_i \hat{\pi}_i(N-i)\right) + \frac{1}{1-cd}\sum_j j\hat{\pi}_j(j\frac{R_j}{N})k \\
&= \left(\frac{-1}{1-cd} + \frac{N}{Nd} - \frac{1}{Nd}\sum_i i\hat{\pi}_i\right).\sum_j j\hat{\pi}_j + \frac{1}{1-cd}\sum_j j\hat{\pi}_j(j\frac{R_j}{N})k \\
&= \left(\frac{-1}{1-cd} + \frac{1}{d} - \frac{Nk}{Nd}\right)\sum_j j\hat{\pi}_j + \frac{1}{1-cd}\sum_j j\hat{\pi}_j(j\frac{R_j}{N})k \\
&= \frac{-c}{1-cd}\sum_j j\hat{\pi}_j + \frac{1}{1-cd}\sum_j j\hat{\pi}_j(j\frac{R_j}{N})k \\
&= \frac{N}{1-cd}\sum_j \left(\hat{\pi}_j\frac{j}{N}(-c+k\frac{j}{N}R_j)\right)
\end{aligned}$$

With similar calculations, the inclusive fitness increment (ΔW^{NN}) of non-native mutant

$$\Delta W^{NN} = \frac{N}{1-cd}\sum_j \left(\hat{\pi}_j\frac{N-j}{N}(-c+k\frac{N-j}{N}\tilde{R}_j)\right)$$

Let R denote the relatedness between mother, and average offspring born on the same patch. Then, the mathematical expression of R is as follow

$$R = \sum_j \hat{\pi}_j\left(\frac{j}{N}.\frac{j}{N}.R_j + 2.\frac{j}{N}.\frac{N-j}{N}.0 + \frac{N-j}{N}.\frac{N-j}{N}.\tilde{R}_j\right) \tag{B.4}$$

Now, adding the inclusive fitness of native and non-native mutant, we have

$$\Delta W = \frac{-cN}{1-cd} + \frac{Nk}{1-cd}.\sum_j \left(\hat{\pi}_j(\frac{j}{N})^2R_j + (\frac{N-j}{N})^2\tilde{R}_j\right)$$

and using (B.4), the inclusive fitness increment

$$\Delta W = \frac{N}{1-cd}(-c+kR) \tag{B.5}$$

The ESS condition is obtained by solving $\Delta W = 0$ which is exactly same as Taylor's (1988) result.

Appendix C

Stable dispersal rates

Here we will present the data of stable dispersal rates of natives and non-natives calculated by the procedure described in section 2.4. We also present Taylor's (1988) unconditional dispersal rate calculated by using the formula described in section 2.2, equation (2.3). Finally, the population-average dispersal rate of individuals (when dispersal is conditioned on its migration status), calculated by the formula described in section 2.4, is presented in the following tables.

Table C.1: Stable dispersal rates

Patch Size	Dispersal Rates	Cost of dispersal								
		c=0.1	c=0.2	c=0.3	c=0.4	c=0.5	c=0.6	c=0.7	c=0.8	c=0.9
N=2	d_N^*	0.8273	0.7009	0.6087	0.5414	0.4923	0.4563	0.4200	0.3804	0.3435
	d_{NN}^*	0.8178	0.6624	0.5212	0.3833	0.2386	0.0750	0	0	0
	Taylor	0.8199	0.6782	0.5696	0.4866	0.4226	0.3725	0.3323	0.2997	0.2727
	Model	0.8197	0.6768	0.5668	0.4842	0.4235	0.3799	0.3587	0.3439	0.3275
N=3	d_N^*	0.7555	0.6006	0.5029	0.4391	0.3847	0.3327	0.2885	0.2518	0.2216
	d_{NN}^*	0.7280	0.4980	0.2882	0.0817	0	0	0	0	0
	Taylor	0.7370	0.5556	0.4369	0.3571	0.3009	0.2596	0.2280	0.2032	0.1831
	Model	0.7358	0.5498	0.4286	0.3507	0.3127	0.2864	0.2608	0.2370	0.2156
N=4	d_N^*	0.6929	0.5250	0.4303	0.3588	0.2973	0.2490	0.2117	0.1828	0.1601
	d_{NN}^*	0.6409	0.3454	0.0807	0	0	0	0	0	0
	Taylor	0.6630	0.4642	0.3505	0.2799	0.2324	0.1985	0.1731	0.1535	0.1378
	Model	0.6598	0.4532	0.3377	0.2882	0.2539	0.2233	0.1972	0.1753	0.1571
N=5	d_N^*	0.6386	0.4671	0.3714	0.2942	0.2372	0.1958	0.1654	0.1424	0.1247
	d_{NN}^*	0.5572	0.2062	0	0	0	0	0	0	0
	Taylor	0.5985	0.3961	0.2914	0.2295	0.1890	0.1605	0.1395	0.1233	0.1104
	Model	0.5924	0.3808	0.2888	0.2459	0.2094	0.1800	0.1566	0.1380	0.1230

Table C.2: Stable dispersal rates (Continued)

Patch Size	Dispersal Rates	Cost of dispersal								
		c=0.1	c=0.2	c=0.3	c=0.4	c=0.5	c=0.6	c=0.7	c=0.8	c=0.9
N=6	d^*_N	0.5918	0.4218	0.3199	0.2459	0.1954	0.1603	0.1351	0.1164	0.1020
	d^*_{NN}	0.4774	0.0786	0	0	0	0	0	0	0
	Taylor	0.5430	0.3443	0.2489	0.1943	0.1591	0.1347	0.1167	0.1030	0.0921
	Model	0.5337	0.3257	0.2573	0.2117	0.1765	0.1497	0.1293	0.1135	0.1009
N=7	d^*_N	0.5512	0.3837	0.2781	0.2096	0.1652	0.1352	0.1140	0.0983	0.0863
	d^*_{NN}	0.4015	0	0	0	0	0	0	0	0
	Taylor	0.4954	0.3040	0.2170	0.1683	0.1374	0.1160	0.1004	0.0884	0.0790
	Model	0.4828	0.2891	0.2299	0.1846	0.1517	0.1277	0.1099	0.0962	0.0855
N=8	d^*_N	0.5160	0.3475	0.2443	0.1819	0.1428	0.1168	0.0985	0.0850	0.0747
	d^*_{NN}	0.3296	0	0	0	0	0	0	0	0
	Taylor	0.4545	0.2719	0.1923	0.1485	0.1208	0.1019	0.0880	0.0775	0.0692
	Model	0.4389	0.2684	0.2066	0.1628	0.1326	0.1112	0.0955	0.0835	0.0741
N=9	d^*_N	0.4853	0.3158	0.2169	0.1601	0.1255	0.1027	0.0867	0.0749	0.0659
	d^*_{NN}	0.2613	0	0	0	0	0	0	0	0
	Taylor	0.4193	0.2457	0.1726	0.1328	0.1079	0.0908	0.0784	0.0689	0.0615
	Model	0.4010	0.2493	0.1868	0.1453	0.1176	0.0984	0.0843	0.0737	0.0654
N=10	d^*_N	0.4584	0.2880	0.1943	0.1428	0.1118	0.0915	0.0774	0.0669	0.0589
	d^*_{NN}	0.1967	0	0	0	0	0	0	0	0
	Taylor	0.3887	0.2241	0.1565	0.1201	0.0974	0.0819	0.0706	0.0621	0.0554
	Model	0.3682	0.2319	0.1700	0.1310	0.1056	0.0881	0.0755	0.0660	0.0585

Appendix D

Numerical procedure to find stable dispersal rates of Natives and Non-natives

```
N=2;
c=0.5;
digits(10);
K=@(D)  (1-D)/(1-c*D);
R=@(D)  1/(N-(N-1)*(K(D))^2);
IF=@(D)  -c + K(D)*R(D);
Taylor=fzero(IF, 0.5);
Sigma=[0.01, 0; 0, 0.01];
dn=0.4;
dnn=0.3;
tol=1;
while tol > 10^(-7)
    [DeltaN, DeltaNN]=NumericalTest(N,dn,dnn,c);
        % Need to exert control over the size of the IF effects
```

```
    ON=ceil(log10(abs(DeltaN)));
    ONN=ceil(log10(abs(DeltaNN)));
    if ON > 0 || ONN > 0
        MaxO=max(ON,ONN);
        DeltaN=DeltaN*10^(-(MaxO+1));
        DeltaNN=DeltaNN*10^(-(MaxO+1));
    end
    next=[dn; dnn]+Sigma*[DeltaN;DeltaNN];
    tol=norm([dn-next(1), dnn-next(2)]);
   dn=next(1);
   dnn=next(2);
end
[Pi,P,NLC]=PI(N,dn,dnn,c);
indx=0:N;
s=dn*indx+(N-indx)*dnn;
% Outputs are dstar, dn, dnn and Taylor
dstar=(s*Pi)/N
dn
dnn
Taylor
```

```
function [DeltaN,DeltaNN]=NumericalTest(N,dn,dnn,c)
% Calling functions that we need
R=Relatedness(N,dn,dnn,c);
[Vn,Vnn]=RvSuccess(N,dn,dnn,c);
[Pi,P,NLC]=PI(N,dn,dnn,c);
a1=0;a2=0;b1=0;b2=0;c1=0;c2=0; % initialization
for i=0:N
for j=0:N
   % Fitness increment for native
```

```
    t1=j*(1-dn)+(N-j)*(1-dnn);
    t2=Vn(i+1)*P(i+1,j+1);
    t3=j*Pi(j+1);
  a1=a1-t2*(i/t1)*t3;
  pj=t1/(t1+(1-c)*NLC);
  b1=b1+(t2*t3*i*j*(1-dn)/t1^2)*
 (1-pj*(1-pj)*(i/pj-(N-i)/(1-pj)))*R(j+1);
  c1=c1+Vnn(i+1)*Pi(i+1)*(N-i)*t3/NLC;
  % Fitness increment for non native
  t4=(N-j)*Pi(j+1);
  a2=a2-t2*(i/t1)*t4;
  b2=b2+(t2*i*(N-j)*(1-dnn)/t1^2)*
 (1-pj*(1-pj)*(i/pj-(N-i)/(1-pj)))*Pi(j+1);
  c2=c2+Vnn(i+1)*Pi(i+1)*(N-i)*t4/NLC;
  end
end
DeltaN=a1+b1+c1;
DeltaNN=a2+b2+c2;
%%%%%%%%%%END OF A FUNCTION%%%%%%%
function [Pi,P,NLC]=PI(N,dn,dnn,c)
% This function will find patch frequency at equilibrium
indx=0:N;
nlc=indx*dn+(N-indx)*dnn;     % Competitive effort from j patch
Q0=ones(N+1,1);
Q0=Q0./sum(Q0);
ct=0;
err=1;
PP=zeros(N+1);
while err>10^(-9)
    for k=0:N
      lc=(1-dn)*indx+(1-dnn)*(N-indx);
      pj=lc./(lc+(1-c)*nlc*Q0);
```

```
      PP(k+1,:)=nchoosek(N,k).*((pj).^k).*(1-pj).^(N-k);
    end
 Q=PP*Q0;
 err=norm(Q-Q0);
 Q0=Q;
end
Pi=Q;                      % Returning euqilibrium patch freq;
P=PP;                      % Returning transition prob matrix;
NLC=nlc*Q;
%%%%%%%%% END OF A FUNCTION%%%%%%%
function R=Relatedness(N,dn,dnn,c)
indx=0:N;
nat=indx*(1-dn);
nonnat=(N-indx)*(1-dnn);
lc=nat+nonnat;
natsuc=(nat./lc).^2;
nonnatsuc=(nonnat./lc).^2;
% calling transition prob matrix P, patch frequency Pi
[Pi,P,NLC]=PI(N,dn,dnn,c);
M1=zeros(N);
M2=M1;
 for j=1:N
     M1(j,:)=P(j+1,2:end).*(Pi(2:end)/Pi(j+1))'.*natsuc(2:end);
 end
for j=0:N-1
    M2(j+1,:)=P(j+2,1:end-1).*(Pi(1:end-1)/Pi(j+2))'
.*nonnatsuc(1:end-1);
end
Rjbar=1./(N-indx(1:end-1));
s2=M2*Rjbar';    % is the product of Rj bar with non local part
R=0.1*ones(1,N);
i=1:N;err=1;
```

```
oneByI=1./i;
Sc=(i-1)./i;
while err>10^(-6)
    Rj=Sc.*(M1*R'+s2)'+oneByI;
    err=norm(R-Rj);
    R=Rj;
end
R=[0,R];
%%%%%%%%% END OF FUNCTION%%%%%%
function [Vn,Vnn]=RvSuccess(N,dn,dnn,c)
j=0:N;
[Pi,P,NLC]=PI(N,dn,dnn,c);
A=zeros(N+1);B=A;C=A;D=A;  % N by N matrix to store alphaij, ...
    betaij, gamaij, ∆ij
lc=(1-dn)*j+(1-dnn)*(N-j);     % Local pressure on j patch
nat_nat=(1-dn)./lc;
nonnat_nat=(1-dnn)./lc;
nat_nonnat=dn/NLC;
nonnat_nonnat=dnn/NLC;
for k=0:N
    A(:,k+1)=nat_nat(k+1)*j.*P(:,k+1)';
    B(:,k+1)=nonnat_nat(k+1)*j.*P(:,k+1)';
    C(:,k+1)=nat_nonnat*((N-j).*Pi');
    D(:,k+1)=nonnat_nonnat*((N-j).*Pi');
end
W=zeros(2*(N+1));
W(1:N+1,1:N+1)=A;
W(1:N+1,N+2:2*(N+1))=B;
W(N+2:2*(N+1),1:N+1)=C;
W(N+2:2*(N+1),N+2:2*(N+1))=D;
[vec,val]=eig(W');
vec=vec(:,3)/vec(N+2,3);
```

```
Vn=vec(1:N+1);
Vnn=vec(N+2:end);
%%%%%%%%% END OF FUNCTION%%%%%
```

Appendix E

Simulation of stable dispersal rates of Natives and Non-natives

```
% Simulation to find ESS level of native and non-native ...
    dispersal rate %
%-------Parameters---------
Nruns=50;
T=5001;          % Total number of generations to simulate
P=200;           % Number of Patches
mutationScale=0.01;
N=2;             % Number of individuals per patch
c=0.3;            %cost of dispersal
n=1;             % native code
nn=2;            % non-native code
%-------Simulations--------
datan=zeros(Nruns,T);  % Array of arrays to store evolutionary ...
    histories of dn
datann=zeros(Nruns,T); % Array of arrays to store evolutionary ...
    histories of dnn
```

```
dstar=zeros(Nruns,T);
for Run=1:Nruns         % Initialize the run
   d=rand()*rand(N,P,2);   % Initial population dispersal rates
   dnew=zeros(N,P,2);      % Placeholder for next-gen dispersal ...
       rates
   X=random('binomial', 1, 0.5, N, P); % Initial dispersal status
   Xnew=zeros(N,P);        % Next-gen dispersal status
for t=1:T
    dAvg=mean(d);       % stores patch-average dispersal rates
    dAvgAvg=mean(dAvg); % stores global average dispersal rate
    datan(Run,t)=dAvgAvg(:,:,n);    % record native data
    datann(Run,t)=dAvgAvg(:,:,nn);  % record non-native data
    dX=d(:,:,n).*X + d(:,:,nn).*(1-X);
    dAvgX=mean(dX);     % stores patch-average expressed ...
       dispersal rates
    dAvgAvgX=mean(dAvgX); % stores dispersal rate
    dstar(Run,t)=dAvgAvgX; % population-average dispersal

    if isnan(dAvgAvgX)==1
        break
    end
    k=(1-dAvgX)./((1-dAvgX) + (1-c)*dAvgAvgX);
        for j=1:P
        for i=1:N
            x=rand();
            if x<k(j)
                 % Winner is local
            Xnew(i,j)=1;
            p=(1-dX(:,j))/sum(1-dX(:,j)); % a column prob vector
            winner=MyMnrnd(1,p');
            winnerN=d(winner,j,n);        % winner is native
            winnerNN=d(winner,j,nn);      % winner is non-native
```

```
        else
            % Winner is not local
        Xnew(i,j)=0;
        p=dAvgX/sum(dAvgX,2);           % a row prob vector
        momPatch=MyMnrnd(1,p);
        q=dX(:,momPatch)/sum(dX(:,momPatch)); % a column ...
            prob vector
        winner=MyMnrnd(1,q');
        winnerN=d(winner,momPatch, n); % winner is native
        winnerNN=d(winner,momPatch, nn);  % winner is non-native
        end
        %----------mutate offspring-------------
        winnerN=winnerN+mutationScale*randn();
        if winnerN > 1
            winnerN=1;
        elseif winnerN < 0
            winnerN=0.00001;
        else
            winnerN;
        end
        winnerNN=winnerNN+mutationScale*randn();
        if winnerNN > 1
            winnerNN=1;
        elseif winnerNN < 0
            winnerNN=0.00001;
        else
            winnerNN;
        end
        dnew(i,j,n)=winnerN;
        dnew(i,j,nn)=winnerNN;
    end
end
```

```
    d=dnew; % update
    X=Xnew;
end
end
%-------------- Summary Statistics--------------
dSTAR=mean(dstar);     % mean  dispersal over all runs
AvgDatan=mean(datan);
TwoSEsn=2*std(datan)/sqrt(Nruns); % standard error of native data
NaboveCI=AvgDatan + TwoSEsn;       % upper limit of CI
NbelowCI=AvgDatan - TwoSEsn;       % lower limit of CI

AvgDatann=mean(datann);  % mean dispersal rate of non-natives ...
    over all runs
TwoSEsnn=2*std(datann)/sqrt(Nruns);  % standard error of ...
    non-native data
NNaboveCI=AvgDatann + TwoSEsnn;      % upper limit of CI
NNbelowCI=AvgDatann - TwoSEsnn;      % lower limit of CI
figure
hold on;
plot([0,T-1], [0.6087 ,0.6087], '--r', 'LineWidth', 1)
plot([0,T-1], [0.5212, 0.5212], '--k', 'LineWidth', 1)
plot(0:(T-1), AvgDatan, '-r', 'LineWidth', 2)
plot(0:(T-1), NaboveCI, '-r', 'LineWidth', 1)
plot(0:(T-1), NbelowCI, '-r', 'LineWidth', 1)
plot(0:(T-1), AvgDatann, '-k', 'LineWidth', 2)
plot(0:(T-1), NNaboveCI, '-k', 'LineWidth', 1)
plot(0:(T-1), NNbelowCI, '-k', 'LineWidth', 1)
axis([0,T-1, 0,1])
xlabel('Time in generations', 'FontName', 'Arial', 'FontSize', 16)
ylabel('Average dispersal rate, d', 'FontName', 'Arial', ...
    'FontSize', 16)
box on
```

```
hold off
```

```
function Y = MyMnrnd( nTrials,p )
% A simple version of the builtin mnrnd command
%   This function will generate a multinomial(nTrials,p) random ...
    variable
     N=numel(p);
    CumP=NaN(1,N);
      for i=1:N
        CumP(i) = sum(p(1:i));
    end
    CumP(N) = 1;
    X=rand(1,nTrials);
    Y=NaN(1,nTrials);
    for t=1:nTrials
        for i=1:N
            if X(1,t) ≤ CumP(i)
                Y(1,t)=i;
                break
            end
        end
    end
end
```

Appendix F

Simulation of stable dispersal rate of Natives

```
% Simulation to find ESS level of native dispersal rate %
%-------Parameters---------
Nruns=50;
T=5001;          % Total number of generations to simulate
P=200;           % Number of Patches
mutationScale=0.01;
N=2;             % Number of individuals per patch
c=0.8;           %cost of dispersal
n=1;             % native code
nn=2;            % non-native code
%-------Simulations--------
datan=zeros(Nruns,T);  % Array of arrays to store evolutionary ...
    histories of dn
dstar=zeros(Nruns,T);
for Run=1:Nruns          % Initialize the run
     d=rand()*rand(N,P,2);    % Initial population dispersal rates
```

```
     dnew=zeros(N,P,2);      % Placeholder for next-gen ...
        dispersal rates
     X=random('binomial', 1, 0.5, N, P); % Initial dispersal status
     Xnew=zeros(N,P);        % Next-gen dispersal status
     d(:,:,nn)=0.00001;
for t=1:T
    dAvg=mean(d);       % stores patch-average dispersal rates
    dAvgAvg=mean(dAvg); % stores global average dispersal rate
    datan(Run,t)=dAvgAvg(:,:,n); % record native data
    dX=d(:,:,n).*X + d(:,:,nn).*(1-X);
    dAvgX=mean(dX);
    dAvgAvgX=mean(dAvgX);  % stores dispersal rate
    dstar(Run,t)=dAvgAvgX;  % population-average dispersal

    if isnan(dAvgAvgX)==1
        break
    end
    k=(1-dAvgX)./((1-dAvgX) + (1-c)*dAvgAvgX);
    for j=1:P
        for i=1:N
            x=rand();
            if x<k(j)
                % Winner is local
             Xnew(i,j)=1;
             p=(1-dX(:,j))/sum(1-dX(:,j)); % a column prob vector
             winner=MyMnrnd(1,p');
             winnerN=d(winner,j,n);         % winner is native
             winnerNN=d(winner,j,nn);       % winner is non-native
            else
                % Winner is not local
             Xnew(i,j)=0;
             p=dAvgX/sum(dAvgX,2);          % a row prob vector
```

```
             momPatch=MyMnrnd(1,p);
             q=dX(:,momPatch)/sum(dX(:,momPatch));% a column ...
                 prob vector
             winner=MyMnrnd(1,q');
             winnerN=d(winner,momPatch, n); % winner is native
             winnerNN=d(winner,momPatch, nn);  % winner is ...
                 non-native
            end
            %-----------mutate offspring--------------
            winnerN=winnerN+mutationScale*randn();
            if winnerN > 1
                winnerN=1;
            elseif winnerN < 0
                winnerN=0.00001;
            else
                winnerN;
            end
            dnew(i,j,n)=winnerN;
            dnew(i,j,nn)=winnerNN;
        end
    end
    d=dnew; % update
    X=Xnew;
end
end
%-------------- Summary Statistics--------------
dSTAR=mean(dstar);     % mean population-average dispersal over ...
    all runs
AvgDatan=mean(datan);  % mean dispersal rate of natives over all ...
    runs
TwoSEsn=2*std(datan)/sqrt(Nruns); % standard error of native data
NaboveCI=AvgDatan + TwoSEsn;        % upper limit of CI
```

```
NbelowCI=AvgDatan - TwoSEsn;       % lower limit of CI
figure
hold on;
plot([0,T-1], [0.3804 ,0.3804], '--r', 'LineWidth', 1)
plot(0:(T-1), AvgDatan, '-r', 'LineWidth', 2)
plot(0:(T-1), NaboveCI, '-r', 'LineWidth', 1)
plot(0:(T-1), NbelowCI, '-r', 'LineWidth', 1)
axis([0,T-1, 0,1])
xlabel('Time in generations', 'FontName', 'Arial', 'FontSize', 16)
ylabel('Average dispersal rate, d', 'FontName', 'Arial', ...
    'FontSize', 16)
box on
hold off
```

```
function Y = MyMnrnd( nTrials,p )
% A simple version of the builtin mnrnd command
%   This function will generate a multinomial(nTrials,p) random ...
    variable
     N=numel(p);
    CumP=NaN(1,N);
      for i=1:N
        CumP(i) = sum(p(1:i));
    end
    CumP(N) = 1;
    X=rand(1,nTrials);
    Y=NaN(1,nTrials);
    for t=1:nTrials
        for i=1:N
            if X(1,t) ≤ CumP(i)
                Y(1,t)=i;
```

```
                break
            end
        end
    end
end
```

Appendix G

Numerical procedure to find ESS using branching process

```
n=20;
Δ=1/n;
N=2;c=0.1;
data=[];poly=zeros(n,n);
    for i=0:n
        da=i*Δ;
        crt=bpnew(N,da,da,c);
            for j=0:n
                dA=j*Δ;
                ext=bpnew(N,dA,da,c);
                  if ext≤crt
                    data=[data;da,dA];
                    poly(j,i)=dA;
                end
            end
    end % execution completes here
```

```
 %finding the values for interpolation
 inter=zeros(n,2);ct=n;
 for i=1:n
     x=poly(:,i);
     m=min(x(x≠0));mm=max(x);
     if mm==m
       ct=i;
     end
         inter(i,1)=i*Δ;
     if i>ct
         inter(i,2)=m;
     else
         inter(i,2)=mm;
     end
 end  % values for interpolation found out
 % generating x & y for second isoclines
 pcoeff=polyfit(inter(:,1),inter(:,2),10);
 xp=0:Δ:1;
 yp=polyval(pcoeff,xp);
 %finding ESS d
  x0=0;err=1;
 while err>10^(-3)
     x=polyval(pcoeff,x0);
     err=abs(x0-x);
     x0=x;
 end
 x % ESS done
%generating figure
  figure;
  hold on
  plot(data(:,1),data(:,2),'--rs','LineWidth',2,...
       'MarkerEdgeColor','k','MarkerSize',5);
```

```
    plot([0,1],[0,1],'-k','LineWidth',2);
    xlabel('Dispersal of wild-types','FontName', 'Arial', ...
        'FontSize', 14);
    ylabel('Dispersal of mutants','FontName', 'Arial', ...
        'FontSize', 14);
    plot(xp,yp);
    axis([0,1  ,0,1]);
    box on
```

```
function ext=bpnew(N,D,d,c)
%preliminary work for FL
p=((1-D)*(1:N)./((1-d)*...
     (N-(1:N))+(1-D)*(1:N)+N*(1-c)*d))';
P=zeros(N:N);
 for j=1:N
     P(:,j)=nchoosek(N,j)*((p.^j).*((1-p).^(N-j)));
 end
 oneminusP=(1-sum(P'))';
 PP=[oneminusP,P];
 %preliminary work for FNL
 m=(1-c)*d/(1-c*d);
 %Iterating dynamical system to find fixed point
 z0=zeros(N,1);
 err=1;
    while err>10^(-9)
        FL=PP*[1;z0];
        FNL=exp((1:N).*(m*D/d)*(z0(1)-1));
        z=FL.*(FNL)';
        err=norm(z-z0);
        z0=z;
```

```
    end
ext=prod(z);
end
```