

Dispersal evolution in fragmented habitats: the interplay between the tendency and the ability to disperse

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ABSTRACT

Questions: How will two dispersal traits, one determining dispersal ability and the other determining dispersal tendency, affect each other's evolutionary dynamics in a fragmented landscape? Which properties of fragmented habitats lead to evolutionary interactions between these two traits and which allow the traits to evolve independently?

Mathematical method: A population genetic model with explicit ecological costs. The mean fitness of the population is maximized on S. Wright's adaptive topography.

Key assumptions: Two haploid (or diploid) loci, each with two alleles. The first locus describes dispersal 'tendency', where the strength of environmental fluctuations and the distance separating suitable habitats determines the cost of sedentary behaviour relative to the cost of dispersal. The second locus determines dispersal 'ability', where there is a trade-off between survival in the local habitat (favouring low dispersal ability type) and survival during a dispersal event (favouring high dispersal ability type).

Conclusions: The evolutionary relationships between these dispersal traits range from simple monotonic trajectories, where the traits evolve independently, to non-linear dynamics, where the evolution of one trait strongly depends on the other's evolution. One example of non-linearity: the same ecological conditions may either allow the fixation or the loss of dispersal traits simply depending on the initial allelic frequencies of dispersal traits. This result leads to a novel colonization bias hypothesis. Non-linear dynamics are found when habitats have intermediate levels of environmental fluctuation and/or when the distance between habitats is large and when dispersal tendency has high genetic penetrance (*sensu* Falconer, 1981). When dispersal tendency and ability traits exhibit non-linear dynamics, our view of their evolution will be seriously distorted if both are not studied simultaneously.

Keywords: adaptive landscape, co-evolution, colonization, evolutionary dynamics, islands, penetrance.

INTRODUCTION

Dispersal in fragmented habitats such as oceanic archipelagos, mountain ranges and forest patches has been of particular interest to evolutionary biologists and biogeographers

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because of its direct influence on a multitude of population level ecological and evolutionary processes (e.g. Mayr and Diamond, 2001). Much theoretical research has focused on identifying the ecological conditions favouring dispersal within such fragmented areas. Fragmented habitats pose a great problem for dispersing individuals because unlike in more continuous areas, individuals must face the prospect of dispersing into and across unsuitable environments that provide less opportunity for rest and are inadequate for establishment (Mayr, 1942). For selection to favour individuals that have the behavioural inclination to disperse away from a local habitat, not only must there be sufficient physical ability to survive crossing the hostile environment, but individuals must then also be capable of successfully establishing once they reach a suitable habitat (see Johnson and Gaines, 1990).

Most models have focused on understanding how the evolution of dispersal behaviour is affected by the properties of suitable habitats, in terms of either the local incentive to disperse or establishment success after dispersal. These models have suggested that dispersal into novel habitats is favoured when resource quality in different habitats fluctuates independently over time (Levin *et al.*, 1984), when local populations experience cyclic or chaotic growth dynamics (Holt and McPeck, 1996; Doebeli and Ruxton, 1997; Parvinen, 1999) or go extinct (Van Valen, 1971; Olivieri *et al.*, 1995), when relatives compete for local resources (Hamilton and May, 1977) or experience strong inbreeding depression (Bengtsson, 1978; Crespi and Taylor, 1990), and when populations adapt to divergent selective regimes of different habitats (Kisdi, 2002).

Much less theoretical attention has been paid to how the process of dispersal affects the evolution of dispersal behaviour, even though empiricists have long thought that dispersal across unsuitable environments carries a high cost (e.g. Darwin, 1859; Carlquist, 1974; Lomolino, 1984; Hanski, 1986; Johnson and Gaines, 1990). The above models assume a fixed cost to dispersal without explicitly considering the source of that mortality. In reality, the cost of a dispersal event is a direct consequence of the physical ability of individuals to survive while crossing habitat gaps. In effect, the assumption of a fixed dispersal cost implies that all individuals are equally able to survive while dispersing. A brief look at the empirical literature suggests that this assumption is unlikely to be met in nature because individuals within populations differ in their ability to successfully disperse across unsuitable habitats. This is evident in insects during flight (e.g. Rose, 1972; Dobzhansky, 1973; Dingle, 1979; Harrison, 1980; Gunn and Gatehouse, 1993; Schumacher *et al.*, 1997a,b), plant seeds transported across oceans and in the air (Sykes and Godley, 1968; Carlquist, 1974; Wickens, 1979), small island mammals swimming in lakes and the ocean (Lawlor, 1982; Lomolino, 1983, 1984; Hanski *et al.*, 1991), marine planktonic larvae (Williams *et al.*, 1973; Koehn and Williams, 1978) and island lizards floating in sea water (Schoener and Schoener, 1984). Some studies directly measure or infer dispersal survivorship in the field, while others measure some correlate of dispersal survivorship such as the longest travelling duration until exhaustion in the laboratory. In insects, this variation has a strong additive genetic basis (see Dingle, 1979; Roff and Fairbairn, 1991). Moreover, field studies provide evidence that different populations of the same species vary with respect to their individuals' dispersal ability (Darlington, 1943; den Boer, 1970; Dingle, 1978; Zera, 1981; Lawlor, 1982; Lomolino, 1983, 1984; Liebherr, 1988; Hanski *et al.*, 1991; Paterson and Denno, 1997).

Therefore, the empirical data suggest that the cost of dispersing across unsuitable environments is not a fixed value, but is likely to vary within and between populations. If so, our understanding of the evolution of dispersal behaviour based on a fixed dispersal cost may be oversimplified or even misleading because dispersal cost is likely to evolve together with dispersal behaviour. Furthermore, dispersal behaviour might determine to what extent dispersal ability traits will experience within- versus between-habitat selection pressure. This interdependence might force the two dispersal traits to co-evolve in fragmented habitats.

In effect, the evolution of dispersal behaviour might not only depend on the properties of suitable habitats, but also on the outcome of these evolutionary dynamics.

This possibility raises an interesting, but yet unanswered question: When, if ever, should we expect these two dispersal traits to influence each other's evolution in nature? Moreover, how will these interactions change our expectation of the evolutionary trajectory and outcome of each trait? If dispersal behaviour and dispersal ability interact, it will no longer be justifiable, at least under some circumstances, to study the evolution of these traits in isolation. It is also important to identify ecological and genetic conditions where these traits fail to affect each other's evolution.

A GENERAL MODEL

To begin to address this question theoretically, this paper describes a spatially implicit, but general and analytical model for the evolutionary dynamics of dispersal tendency and dispersal ability. I explicitly treat dispersal tendency and dispersal ability as separate traits. This means that the traits have separate functions: dispersal tendency determines the probability of dispersal and dispersal ability determines the likelihood of survival during dispersal (but see Discussion). For simplicity, both traits are modelled as haploid loci, each with two alternative alleles (diploidy does not alter the qualitative results of the model; see Discussion).

The dispersal tendency locus (T) determines the probability that individuals remain in the local habitat in which they were born (allele t – 'sedentary tendency') or disperse away from it by entering the inhospitable space beyond its borders (allele T – 'dispersing tendency'). The frequency of allele t is p_t and the frequency of allele T is p_T , with $p_T + p_t = 1$ within populations. The dispersal probability m_t is for genetically sedentary individuals and the dispersal probability m_T is for genetically dispersing individuals, where $m_T > m_t$ in the model. The dispersal ability locus (A) determines whether individuals will exhibit weak dispersal ability (allele a) or stronger dispersal ability (allele A). The frequency of allele a is p_a and the frequency of allele A is p_A , with $p_A + p_a = 1$. The four possible haplotypes and their frequencies in each population are shown in Table 1. These mate randomly within each local habitat to produce the next generation of offspring with frequencies: $x'_1 = x_1 - rD$, $x'_2 = x_2 + rD$, $x'_3 = x_3 + rD$, $x'_4 = x_4 - rD$, where r is the recombination rate between the two loci and D is their linkage disequilibrium (Hedrick, 2000).

I assume that after random local mating, individuals experience different ecological costs that are incorporated into the total cost functions of each haplotype as follows:

$$c_{AT} = l_A + d_A m_T + (s_e)(1 - m_T) \quad (1a)$$

$$c_{aT} = l_a + d_a m_T + (s_e)(1 - m_T) \quad (1b)$$

$$c_{At} = l_A + d_A m_t + (s_e)(1 - m_t) \quad (1c)$$

$$c_{at} = l_a + d_a m_t + (s_e)(1 - m_t) \quad (1d)$$

To keep the model general and simple so that its analysis remains analytical, the costs above only implicitly describe the ecological context and do not involve a spatially explicit model with density-dependent effects (e.g. Travis *et al.*, 1998; Murrell *et al.*, 2002; Rousset and Gandon, 2002; Cadet *et al.*, 2003). I will later discuss how incorporating these factors might alter my results.

Table 1. The four haplotypes and their frequencies in each local population

Haplotypes	Names	Frequency
<i>AT</i>	Strong ability – dispersal behaviour	$x_1 = p_A p_T + D^*$
<i>aT</i>	Weak ability – dispersal behaviour	$x_2 = p_a p_T - D$
<i>At</i>	Strong ability – sedentary behaviour	$x_3 = p_A p_t - D$
<i>at</i>	Weak ability – sedentary behaviour	$x_4 = p_a p_t + D$

* D is the linkage disequilibrium between the two loci, where $D = (x_1 x_4) - (x_2 x_3)$.

First, all individuals experience costs associated with their dispersal ability phenotype in a local habitat: l_a for weak dispersal ability and l_A for strong dispersal ability. I let the weak dispersal ability phenotype be the optimal strategy within a local habitat such that $l_a < l_A$, where the local selective difference is $\Delta l = l_A - l_a$. I assume that the weak disperser allocates less energy to the production of dispersal ability structures, such as wing muscles, and will therefore be able to use this extra energy for fecundity or other fitness components [for birds, see Greenewalt (1975), Chai and Dudley (1999); for insects, see Dingle (1979), Roff (1986), Roff and Fairbairn (1991), Roff and Bradford (1996)]. Hence, in a suitable environment, not requiring long-distance dispersal, this phenotype is at a relative advantage. Alternatively, what has been called a ‘weak’ dispersal ability may also be thought of as an adaptation to manoeuvring within a local habitat, while ‘strong’ ability may be regarded as an adaptation for longer-distance dispersal that is less effective in local manoeuvrability (see Pennycuik, 1975; Terres, 1980; Burton, 1990).

After local selection, individuals either disperse into habitat gaps or remain within their original habitat, according to their dispersal tendency haplotype. Dispersing individuals experience dispersal mortality costs on their way to other habitats: d_a for haplotypes with weak dispersal abilities and d_A for haplotypes with strong dispersal abilities. Accordingly, I assume that $d_A < d_a$, where the dispersal selection difference is $\Delta d = d_a - d_A$ (e.g. Lomolino, 1983, 1984; Hanski *et al.*, 1991).

I further assume that habitats may fluctuate in time and space as a result of stochastic, localized environmental disturbances (*sensu* Levin *et al.*, 1984). This creates spatial heterogeneity in local population dynamics, such that disturbed populations fall below their carrying capacity, while undisturbed populations remain at their carrying capacity (Levin *et al.*, 1984). In this case, the dispersal haplotype is benefited because it may disperse from stable to expanding populations (e.g. Olivieri *et al.*, 1995; Parvinen, 1999) and this benefit is directly proportional to the strength and frequency of local environmental disturbances (*sensu* Levin *et al.*, 1984). In the extreme case, dispersal has greatest benefit in a metapopulation context where local populations go extinct and are then recolonized by dispersing haplotypes (Van Valen, 1971; Olivieri *et al.*, 1995). I incorporate this effect into the model by assuming that the cost to sedentary behaviour, s_e , roughly increases with the strength of localized environmental fluctuations.

The probability that an individual of a certain haplotype experiences either dispersal mortality or sedentary cost is determined by the individual’s probability of dispersal, m_T or m_t for dispersal and sedentary haplotypes, respectively (see above). In effect, the dispersal rates determine the proportion of individuals of a certain haplotype experiencing the two alternative selective costs (see equations 1). Finally, I assume that all populations start out with the same allelic frequency at the two dispersal loci. A two-patch computer simulation

(available upon request) shows that spatial heterogeneity in allelic frequency does not alter the qualitative results.

After all of the above ecological costs have been incorporated into the total cost functions above, the absolute fitness of each haplotype simply becomes

$$w_i = 1 - c_i \quad (2)$$

Therefore, the mean fitness in each local population after reproduction is

$$\bar{w} = w_{AT}(x_1 - rD) + w_{aT}(x_2 + rD) + w_{At}(x_3 + rD) + w_{at}(x_4 - rD) \quad (3)$$

DESCRIBING EVOLUTIONARY DYNAMICS

To understand how the two dispersal traits affect each other's evolutionary dynamics, I describe a diverse set of ecological cost-benefit scenarios by deriving the adaptive topography for each scenario designated by the above fitness functions in equations (1). The adaptive landscape for a given scenario describes the mean fitness of the population given in equation (3) as a function of allelic frequencies and D of the two dispersal loci. In this model, I optimize the mean fitness of the population, assuming frequency-independent selection. The shape of the topography describes the evolutionary dynamics (trajectories) of dispersal evolution from all possible points on the landscape. Furthermore, the evolutionary stable point(s) on the landscape are inferred from the shape of the topography and are the point(s) on the landscape where all local trajectories converge (Wright, 1932, 1969). A stable point represents the optimal frequency of dispersal tendency and ability alleles in the population for each ecological scenario. The adaptive topographies are determined algebraically under the assumption that initial linkage disequilibrium, D_o , between the two traits is zero (Hedrick, 2000). I later show numerically that relaxing this assumption to include varying degrees of D_o does not alter the qualitative results developed here analytically. By manipulating the mean fitness equation (3), one finds

$$\bar{w} = E \left[p_A - \frac{w_{at} - w_{aT}}{E} \right] \left[p_T - \frac{w_{at} - w_{At}}{E} \right] + \left[\frac{w_{AT}w_{at} - w_{aT}w_{At}}{E} \right] \quad (4)$$

where $E = w_{AT} + w_{at} - w_{aT} - w_{At}$ [additive epistasis (Hedrick, 2000)]. Upon substituting the ecological costs in equations (1) into equation (2) and simplifying,

$$E = (d_a - d_A) \times (m_T - m_t) \quad (5)$$

which is always positive under the fitness functions in this model (see Appendix for calculations). A curve with constant mean fitness (i.e. an isocline) is a hyperbola with asymptotes parallel to the axes of a two-dimensional adaptive topography, one asymptote at

$$p_A = \frac{w_{at} - w_{aT}}{E} \quad (6a)$$

and the other at

$$p_T = \frac{w_{at} - w_{At}}{E} \quad (6b)$$

Upon substituting the fitness functions in equation (2) into equations (6a) and (6b), the asymptotes become

$$p_A = \frac{(d_a - s_e)}{(d_a - d_A)} \quad (7a)$$

and

$$p_T = \frac{\left[\frac{\Delta l}{\Delta d} - m_t \right]}{(m_T - m_t)} \quad (7b)$$

(see Appendix for calculations). Depending on the ecological parameters in equations (7a) and (7b), each (p_A and p_T) asymptote may be less than 0, between 0 and 1, or greater than 1. Since the asymptotes are parallel to the axes of a two-dimensional adaptive topography, their intersection point may be found (Fig. 1a). If both asymptotes are between 0 and 1, they intersect at the centre of the topography (Fig. 1a: 1). Eight other qualitatively different intersection points are also possible, depending on the value of each asymptote (Fig. 1a: 2–9). The p_A asymptote moves down or up with respect to the centre of the topography, depending on whether it is negative or greater than 1, respectively. Similarly, the p_T asymptote moves left or right with respect to the centre of the topography, depending on whether it is negative or greater than 1, respectively.

The intersection of the asymptotes determines two critical aspects of the topography. First, equation (4) shows that all curves of constant mean fitness are hyperbolas (isoclines) of the form $p_A * p_T = k$, where k is a constant that increases with increasing mean fitness (since $E > 0$; see above). Since the isoclines translate along each asymptote by the amounts in equations (7a) and (7b), I plot $p_A * p_T = k$ for many values of k to infer the shapes of nine qualitatively different topographies (Fig. 1b: 1–9).

To visualize the relationship between all nine topographies and infer the direction of evolution in each, I simply plot all nine topographies on a common topography with respect to its origin (see Fig. 2). For instance, topography #1 in Fig. 1 is placed at the centre of the common topography because both of its asymptotes cross its origin, while topography #8 is

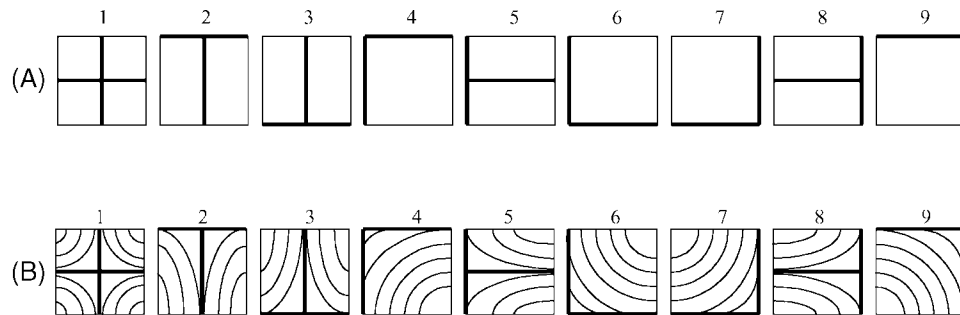


Fig. 1. The construction of all nine qualitatively different adaptive topographies of evolution between dispersal tendency and dispersal ability traits. (A) Nine qualitatively different intersection points of p_A and p_T asymptotes when each asymptote (designated as bold lines) is less than 0, between 0 and 1, or greater than 1, in equations (7a) and (7b) (see text). (B) Isoclines of constant mean fitness are translated along each asymptote by the amounts in equations (7a) and (7b) (see text). This determines the shape of topography.

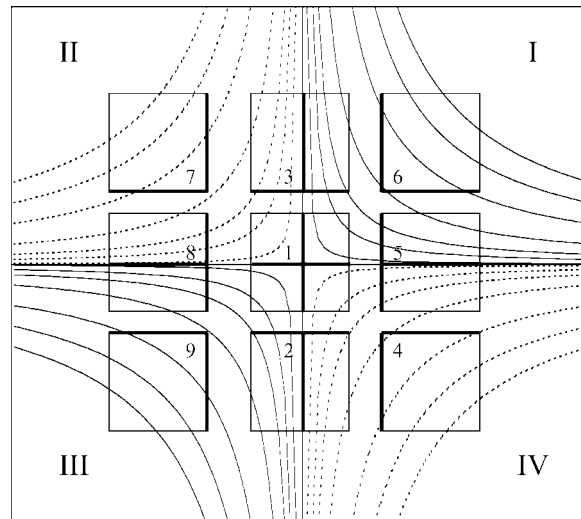


Fig. 2. All nine topographies constructed in Fig. 1 are plotted on a common surface, with respect to its origin. For visual clarity, I place each topography (except topography #1) slightly away from the origin, but still according to its intersection point (designated by the intersection of its asymptotes, shown in bold). The general surface is subdivided into four quadrants (I–IV). The direction of evolution of any point in quadrants I and III is away from the common origin (solid isoclines), whereas in quadrants II and IV the direction of evolution is towards the common origin (broken isoclines) (see text).

placed to the left of the centre of the common topography because its p_T asymptote was shifted to the right of its origin (Fig. 2).

Since k increases with mean fitness (see above), to infer the direction of increasing mean fitness for each topography, we need to know the sign of k . This depends on the sign of p_A and p_T asymptotes in equations (7a) and (7b). Where both asymptotes are positive or negative, k is positive and mean fitness increases away from the origin (quadrants I and III in Fig. 2). When the asymptotes differ in sign, k is negative and the mean fitness increases towards the origin (quadrants II and IV in Fig. 2). Thus, quadrants determine the direction of evolution for any given point on the topography.

High penetrance dispersal

I begin with the simplest biological case: the proportion staying within a habitat versus dispersing away from it is determined by the dispersal tendency locus, such that all dispersing haplotypes disperse ($m_T = 1$) and all sedentary haplotypes remain within their original habitat ($m_i = 0$). I do not imply that natural systems ever exhibit this extreme scenario, but the interest here is to analyse situations where genetics plays a dominant role in dispersal behaviour such that dispersal probabilities may have high penetrance (*sensu* Falconer, 1981).

Sedentary behaviour with weak dispersal ability

First, consider the ecological condition where populations rarely, if ever, experience environmental fluctuations such that $s_e < d_A$. This condition corresponds to the p_A

asymptote > 1 (see equation 7a). In addition, imagine that the dispersal process across habitat gaps does not pose a major problem for weak dispersers such that local selection for weak dispersers is actually greater than dispersal selection for strong dispersers. This condition is likely when the distance between suitable habitats is short and corresponds to p_T asymptote > 1 , since $\Delta l / \Delta d > m_T$, where $m_T = 1$ (see equation 7b). Not surprisingly, the adaptive topography leads towards the fixation of the sedentary and weak dispersal ability haplotype (Fig. 3A). In effect, both a and t alleles fail to influence each other's evolutionary direction and result in a monotonic process.

What happens, however, when these conditions are altered to allow for stronger environmental fluctuations or for a more costly dispersal process? Will the system still evolve sedentary behaviour with a weak dispersal ability strategy? The answer is yes, although the evolutionary trajectory does change substantially.

First, I allow for stronger environmental fluctuations such that now $d_A < s_e < d_a$ (here the p_A asymptote is between 0 and 1; see equation 7a), but still keep local selection greater than dispersal selection such that $\Delta l > \Delta d$ (here the p_T asymptote > 1 ; see above). Figure 3B shows the dynamics. Since no individual can avoid the local costs (even if that individual will eventually disperse), weak dispersal ability begins to increase in frequency (trajectory towards the bottom of the graph). Despite at first the population evolving in the direction of higher dispersal tendency frequency, the sedentary tendency allele eventually fixes in the population. The final outcome is the loss of both dispersal traits, even though dispersal alleles would have increased to fixation if the population maintained many strong dispersers. The evolution of dispersal tendency strongly depends on the evolution of dispersal ability in this scenario.

Now, let environmental fluctuations again be minimized, such that $s_e < d_A$ (here the p_A asymptote > 1 ; see above), but increase the cost of dispersal across habitat gaps, such that dispersal selection for strong ability becomes greater than local selection against them (the p_T asymptote is now between 0 and 1 such that $m_i < \Delta l / \Delta d < m_T$, where $m_i = 0$ and $m_T = 1$; see equation 7b). Here, strong dispersers increase in frequency when the system starts out with a high frequency of dispersing individuals (right-hand side of Fig. 3C). However, because dispersal tendency is at an overall disadvantage, the population becomes increasingly less exposed to dispersal selection over time and evolution ultimately fixes the weak dispersal allele. Here, the weak ability allele, despite being at a selective disadvantage when the population has many dispersing individuals, nevertheless evolves with the evolution of sedentary behaviour. Here, the evolution of dispersal ability strongly depends on the evolution of dispersal tendency.

Considering all three ecological scenarios leading towards the evolution of sedentary behaviour with weak ability, I find it is not necessary for selection to favour both traits all the time for this strategy to evolve in nature, but only one. This effectively means that dispersal tendency evolves even when environmental fluctuations are of intermediate strength and weak dispersal ability evolves even when dispersal selection against it is stronger than local selection for it.

Dispersal tendency with weak dispersal ability

When populations experience maximum environmental fluctuations such that $s_e > d_a$ (here the p_A asymptote < 0 ; see equation 7a), but dispersal distances between suitable habitats are small to make $\Delta l > \Delta d$ (see above), not surprisingly the haplotype with dispersal tendency and weak dispersal ability (aT) evolves in the system (Fig. 3D). What is perhaps unusual is

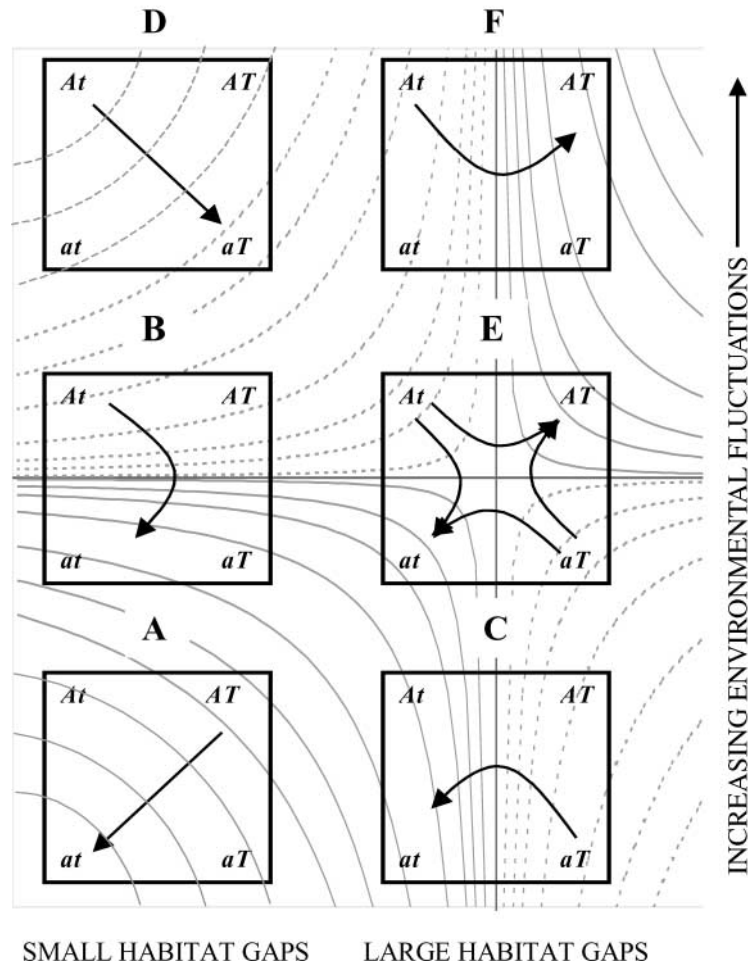


Fig. 3. Six possible adaptive topographies (A–F) of evolution between dispersal tendency and dispersal ability when dispersal tendency has high genetic penetrance (see text). For all topographies, the frequency of the strong dispersal ability allele within populations (p_A) runs along the y-axis and the frequency of the dispersal tendency allele (p_T) runs along the x-axis. Arrows provide an example of evolutionary dynamics (trajectories) and point in the direction of evolutionarily stable strategies of dispersal tendency and ability, described in Table 1. The background surface represents the general shape of isoclines derived in Figs. 1 and 2. It describes the mean fitness surface of each topography and also illustrates the mathematical relationship between the different topographies according to equations (7a) and (7b). The strength of environmental fluctuations increases from bottom to top (p_A asymptote in equation 7a decreases), while habitat gaps increase from left to right (p_T asymptote in equation 7b decreases).

that this strategy results in the mismatch or decoupling of dispersal tendency and ability phenotypes, but this result is completely expected based on the ecological circumstances. Here, these traits evolve in a monotonic fashion without influencing each other's evolutionary direction. This result might explain the observations of Gressitt and Weber (1959), who

found that some insect species in Southern Atlantic islands are very active in air despite being relatively weak flyers compared with other insects.

Sedentary behaviour with weak ability or dispersal tendency with strong ability

Probably the most interesting consequence of the interaction between the evolution of dispersal tendency and dispersal ability traits is the result described below. Let environmental fluctuations have intermediate values, such that $d_A < s_e < d_a$ (see above), and keep habitat gaps large, such that $\Delta l < \Delta d$ (see above). The dynamics here produce two locally stable adaptive peaks separated by an unstable maladaptive valley with an internal saddle point (Fig. 3E). This means that identical ecological conditions may either give rise to the evolution of sedentary behaviour with weak dispersal ability (*at*) or to the evolution of dispersal tendency with strong dispersal ability (*AT*).

Which strategy will actually evolve strictly depends on evolutionary initial conditions. When populations start out with a high frequency of sedentary alleles or weak ability alleles, these traits evolve over time (haplotype *at*). On the other hand, when either dispersing alleles or strong ability alleles are initially common among populations, evolution then fixes both of these traits (haplotype *AT*). Importantly, this occurs even though these alleles are initially in linkage equilibrium. The result is an intrinsic consequence of the mutual positive feedback between the fitness of the two traits under this scenario.

Thus, when habitats have intermediate environmental fluctuations and are separated by large distances, to predict the evolutionary trajectory and outcome of each dispersal trait one must account for the initial frequencies of these alleles among the ancestral populations. Failure to do so results in a seriously distorted view of the evolution of both dispersal tendency and dispersal ability traits. For instance, without knowing the initial conditions, it would be impossible to predict the final evolutionary direction of these two traits by sampling the first set of trajectories that all seem to converge towards a polymorphic state. Furthermore, this finding shows that these dispersal traits may evolve even when both are at a selective disadvantage at some part of the landscape.

Dispersal tendency with strong dispersal ability

Finally, I explored the last ecological condition with high penetrance dispersal, shown in Fig. 3F. Here, I allow both maximum environmental fluctuations, such that $s_e > d_a$ (see above), and dispersal selection to be greater than local selection, such that $\Delta l < \Delta d$ (see above). As expected, haplotype *AT* evolves. However, despite the fact that here sedentary behaviour and weak ability are both more costly alleles, the evolution of dispersal traits only evolves by a non-linear trajectory. This is because only when dispersal tendency evolves to a certain threshold frequency in the population will the benefits of strong dispersal ability be realized to give the haplotype *AT*. Again, the evolutionary fate of dispersal ability strongly depends on the evolution of dispersal tendency.

In conclusion, when dispersal penetrance is high, only two of the six scenarios allow the dispersal tendency and ability traits to evolve independently of one another. All other landscapes give rise to strong evolutionary interdependence between the two traits. The most extreme example of co-evolution occurs when habitats experience intermediate environmental fluctuations and are separated by large distances. Do these conclusions change once dispersal tendency has low genetic penetrance? I address this question in the following section.

Low penetrance dispersal

When dispersal tendency has low penetrance, there is a disconnection between an individual's genotype of dispersal and its actual probability of dispersal, such that some individuals in the population fail to behave based on their genetic predisposition. The environment is likely to influence the average penetrance in the population (Falconer, 1981). Larger and more ecologically heterogeneous habitats might reduce the probability of dispersal even for haplotypes that are genetically inclined to disperse ($m_T < 1$), while smaller and simpler habitats might have the opposite effect ($m_i > 0$) (see Darlington, 1943; MacArthur and Wilson, 1967, p. 158). Similarly, when local cues to disperse are frequent and strong, both genetically dispersive and sedentary individuals are likely to do so at a high rate, while dispersal is likely to be low for both with relatively rare and weak local dispersal cues. By definition, m_i is still less than m_T .

Whether incomplete dispersal penetrance (i.e. when $m_T < 1$ or $m_i > 0$) alters the previous adaptive topography strictly depends on whether local selection is greater or less than dispersal selection. Only when $\Delta l < \Delta d$, such that $m_i < \Delta l / \Delta d < m_T$ (i.e. when habitats gaps are large), can incomplete penetrance alter the outcome obtained with high penetrance dispersal. If $\Delta l > \Delta d$, such that $\Delta l / \Delta d > m_T$, the $\Delta l / \Delta d$ ratio is already greater than 1. Thus, even if m_T falls below 1 (i.e. because some genetically dispersive individuals remain sedentary), the above relationship is still maintained (Figs. 4A, B, D). On the other hand, when $\Delta l < \Delta d$, if some genetically dispersive individuals remain sedentary such that m_T decreases below 1, $\Delta l / \Delta d$ might become greater than m_T , changing the previous relationship $m_i < \Delta l / \Delta d < m_T$. Similarly, if some genetically sedentary individuals disperse such that m_i increases above 0, m_i might become greater than $\Delta l / \Delta d$, again changing the previous relationship $m_i < \Delta l / \Delta d < m_T$. Figure 4 shows how the topographies in Figs. 3C, E and F change when m_T falls enough below 1 (left side shift) or m_i increases enough above 0 (right side shift). Of course, whether the change in m_T or m_i changes the above relationship strictly depends on the relative strength of dispersal selection over local selection (i.e. ratio $\Delta l / \Delta d$).

The most interesting feature of this result is that it describes how simply altering the genetic penetrance of dispersal tendency dramatically changes the evolutionary dynamics of dispersal traits, despite the ecological conditions remaining the same. Even more noteworthy is that by reducing dispersal penetrance in a certain way (i.e. when m_i becomes > 0), I encounter trajectories and stable outcomes of dispersal trait evolution that are not possible with complete dispersal penetrance (compare Figs. 3 and 4). To understand this latter result, I focus on the right side of Fig. 4, describing how incomplete dispersal tendency penetrance produces novel evolutionary dynamics.

Sedentary behaviour with strong dispersal ability ('psychological barriers to dispersal')

Above I described an ecological condition where environmental fluctuations are minimum, such that $s_e < d_A$, and dispersal selection is greater than local selection, such that $\Delta l < \Delta d$ (Fig. 3C). Populations evolved sedentary behaviour with weak dispersal ability when no genetically sedentary individual dispersed. By now allowing some proportion of genetically sedentary individuals to disperse, such that $\Delta l / \Delta d < m_i$, we change the evolutionary dynamics of dispersal by fixing the haplotype At (Fig. 4C). Here, individuals are genetically sedentary, but maintain strong dispersal abilities. In fact, Ernst Mayr and his co-workers frequently described this mismatched dispersal phenotype among the Northern Melanesian

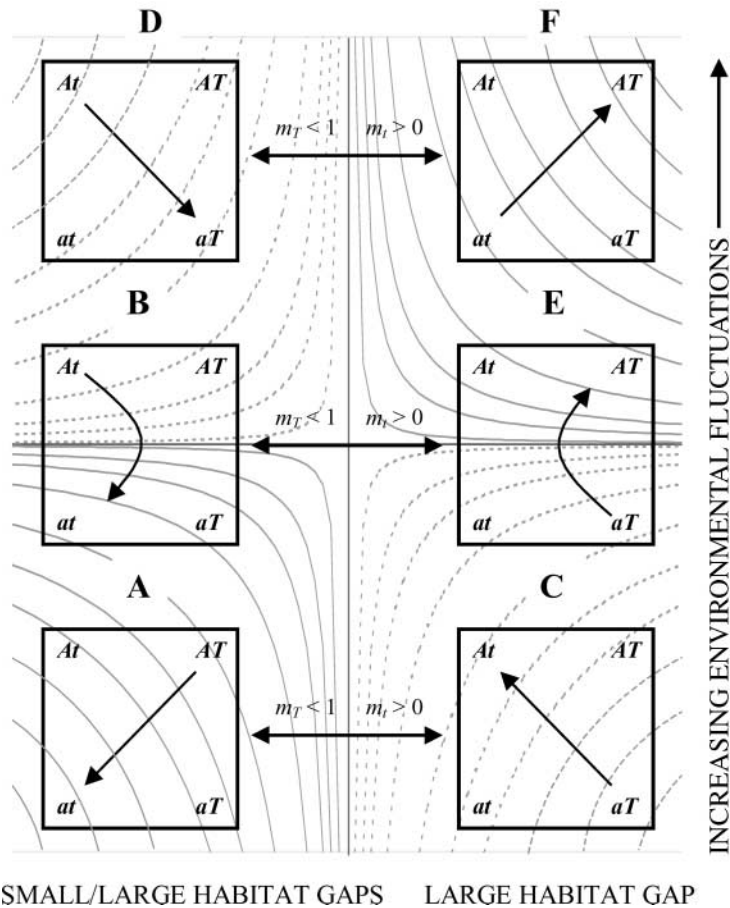


Fig. 4. Six possible adaptive topographies (A–F) of evolution between dispersal tendency and dispersal ability when dispersal tendency has low (incomplete) genetic penetrance (see text). For a detailed description of topographical features, see Fig. 3. When local selection is greater than dispersal selection (i.e. small habitat gaps), low penetrance does not change the dynamics in Fig. 3 (topographies A, B and D). When dispersal selection is greater than local selection (i.e. large habitat gaps), topographies C, E and F in Fig. 3 (for high penetrance) may change when m_T and/or m_t have low penetrance (left and right shifts, respectively). Note that topographies A, B and D are the same as in Fig. 3, except that m_T is now less than 1 (and habitat gaps may be large). Topographies C, E and F are only produced when dispersal behaviour has low penetrance.

bird species as ‘psychological barriers to dispersal’ (see Mayr, 1942, 1963, pp. 567–568; Mayr and Vaurie, 1948; Mayr and Diamond, 2001, p. 298). The ESS dispersal rate of sedentary individuals depends on the specific parameters of $\Delta//\Delta d$, but if this ratio is close to zero (i.e. when habitat gaps are large), very few sedentary individuals need to disperse every generation to satisfy $\Delta//\Delta d < m_t$. Here dispersal tendency and ability alleles evolve independently of one another, without evolutionary interactions.

Dispersal tendency with strong dispersal ability

With complete dispersal penetrance, as the strength of environmental fluctuations was increased, such that $d_A < s_e < d_a$ or $s_e > d_a$, and dispersal selection was greater than local selection, evolution either led to two locally stable peaks (Fig. 3E) or to the non-linear fixation of dispersal traits (Fig. 3F). By allowing some genetically sedentary individuals to disperse, such that $\Delta/\Delta d < m_i$, changes these previous topographies in favour of the evolution of dispersal traits (Figs. 4E and 4F). This result is explained by the fact that with some genetically sedentary individuals dispersing, more ability alleles are exposed to the dispersal selection regime than before. Note that when this happens, evolutionary history no longer plays a role in the evolution of the two dispersal traits (compare Figs. 3E and 4E).

Do populations with low dispersal tendency penetrance display more or less evolutionary interaction between these traits than populations with high dispersal tendency penetrance? Comparing Figs. 3 and 4, it is evident that as the penetrance of dispersal tendency is reduced, the two dispersal traits become less interactive; with high penetrance dispersal, four of six topographies display evolutionary interactions, whereas with low penetrance dispersal, only two of six topographies do so.

Finally, I note that the analytical results above were confirmed by a numerical iteration of the recursive equations for the haplotype frequencies after random mating within each local patch and identical selection in each patch in a two-patch simulation:

$$x_1^* = w_{AT} (x_1 - rD) / \bar{w} \quad (8a)$$

$$x_2^* = w_{aT} (x_2 + rD) / \bar{w} \quad (8b)$$

$$x_3^* = w_{At} (x_3 + rD) / \bar{w} \quad (8c)$$

$$x_4^* = w_{at} (x_4 - rD) / \bar{w} \quad (8d)$$

Importantly, this approach also shows that the qualitative results derived above, with the assumption of initial equilibrium between the two dispersal traits, are maintained when initial linkage disequilibrium D_o is incorporated. These results hold for any value of initial D_o , as long as the two traits have a positive recombination rate r between them. In the simulation, recombination breaks down the initial D_o after a few generations. From this point, because of directional natural selection in the system, positive linkage disequilibrium is built up again, and then finally declines to zero with the fixation of alleles in both patches (see Hedrick, 2000, for graphical depiction).

DISCUSSION

Evolution of dispersal tendency in fragmented habitats must overcome the high mortality cost of dispersing across unsuitable terrain. The cost associated with the dispersal process is a direct consequence of the physical dispersal ability of individuals, which in light of empirical evidence (see above) is likely to be an evolving property of the population. As dispersal ability evolves, it might not only affect the evolutionary dynamics of dispersal tendency, but may also be affected by the latter. But under which ecological conditions should we expect this to happen? And if these traits do influence each other's evolution, how does this change the way we view each trait's evolutionary dynamics? To answer these questions, I have formally explored the evolutionary relationship between these two dispersal traits under a diverse set of cost-benefit conditions. My results give rise to four

basic evolutionary strategies: the two matching strategies describe a situation where individuals either lose both the tendency and strong ability to disperse across habitat gaps or fix these traits; and the mismatching strategies describe a situation where individuals are either forced to disperse across habitat gaps with weak abilities or remain sedentary despite having the strong ability to disperse.

Throughout this paper, I have described different types of evolutionary relationships between these two dispersal traits, ranging from simple monotonic trajectories, where traits are evolving independently, to non-linear dynamics, where either the evolution of one or both of the traits strongly depends on the other's evolution. Therefore, we may be fairly confident that these dispersal traits are capable of evolutionary interaction. However, I must qualify this statement by noting that whether they do interact, and to what extent they interact, depends on the ecological and genetic circumstances. The model parameters may be subdivided into three major categories: First, I asked what will be the relative cost to sedentary behaviour compared with the cost of dispersal across habitat gaps? This relationship depends on the property of suitable habitats (where I explore varying strength of environmental fluctuations) versus the average distance separating the habitats. Second, I asked what is the relative selection pressure within local habitats (in favour of weak dispersal ability) compared with selection during dispersal (in favour of stronger dispersal ability)? This relationship depends on the relative energetic cost of having a stronger dispersal ability phenotype versus the average distance separating the habitats. Finally, I altered the genetic penetrance of dispersal tendency from high penetrance to low penetrance (*sensu* Falconer, 1981). Below I summarize how this ecological and genetic setting affects the evolutionary dynamics of dispersal tendency and ability traits.

First, I found that for dispersal tendency and dispersal ability to evolve in an independent fashion, the ecological conditions must be such that both alleles are selectively advantageous throughout the whole landscape, regardless of the frequency of the other allele. Each matching and mismatching strategy evolves in this linear fashion (Figs. 3 and 4). An important result is that mismatching strategies only display monotonic trajectories. Under these cases, the ecological conditions are so extreme that the evolution of each trait has little impact on the other. To summarize, the two dispersal traits will evolve independently in: (1) highly stable habitats, separated by small distances (*at*-strategy); (2) highly unstable habitats, separated by small distances (*aT*-strategy); and when low penetrance is combined with (3) highly unstable habitats, far apart (*AT*-strategy); and (4) highly stable habitats, far apart (*At*-strategy).

When populations occupy habitats with intermediate levels of environmental fluctuations, I found that dispersal tendency and dispersal ability traits always display significant non-linear evolutionary dynamics, regardless of the distance separating individual habitats. Furthermore, as long as the penetrance of dispersal tendency is high, non-linear dynamics are also always produced when habitat gaps are large, regardless of the habitats' stability. Under these circumstances, our understanding of the trajectory and outcome of dispersal tendency and ability will be seriously distorted if we do not consider the evolution of both traits together. For instance, I have described instances where one would have predicted the very opposite outcome for the evolution of dispersal tendency or ability if the other trait remained fixed in the population. This is because I find that these traits, under these conditions, exhibit 'threshold effects' – the direction of evolution of one trait changes course when the other trait reaches a certain frequency.

The most impressive example of such evolutionary interdependence between these two traits occurs when intermediate environmental fluctuations combine with large habitat gaps. When populations reside in these landscapes and dispersal tendency penetrance is relatively high, the evolutionary dynamics of each trait not only depend on the other's evolution, but here also depend on the initial frequency of both traits among the ancestral populations (Fig. 3E). In other words, the evolutionary fate of dispersal tendency or ability is ultimately determined by the other's early evolutionary history. Remarkably, the outcome could either lead to the fixation or complete loss of dispersal-related traits under this same ecological condition.

This result is likely to have implications for the evolution of dispersal tendency and ability traits after colonization events into novel environments. This is because the colonization process itself could potentially bias the allelic frequency of founder individuals with greater tendencies to disperse into habitat gaps and with stronger dispersal abilities. This initial condition could then bias the evolutionary trajectory towards the dispersal, strong ability strategy (i.e. colonization bias hypothesis). Possible examples of this phenomenon exist in empirical studies (see Lindroth, 1953; Mayr, 1963, p. 569; Mayr, 1964, p. 44; den Boer, 1970; Lawlor, 1982; Lomolino, 1984; Hanski *et al.*, 1991; Thomas *et al.*, 2001; Jansson and Dynesius, 2002; but see Simmons and Thomas, 2004).

My conclusions are based on the genetics of haploid organisms where each dispersal trait is governed by a single locus, each with two alleles, despite the possibility that in many cases these traits could be polygenic [but see Roff (1994) for many single-locus examples]. The main value of this approach is that I am able to model dispersal evolution analytically, revealing the general properties of evolutionary dynamics between dispersal tendency and dispersal ability. This analytical approach identified all mathematically possible dynamics and outcomes of evolution. Furthermore, it clarified the precise mathematical relationship between these various scenarios. Numerical simulation studies often lack these attributes (e.g. Gavrilets, 2003). Nevertheless, when I introduced diploidy into the model, with heterozygotes having intermediate phenotypic values, the results still remained the same. If heterozygote phenotypes produce overdominance, the model is likely to give stable dimorphisms (e.g. Feldman and Libermann, 1979), but at present it is unclear whether overdominance is likely for these dispersal traits.

There are, however, a few assumptions that, if violated, could potentially alter my results. First, I assumed complete functional separation of the two dispersal traits, such that both the individual's tendency and ability to disperse was only directly affected by its appropriate trait. Relaxing this assumption to include situations where each function is affected by both traits ultimately reduces this model to a single dispersal locus case (reviewed by Johnson and Gaines, 1990), in which case no evolutionary interaction is expected.

Second, this model should be thought of as a first general description of the evolutionary interaction between dispersal tendency and dispersal ability traits because evolution here is modelled in a spatially implicit context only. Future work is necessary to numerically simulate these analytical results in a multi-patch setting with specific geographical distances separating habitats (Heino and Hanski, 2001; Murrell *et al.*, 2002) and actual environmental fluctuations in habitat quality (Friedenberg, 2003). Now that a general analytical model exists for the simultaneous evolution of these dispersal traits, we are in a position to explore more specific values of environmental fluctuations (Travis and Dytham, 1999) and geographical distances (Rousset and Gandon, 2002) that are predicted here to alter the evolutionary dynamics and outcomes of these traits. Furthermore, the numerical simulations should incorporate other aspects of the relevant biology of dispersal evolution, such as density-dependent selection for dispersal

tendency (e.g. Levin *et al.*, 1984), distance-dependent selection for dispersal ability (e.g. Murrell *et al.*, 2002) and kin selection (Hamilton and May, 1977). At present, my model assumes that these other forms of selection have a negligible affect on the relative fitness of these dispersal-related traits compared to the factors that I have modelled. This might be a fair assumption for some but not all organisms in nature. I expect that density-dependent and kin selection will give rise to stable polymorphism with some proportion of individuals genetically sedentary and another proportion genetically dispersive and may help to identify additional conditions where these traits interact evolutionarily.

In general, this model provides an important example of why we need to study the joint evolution of dispersal behaviour and other traits (see also Klinkhamer *et al.*, 1987; Venable and Brown, 1988; Ezoe, 1998; Ferriere *et al.*, 2000; Levin and Muller-Landau, 2000; Ronce *et al.*, 2000; Kisdi, 2002), and should further our interest in evolutionary dynamics between functionally related ecological traits.

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APPENDIX

Calculations of E (additive epistasis)

If $E = w_{AT} + w_{at} - w_{aT} - w_{At}$ (see equation 4) and substituting equations (1) into equation (2) for each w_i , we get:

$$E = (1 - l_A - d_A m_T - s_e + s_e m_T) + (1 - l_a - d_a m_t - s_e + s_e m_t) - (1 - l_a - d_a m_T - s_e + s_e m_T) - (1 - l_A - d_A m_t - s_e + s_e m_t) \quad (A1)$$

After simplification:

$$E = -d_A m_T - d_a m_t - d_a m_T - d_A m_t \quad (A2)$$

and then:

$$E = (d_a - d_A) * (m_T - m_t) \quad (A3)$$

Because d_a is always greater than d_A and m_T is always greater than m_t (see above), E is always positive in this model.

Calculations of p_A asymptote

If $p_A = (w_{at} - w_{aT})/E$ and substituting equations (1) into equation (2) for each w_i , we get:

$$p_A = \frac{1 - l_a - d_a m_t - s_e + s_e m_t - 1 + l_a + d_a m_T + s_e - s_e m_T}{-d_A m_T - d_a m_t - d_a m_T - d_A m_t} \quad (A4)$$

After simplification:

$$p_A = \frac{-d_a m_t + d_a m_T + s_e m_t - s_e m_T}{-d_A m_T - d_a m_t - d_a m_T - d_A m_t} \quad (A5)$$

and then:

$$p_A = \frac{(m_T - m_t) * (d_a - s_e)}{(d_a - d_A) * (m_T - m_t)} \quad (A6)$$

and:

$$p_A = (d_a - s_e)/(d_a - d_A) \quad (\text{A7})$$

Calculations of p_T asymptote

If $p_T = (w_{at} - w_{Ad})/E$ and substituting equations (1) into equation (2) for each w_p , we get:

$$p_T = \frac{1 - l_a - d_a m_t - s_e + s_e m_t - 1 + l_A + d_A m_t + s_e - s_e m_t}{-d_A m_T - d_a m_t - d_a m_T - d_A m_t} \quad (\text{A8})$$

After simplification:

$$p_T = \frac{l_A - l_a - m_t * (d_a - d_A)}{(d_a - d_A) * (m_T - m_t)} \quad (\text{A10})$$

and then:

$$p_T = \frac{\frac{(l_A - l_a)}{(d_a - d_A)} - m_t}{(m_T - m_t)} \quad (\text{A11})$$