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Speciation through the learning of habitat features

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Abstract

Learning of environmental features can influence both mating behaviour and the location where young are produced. This may lead to speciation in three steps: (i) colonization of a new habitat, (ii) genetic divergence of the two groups by adaptation to the habitats, and (iii) a decrease of genetic mixing between the lineages (similar to reinforcement). In a previous paper we showed that steps (i) and (ii) occur readily for a wide range of fixed mating and habitat preferences. Here, we study whether this can ultimately lead to speciation through selective changes in these preferences.

We show that this indeed occurs, and, furthermore, it is very general: for a large class of models there is selection toward producing young more frequently in the natal habitat. Once habitat preference is strong, there is selection toward stronger assortative mating. Even when steps (i) and (ii) initially fail, genetic divergence may succeed at a later evolutionary stage, after which a decrease of genetic mixing completes speciation. Our results show that speciation by the learning of habitat features is an extremely effective mechanism.

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1. Introduction

The potential impact of learning on evolutionary processes has been noted only occasionally (e.g., ten Cate and Bateson, 1988; Grant and Grant, 1997; Irwin and Price, 1999; Owens et al., 1999; ten Cate and Vos, 1999; Slabbekoorn and Smith, 2002), and the amount of theoretical studies investigating it is limited (e.g., Laland, 1994a,b; Aoki et al., 2001; Ellers and Slabbekoorn, 2003; Beltman et al., 2003, 2004). Studies of speciation usually focus on the geographical mode of speciation (see Mayr, 1942, 1963; Schilthuizen, 2001; Turelli et al., 2001; Gavrillets, 2004; Coyne and Orr, 2004). Indeed, a multitude of models has been produced

to investigate speciation in the presence of gene flow (e.g., Maynard Smith, 1966; Pimm, 1979; Kawecki, 1997; Dieckmann and Doebeli, 1999; Higashi et al., 1999; Kondrashov and Kondrashov, 1999; Gavrillets, 2000; van Doorn and Weissing, 2001; Gavrillets and Waxman, 2002; Fry, 2003), ignoring the potential role of learning.

Learning can influence speciation when the mating behaviour of individuals depends on their experience, which happens in many species. Sexual imprinting (reviewed in ten Cate and Vos, 1999), the acquisition of mate preferences through learning the characteristics of parents or siblings early in life (Lorenz, 1937), provides an example. Mating behaviour can also be influenced by the learning of environmental (habitat) features. For instance, specialist brood-parasitic Viduidae learn the songs of their foster species. Males learn to produce these songs (Payne et al., 1998), and females use the songs they heard early in life (i) to find suitable mates, and (ii) to locate host nests (Payne et al., 2000).

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In this example the habitats are the foster species, and the learned habitat features their songs. The learning of habitat features also occurs in other animal species such as fish, insects and mammals. West-Eberhard (2003) and Beltman et al. (2004) discuss several examples, but a more extensive review is provided by Davis and Stamps (2004), who refer to this phenomenon as “natal habitat preference induction”. They suggest that it has been understudied, in part because scientists working with different taxa have used different terms to describe it (e.g., Hopkins’ host selection principle, or habitat imprinting). Well-known examples are fish species that imprint olfactorily at a young age on their local habitat, and use this learned information as adults for homing (e.g., salmon), or insects that prefer to feed on the food plant they have experienced since their birth. The learned host, habitat, or food features can influence both mating behaviour (here referred to as mating preference) and the location where young are produced (here referred to as habitat preference).

As a consequence of habitat imprinting, females normally produce their young in the same habitat as they grew up in. They may, however, accidentally produce their young in another habitat. The frequency of such an event will depend on the strength of the females’ preference for their natal habitat. The young resulting from “accidents” will learn features of the new habitat. Because of this, they will most likely mate with other individuals exploiting the habitat, and adult females will tend to produce their young in the new habitat.

In a previous paper (Beltman et al., 2004) we argued that, through such processes, the colonization of a new habitat may eventually lead to speciation. We used a gene-culture coevolutionary model to study this. It was assumed that population density is regulated separately in each of the two habitats, and that the viability of an individual depends on its genotype as well as on the habitat it exploits. Starting from a population that is specialized on the exploitation of a particular habitat, we studied under what circumstances colonization of a new habitat is possible and whether genetic differences between the subpopulations can arise. We showed that under a wide range of conditions, genetic divergence indeed occurs.

However, in that analysis, the strengths of both the habitat and the mating preference were assumed to be fixed traits. In reality, these traits will be under selective pressure. Furthermore, as long as these preferences are not absolute, there is no complete reproductive isolation. Therefore, our previous results imply only that the first steps toward speciation can occur when individuals imprint on habitat features, but it cannot be concluded that eventually this will indeed lead to divergence into different species. To examine that, we need to study evolutionary changes in habitat and mating preferences.

Selection for changes in habitat preferences is equivalent to selection for migration modification as studied by Karlin and McGregor (1972), Balkau and Feldman (1973), and Karlin and McGregor (1974). However, these authors only consider situations where mating occurs within the habitats, which implies that mating preferences are assumed to be absolute. As a consequence, reproductive isolation is accomplished as soon as the migration fraction is zero. We allow mating frequencies to depend on a mating preference as well as the availability of potential partners from different habitats, and consider evolutionary changes in the strength of this preference.

In the present paper we examine the direction of selection on the two traits by means of the selection differentials. Our main assumptions are that viability selection takes place after density regulation, that density regulation is such that the attractors are fixed points, and that viability selection acts in different directions in the subpopulations. First, we show that under very general conditions there is selection toward an increased habitat preference, regardless of the amount in which different habitats are exploited initially. Subsequently, we show that in a large class of models there is selection toward increased assortative mating as soon as habitat preferences are sufficiently high. These findings together imply that speciation will occur whenever a genetic polymorphism for viabilities in different habitats evolves at high habitat preferences. We examine the conditions under which this occurs for the model discussed by Beltman et al. (2004). We find that, even in cases where successful colonization and genetic divergence does not occur initially, speciation often takes place in the long run. Thus, speciation assisted by the learning of habitat features is an extremely effective mechanism.

2. Description of the model

As before, we consider two habitats, A and B . The viability within a habitat is determined by one diploid locus with two alleles. The three possible genotypes are denoted by g_Ag_A , g_Ag_B , and g_Bg_B . Individuals are further characterized by a cultural trait that is determined by the habitat that they are born into, c_A or c_B . We assume that there is female demographic dominance, and dynamics of females and males are equal, so that it suffices to follow only female dynamics. Generations are discrete and non-overlapping. It is assumed that mating is polygynous, and female preferences depend on male frequencies as well as cultural traits. After or during production of young there is local density regulation, and then viability selection takes place. We here consider a wider class of gene-culture coevolution models than in Beltman et al. (2004) in that we

allow more general forms of density dependence and mate preference.

We denote the probability that a female that was born in habitat x mates with a male from the same habitat by $\rho_x(\alpha)$, where α is the strength of the mating preference. These functions are assumed to be non-negative and non-decreasing in α , approaching one as α tends to infinity.

Females produce their young in the same habitat as they were born in with probability $1 - p$ (we refer to $1 - p$ as the habitat preference). In each habitat there is local density regulation, which is determined by a function Q_x that depends on the density in habitat x . We restrict our attention to functions Q_x of such a form that the only population dynamical attractors are fixed points.

The densities of reproductive adult individuals of the six possible combinations of cultural trait and genotype are denoted by N_i ($i = 1 \dots 6$, see summary in Table 1). Furthermore, we denote the total densities in each habitat by

$$N_A = N_1 + N_2 + N_3,$$

$$N_B = N_4 + N_5 + N_6. \quad (1)$$

Individuals are subject to viability selection, depending on their genotype and the habitat they exploit. In habitat A , individuals carrying more g_A alleles have a higher viability than other individuals, while in habitat B this is the case for individuals carrying more g_B alleles. We denote the viability of the types by w_i (w_1 is the viability of $c_A g_A g_A$ individuals, w_2 that of $c_A g_A g_B$ individuals, etc.). The parameters w_i can range from 0 (no individuals of this type survive) to 1 (all individuals of this type survive).

The model described above is a generalization of that used by Beltman et al. (2004). There we used the following specific forms of the functions $\rho_x(\alpha)$ and Q_x :

$$\rho_A(\alpha) = \frac{\alpha N_A}{\alpha N_A + N_B}, \quad \rho_B(\alpha) = \frac{\alpha N_B}{\alpha N_B + N_A}, \quad (2)$$

and

$$Q_A = \frac{E}{1 + KE((1 - p)N_A + pN_B)},$$

Table 1
The different types of individuals

Type	Density	Cultural trait	Genetic trait
1	N_1	c_A	$g_A g_A$
2	N_2	c_A	$g_A g_B$
3	N_3	c_A	$g_B g_B$
4	N_4	c_B	$g_A g_A$
5	N_5	c_B	$g_A g_B$
6	N_6	c_B	$g_B g_B$

$$Q_B = \frac{E}{1 + KE(pN_A + (1 - p)N_B)}, \quad (3)$$

where E corresponds to female fertility, and K is a positive parameter that determines the carrying capacity (note that a lower K implies a higher carrying capacity). Our present results are, however, valid for any functions that meet the conditions specified previously.

We denote the frequency of allele g_A among those with cultural trait c_A and c_B by respectively g and f , i.e.

$$g = \frac{N_1 + \frac{1}{2}N_2}{N_A}, \quad f = \frac{N_4 + \frac{1}{2}N_5}{N_B}. \quad (4)$$

Furthermore, let β_x be the probability that a female who was born in habitat x produces offspring with paternal allele g_A , i.e.

$$\beta_A = \rho_A(\alpha)g + (1 - \rho_A(\alpha))f,$$

$$\beta_B = \rho_B(\alpha)f + (1 - \rho_B(\alpha))g. \quad (5)$$

In Appendix A it is shown that the dynamics of this system are fully described by a set of recurrence equations for the total densities in each habitat $\{N_A, N_B\}$:

$$\begin{pmatrix} N_A \\ N_B \end{pmatrix}' = \begin{pmatrix} (1 - p)Q_A w_{AA} & pQ_A w_{AB} \\ pQ_B w_{BA} & (1 - p)Q_B w_{BB} \end{pmatrix} \begin{pmatrix} N_A \\ N_B \end{pmatrix}, \quad (6)$$

and a pair of recurrence equations for the frequencies of allele g_A in each habitat $\{g, f\}$:

$$g' = \frac{Q_A}{N_A'} \{(1 - p)w_{AA,1}N_A + pw_{AB,1}N_B\},$$

$$f' = \frac{Q_B}{N_B'} \{pw_{BA,1}N_A + (1 - p)w_{BB,1}N_B\}, \quad (7)$$

where

$$w_{AA} = (w_1\beta_A + w_2(1 - \beta_A))g + (w_2\beta_A + w_3(1 - \beta_A))(1 - g),$$

$$w_{AA,1} = (w_1\beta_A + \frac{1}{2}w_2(1 - \beta_A))g + (\frac{1}{2}w_2\beta_A)(1 - g). \quad (8)$$

The expressions for w_{AB} and $w_{AB,1}$ are found by replacing β_A by β_B and g by f . The expressions for w_{BA} and $w_{BA,1}$ are found by replacing w_1, w_2 and w_3 by respectively w_4, w_5 and w_6 . Finally, the expressions for w_{BB} and $w_{BB,1}$ are found by replacing the w_i ($i = 1, 2, 3$) as well as β_A and g .

3. Results

We study the direction of selection on α and p for the situation that

$$w_1 > w_2 > w_3 \quad \text{and} \quad w_6 > w_5 > w_4. \quad (9)$$

To do this we use the so-called adaptive dynamics approach (Metz et al., 1996; Dieckmann and Law, 1996; Geritz et al., 1998). This implies that we assume that the population is large, and that there are no other factors affecting mate choice besides the mating preference. Furthermore, it is assumed that mutation steps are small, so that mutants closely resemble the resident type, and that mutations are very rare, so that ecological and evolutionary time scales are separated. The last assumption entails that in-between mutation events the population dynamics reaches its attractor, which is in our case an equilibrium. The course of evolution can then be studied by considering which rare mutant types can establish themselves in a population of residents, which of these invasions will lead to replacement of the resident population, and what will be the outcome of a series of such substitution events.

We thus consider a population with resident trait values of the parameters (denoted by p_r and α_r) at its population dynamical equilibrium. Then we calculate the initial growth rate of a rare mutant type with a slightly different value of these traits. If this rate is larger than the growth rate of the resident population (which equals one since it is in equilibrium) the mutant type has a non-zero probability to establish itself. In the terminology of quantitative genetics we study the selection differentials of α and p .

By applying the results of Geritz et al. (2002) to our model, it can be shown that mutants that are able to invade will replace the resident population, as long as the process is not in the vicinity of so-called evolutionary branching points. Such branching points may occur if there is mutual invadability. This means that a mutant, say of type 1, can invade a population consisting of a resident type, here called 2 and that the reverse is also possible: mutants of type 2 can invade a resident population of type 1. It turns out, however, that such situations do not occur here. Thus the selection differentials will tell us the course of evolution.

We only consider situations where the total population does not go extinct, i.e. the total density $N_A + N_B$ remains positive. There are several possibilities: when at equilibrium only allele g_A or g_B is present in the population, we will speak of a (genetically) monomorphic population. When both alleles are present we will call the population polymorphic.

We study the selection differentials of p and α separately. While the evolutionary trajectory may be affected by correlations between these traits, this does not affect our main conclusions about the possibility of speciation.

3.1. Selection on p

We consider the effect of small mutation steps in the value of p . When mutants are rare, density-dependent

components are determined by the resident population. Therefore, the initial growth rate of the mutant population equals the dominant eigenvalue of the matrix in Eq. (6), with p equal to the mutant value p_m , whereas Q_x and the w_{xy} depend on the resident value p_r . We only consider situations where $p_r \neq 0$ or 1. This eigenvalue equals

$$\lambda = \frac{b + \sqrt{D}}{2}, \quad (10)$$

with

$$\begin{aligned} D &= b^2 - 4c, \\ b &= (1 - p_m)(Q_A w_{AA} + Q_B w_{BB}), \\ c &= Q_A Q_B ((1 - p_m)^2 w_{AA} w_{BB} - p_m^2 w_{BA} w_{AB}). \end{aligned} \quad (11)$$

We will show that the derivative of λ to p_m , evaluated at the value $p_m = p_r$ is negative, which means that there is selection in favour of a stronger habitat preference (toward smaller p). This can easily be shown to be equivalent to

$$\left(\sqrt{D} \frac{\partial b}{\partial p_m} + b \frac{\partial b}{\partial p_m} - 2 \frac{\partial c}{\partial p_m} \right)_{p_m=p_r} < 0. \quad (12)$$

Since the resident population is at its equilibrium, $b + \sqrt{D}$ must equal 2 when p_m equals p_r , so the inequality becomes

$$\left(\frac{\partial b}{\partial p_m} - \frac{\partial c}{\partial p_m} \right)_{p_m=p_r} < 0. \quad (13)$$

The derivative of b equals $-b/(1 - p_m)$. From $b + \sqrt{D} = 2$ it further follows that b equals $1 + c$, so the left-hand side of the inequality equals

$$\left(\frac{-1}{1 - p_m} (1 + c) - \frac{\partial c}{\partial p_m} \right)_{p_m=p_r}. \quad (14)$$

Substituting the expressions for c and its derivative gives, after some rearranging,

$$Q_A Q_B \{ (1 - p_r)^2 w_{AA} w_{BB} + p_r (2 - p_r) w_{BA} w_{AB} \} < 1. \quad (15)$$

From Eq. (6) we can derive that at the equilibrium of the resident population

$$\begin{aligned} Q_A &= \frac{N_A}{(1 - p_r) w_{AA} N_A + p_r w_{AB} N_B}, \\ Q_B &= \frac{N_B}{(1 - p_r) w_{BB} N_B + p_r w_{BA} N_A}. \end{aligned} \quad (16)$$

Substituting this and rearranging gives

$$\frac{w_{AA}}{w_{AB}} N_A^2 + \frac{w_{BB}}{w_{BA}} N_B^2 - 2 N_A N_B > 0. \quad (17)$$

Using the definitions of w_{xy} and β_x ($x, y = A, B$) we can derive the following:

$$\begin{aligned} w_{AA} - w_{AB} &= (g-f) \left\{ \frac{(w_1 - w_2)(\rho_A(\alpha)g + \rho_B(\alpha)f)}{+(w_2 - w_3)(\rho_A(\alpha)(1-g) + \rho_B(\alpha)(1-f))} \right\}, \\ w_{BB} - w_{BA} &= (g-f) \left\{ \frac{(w_5 - w_4)(\rho_A(\alpha)g + \rho_B(\alpha)f)}{+(w_6 - w_3)(\rho_A(\alpha)(1-g) + \rho_B(\alpha)(1-f))} \right\}. \end{aligned} \quad (18)$$

In Appendix B it is proved that in polymorphic populations $g > f$. When the viabilities satisfy the inequalities in (9), the right-hand sides of both equations (18) are non-negative. Hence, $w_{AA} > w_{AB}$ and $w_{BB} > w_{BA}$. This implies that in polymorphic resident populations inequality (17) is satisfied for all N_A and N_B .

It remains to be examined whether inequality (17) holds for monomorphic equilibria, where $g = f = 0$ or 1. From (18) we see that in those cases $w_{AA} = w_{AB}$ and $w_{BB} = w_{BA}$. Thus, (17) is satisfied when $N_A \neq N_B$. When $N_A = N_B$ the left hand side of (17) is zero, and thus there is no selection on p .

When the density regulation is the same in both patches, however, $N_A = N_B$ implies that $Q_A = Q_B$, and from (16) it can be seen that in a non-trivial equilibrium $Q_A = 1/w_{AA}$ and $Q_B = 1/w_{BB}$. Hence, this can only occur when $w_3 = w_6$ and $g = f = 0$, or when $w_1 = w_4$ and $g = f = 1$. It turns out that both these equilibria are unstable. This is proven for the case $g = f = 0$ and $w_3 = w_6$ in Appendix C. The proof for the other case is completely analogous. Therefore, this situation cannot occur.

When the forms of the functions Q_A and Q_B differ this may no longer be true. It would have to be examined for specific models whether monomorphic equilibria with $N_A = N_B$ can be stable. If so, there is no selection on p for such resident populations. However, note that this is an exceptional situation. Therefore, in general, selection will cause p to decrease in monomorphic as well as polymorphic resident populations regardless of the value of α .

3.2. Selection on α

We will now examine the direction of selection on α . First note from (5) that whenever $g = f$, β_A and β_B do not depend on α . Therefore, there is no selection on α in monomorphic resident populations.

From the previous results it follows that whatever the initial conditions, in the long run p will evolve to zero. Therefore, for polymorphic populations we only need to study the direction of selection on α for $p_r = 0$. In that

case the recurrence equations for the densities of a rare mutant are given by

$$N'_A = Q_A w_{AA} N_A, \quad N'_B = Q_B w_{BB} N_B, \quad (19)$$

where the w_{xx} depend on the mating preference of the mutant, α_m , and the values of Q_x ($x = A, B$) depend on the mating preference of the resident population, α_r . The growth rate of the mutant population equals the maximum of $Q_A w_{AA}$ and $Q_B w_{BB}$. First consider $\lambda = Q_A w_{AA}$. In that case,

$$\frac{\partial \lambda}{\partial \alpha_m} = Q_A \frac{\partial \beta_A}{\partial \alpha_m} \{ (w_1 - w_2)g + (w_2 - w_3)(1 - g) \}, \quad (20)$$

and from (5)

$$\frac{\partial \beta_A}{\partial \alpha_m} = \frac{\partial \rho_A(\alpha)}{\partial \alpha_m} (g - f). \quad (21)$$

Since $\rho_A(\alpha)$ increases in α and $w_1 > w_2 > w_3$, $\partial \lambda / \partial \alpha_m$ is larger than zero when g is larger than f . In a similar way this can be proven for $\lambda = Q_B w_{BB}$. As we know that $g > f$ for all α_r in polymorphic populations (see Appendix B), this means that there is selection in favour of an increase in mating preference at $p_r = 0$ in polymorphic populations.

3.3. Example

From the previous results we can conclude that in the long run, regardless of the initial resident population, habitat preference will become absolute ($p = 0$) and if the population is polymorphic at that point, mate preference will increase, which will eventually lead to complete reproductive isolation of the populations in the two habitats. Thus, a necessary condition for speciation is that both alleles can coexist at $p = 0$ and high values of α .

3.3.1. Stability of monomorphic equilibria

The possibility of speciation can be studied by looking at the stability conditions of monomorphic equilibria at $p = 0$. As an example, we will consider the model that was examined by Beltman et al. (2004), with Beverton-Holt density dependence (see Eq. (3)) and mating preference functions as in Eq. (2).

At $p = 0$ the recurrence equations for N_A and N_B are as given in (19), and for g and f we find from (7)

$$g' = \frac{w_{AA,1}}{w_{AA}}, \quad f' = \frac{w_{BB,1}}{w_{BB}}. \quad (22)$$

An equilibrium is stable when the Jacobian of the system of recurrence equations for N_A and N_B as well as that of the recurrence equations for g and f both have eigenvalues that are smaller than one in absolute value.

There are four types of genetically monomorphic equilibria: two where only one of the habitats is

occupied, and two where both habitats are occupied. We first consider the situation where only allele g_A occurs and only habitat A is occupied. In Appendix D.1 it is shown that, when the viabilities satisfy (9), the equilibrium is stable if

$$w_1 > 1/E, \quad w_4 < 1/E, \quad w_5 < 2w_4. \quad (23)$$

From symmetry considerations it follows that the equilibrium with only habitat B occupied and allele g_B present is stable if

$$w_6 > 1/E, \quad w_3 < 1/E, \quad w_2 < 2w_3. \quad (24)$$

Note that these conditions do not depend on α .

Next we consider the situation where both habitats are occupied (but the population is genetically monomorphic). In Appendix D.2 it is shown that, when $p = 0$, and the viabilities satisfy the conditions in (9), monomorphic equilibria where both habitats are occupied become unstable when α is sufficiently large.

When initially mating with respect to the cultural trait is random ($\alpha = 1$), a monomorphic equilibrium with only allele g_A and both habitats occupied is stable when (Appendix D.2)

$$\begin{aligned} w_1 &> 1/E, \\ w_4 &> 1/E, \\ 8w_1w_4 &> 3(w_2w_4 + w_1w_5) \\ &+ \sqrt{9(w_2^2w_4^2 + w_1^2w_5^2) - 16w_1w_2w_4w_5}. \end{aligned} \quad (25)$$

From symmetry considerations it follows that a monomorphic equilibrium with only allele g_B and both habitats occupied is stable when

$$\begin{aligned} w_6 &> 1/E, \\ w_3 &> 1/E, \\ 8w_6w_3 &> 3(w_5w_3 + w_6w_2) \\ &+ \sqrt{9(w_5^2w_3^2 + w_6^2w_2^2) - 16w_6w_5w_3w_2}. \end{aligned} \quad (26)$$

When all monomorphic equilibria are unstable at $p = 0$, a polymorphic equilibrium will be attained (since fixed points are the only possible types of attractors) after which the mating preference will increase, which leads to speciation. Whether speciation is guaranteed to occur can thus be derived from conditions (23) to (26). For instance, when $w_4 < 1/E$ and $w_3 < 1/E$, sufficient conditions for speciation are $w_5 > 2w_4$ and $w_2 > 2w_3$.

3.3.2. Conditions for speciation

The conditions for speciation to occur are in reality less strict than those derived from (23) to (26). This is because it is not necessary that all monomorphic equilibria are unstable for a polymorphic equilibrium to be stable. Even when both a monomorphic equilibrium with allele g_A present and one with allele g_B present are stable, there can in addition be a stable

polymorphic equilibrium. The evolutionary outcome then depends on the initial situation.

Fig. 1 illustrates different qualitative outcomes from numerical studies, starting at $p = 0.5$ (no habitat preference) and $\alpha = 1$ (random mating). If monomorphic equilibria are unstable at this point (as in Fig. 1a), a polymorphic equilibrium will be attained. Evolution will then proceed to lower p and higher α , even when a stable monomorphic equilibrium exists (in the black region in Fig. 1a both a monomorphic equilibrium with allele g_A present and a polymorphic equilibrium are stable).

An alternative scenario is shown in Fig. 1b. Here, at the initial point $p = 0.5$ and $\alpha = 1$ a monomorphic equilibrium with allele g_A present is stable. When we start in this equilibrium, evolution proceeds to lower p , but there is no change in α . This leads to instability of the monomorphic equilibria, after which a polymorphic equilibrium is attained, and speciation subsequently occurs.

Speciation does not occur when the system starts in a monomorphic equilibrium, and this equilibrium remains stable on the entire line $\alpha = 1$ (Fig. 1c). Numerical analysis showed that this situation is relatively rare, and occurs mainly when female fertility E is low or the difference between w_2 and w_3 and between w_4 and w_5 is

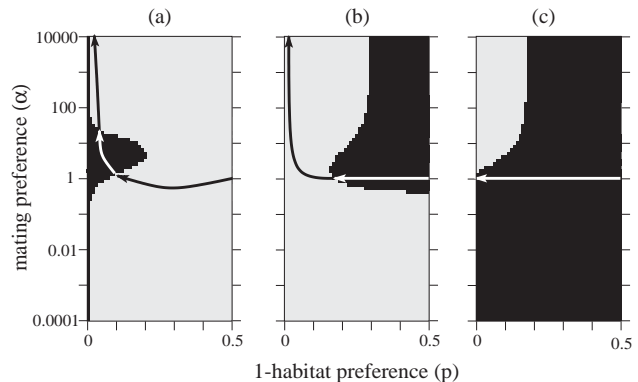


Fig. 1. Prediction of evolutionary trajectories for three qualitatively different parameter settings. In the grey regions a polymorphic equilibrium will be attained because monomorphic equilibria are unstable. In the black region the monomorphic equilibrium with allele g_A present is stable, but a polymorphic equilibrium may be stable as well. Trajectories are shown for the case that the location where young are produced and mating are initially random ($p = 0.5$ and $\alpha = 1$). In (a), a polymorphic equilibrium is immediately attained. In a part of the trajectory a monomorphic equilibrium is stable, but speciation occurs because the polymorphic equilibrium is also stable. In (b) and (c), evolution proceeds to lower p but there is no evolutionary change in α as long as the resident population is in a monomorphic equilibrium. In (b) the decrease of p causes a secondary switch toward the polymorphic equilibrium, after which completion of speciation follows. In (c) the equilibrium switch does not happen, and therefore mating with respect to the cultural trait remains random. Parameters: $K = 0.001$, $w_1 = 1.0$, $w_6 = 1.0$, and in (a) $E = 2$, $w_2 = 0.8$, $w_3 = 0.2$, $w_4 = 0.2$, $w_5 = 0.8$, in (b) $E = 10$, $w_2 = 0.4$, $w_3 = 0.0$, $w_4 = 0.2$, $w_5 = 0.6$, and in (c) $E = 10$, $w_2 = 0.4$, $w_3 = 0.2$, $w_4 = 0.6$, $w_5 = 0.8$.

small. In such cases, evolution will not lead to speciation because genetic diversification does not take place. Instead, although all individuals produce their young exclusively in one of the two habitats, mating with respect to the cultural trait is random. Hence, a clear separation in habitat exploitation of individuals takes place, but not speciation.

3.3.3. Individual-based model

To check the validity of the predicted evolutionary trajectories, we used an individual-based simulation model based on similar assumptions as the recurrence equations (a program written in C, available on request). We consider the situation that the population initially consists of females and males of type $c_A g_A g_A$ with $\alpha = 1$ and $p = 0.5$. Mating, young production, density regulation and viability selection are implemented according to the previously described life history. As in the previous model, population size is not fixed over time but depends on density regulation and viability selection. The traits p and α are inherited from both parents, using additive genetics (note that males carry but do not express these traits). Newborns can have mutations in three characteristics: (i) the probability of egg laying mistakes p , (ii) the strength of the mating preference α , and (iii) the genetic trait that determines viability ($g_A g_A$, $g_A g_B$, or $g_B g_B$). Mutations in the three traits are independent and occur each with a constant probability per generation μ . For mutations in p or α , the mutation step is drawn randomly from a normal distribution with average 0 and standard deviation σ . To avoid biases in the step size of mutations in a certain direction, we transform p and α to a linear scale that varies from $-\infty$ to ∞ before adding mutations (e.g., in the case of α this means taking the logarithm of the α -value of an individual). Subsequently, the mutation is added and the resulting values are transformed back to

their original scale. We apply the same procedure to determine the trait of a young: first the trait values of the two parents are transformed to the linear scale, subsequently their average is taken, and the resulting value is transformed back.

The mathematical analysis showed that, during the evolution of p and α , the population can switch from a boundary equilibrium that contains only one type of allele, to an internal equilibrium that contains both types of alleles (e.g., Fig. 1b). To allow for this in the individual-based model, we include mutations in the genetic trait that determines viability. This is incorporated as a homozygote ($g_A g_A$ or $g_B g_B$) mutating into a heterozygote ($g_A g_B$), or vice versa. This results in a constant, low influx of new mutants in the viability gene, allowing for the process of genetic divergence to occur at different stages of evolution.

Using these simulations we studied the evolution of the three traits over a large number of generations. We did not examine the parameter space exhaustively. Instead, we performed simulations for several parameter settings for which the mathematical analysis predicted qualitatively different results. As expected, the switching between different equilibria is not as clear cut as in the deterministic model, and over evolutionary time there is quite some variation in the evolving traits. Nevertheless, the predictions of the mathematical analysis were confirmed by the individual-based analogue. A typical simulation is shown in Fig. 2: In this example the monomorphic equilibrium with allele g_A present is stable at the initial point ($p = 0.5$ and $\alpha = 1$). There is selection toward lower p (generation 0 to approximately 50,000), and this modifies the stability of the monomorphic equilibrium. As a result, a polymorphic equilibrium is attained. Subsequently, a decrease in genetic mixing leads to completion of the speciation process (generation 50,000–1,000,000).

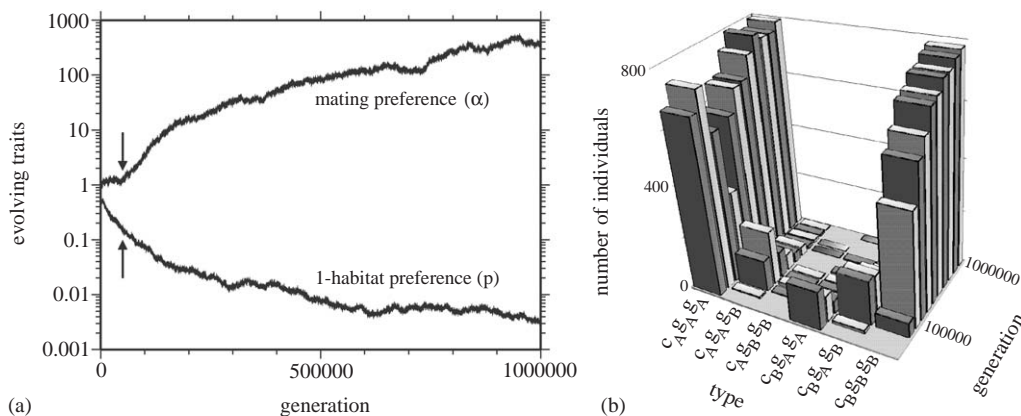


Fig. 2. (a) Evolution of habitat and mating preference in the individual-based simulation model, starting from random mating ($\alpha = 1$) and random young production ($p = 0.5$). (b) The population constitution in the course of evolution. Initially the system is in a monomorphic allele A equilibrium and cannot attain the polymorphic equilibrium. Evolution then proceeds to lower p (there is no selection on α yet). After approximately 50,000 generations (denoted by the arrows in (a)), the polymorphic equilibrium is attained. Genetic mixing then further decreases due to evolution to lower p and higher α . Parameters: $E = 10$, $w_2 = 0.6$, $w_3 = 0.2$, $w_4 = 0.2$, $w_5 = 0.6$, $\mu = 0.001$, $\sigma = 0.25$, $K = 0.0001$.

4. Discussion

We investigated a mechanism that is often ignored in the literature, speciation through the learning of habitat features. When habitat imprinting causes both habitat-dependent assortative mating and a tendency to produce young in this habitat, this may lead to speciation in three steps: (i) colonization of a new habitat, (ii) genetic divergence of the two groups by adaptation to the habitats, and (iii) a decrease of genetic mixing between the lineages. We have previously focussed on the first two steps of this speciation mechanism by analysing a gene-culture coevolutionary model (Beltman et al., 2004). Here we took a more general approach, and investigated whether there is selection in favour of decreased genetic mixing. We showed that for a large class of models there is selection toward producing young more frequently in the habitat that individuals exploit themselves. In addition, once habitat preference is strong and genetic divergence has occurred, there is selection toward stronger habitat-dependent assortative mating due to hybrid inferiority. Speciation is thus guaranteed when genetic divergence occurs at strong habitat preferences. Sufficient conditions for speciation in a particular model can therefore be derived from the stability of genetically monomorphic equilibria at strong habitat preferences. We derived these conditions for the example studied in Beltman et al. (2004). We also demonstrated that the conditions for speciation are in reality less strict because stability of monomorphic equilibria does not imply that polymorphic equilibria are unstable. When polymorphic as well as monomorphic equilibria are stable, the occurrence of speciation depends on the initial situation. For instance, genetic divergence may not occur initially, but evolutionary changes in habitat preference may render a monomorphic equilibrium unstable. In that case, genetic diversification followed by speciation will occur secondarily (e.g., Fig. 1b). Finally, we investigated an individual-based analogue of the model of Beltman et al. (2004), and confirmed the occurrence of speciation predicted by the mathematical analysis.

The models for migration modification, studied by Karlin and McGregor (1972), Balkau and Feldman (1973), and Karlin and McGregor (1974), are closely related to ours. However, there it is assumed that mating preference is absolute, i.e. that α is infinitely large. Speciation is then complete when the migration fraction is zero (or, in our terminology the habitat preference equals one). Furthermore, they do not consider the dynamics of the population densities but assume that these have positive equilibrium values. They showed that for several combinations of viability selection in the two patches, including the ones we consider, there is selection towards decreased migration. Our results generalize theirs in two respects: First, we showed that

if the viabilities satisfy the inequalities in (9) selection towards decreased migration occurs regardless of the value of the mating preference; Second, we explicitly considered a wide variety of models for local density dependence and allowed for the possibility of local extinction. Furthermore, we derived conditions for completion of reproductive isolation through selection towards increased mating preferences.

The decrease of genetic mixing due to hybrid inferiority was originally hypothesized by Dobzhansky (1940) and the process has been termed reinforcement by Blair (1955). It was introduced in the context of geographical speciation: an initial allopatric phase during which genetic differences accumulate is followed by a sympatric phase, during which reinforcement results in reproductive character displacement. According to several theoretical studies, reinforcement of prezygotic isolation is possible under certain conditions (e.g., Liou and Price, 1994; Servedio and Kirkpatrick, 1997; Servedio, 2000; Kirkpatrick, 2001; Sadedin and Littlejohn, 2003; Servedio and Sætre, 2003). Most importantly, it was found that a high hybrid viability and high recombination between alleles affecting mate choice and those affecting hybrid viability oppose reinforcement (Felsenstein, 1981; Trickett and Butlin, 1994; Servedio, 2000). The final step of the speciation mechanism we study is similar to the reinforcement process, although it operates in a different context. Here, the decrease of genetic mixing appears to lack the relatively stringent conditions under which reinforcement is expected to occur. Probably the crucial factor causing this difference in results is the absence of the opposing effect of recombination: Because learning instead of a genetic mechanism determines which of the habitats is preferred, recombination cannot destroy the association between alleles that determine viability and the learned preference. Therefore, our results do not contradict the predictions of previous models that recombination opposes reinforcement (Felsenstein, 1981; Trickett and Butlin, 1994; Servedio, 2000).

We assumed that the trait that determines viability is based on only one locus. It is known that the number of loci for an ecological trait can influence the probability of sympatric speciation (e.g., Kondrashov, 1986). We think that an increase in the number of viability loci in our model may indeed make the step of genetic diversification (studied in Beltman et al., 2004) more difficult, because recombination between these multiple loci may destroy associations between them. However, once genetic diversification has been achieved, the reinforcement step is likely to occur without problem because recombination again forms no obstacle there (see above). However, the presence of multiple viability loci is an interesting extension of the model and remains to be investigated.

We assumed that female mate choice is not costly. It would probably be most realistic to make the cost of female choosiness dependent on the frequency of the preferred males (as is for example the case in Gavrillets and Boake, 1998; Beltman et al., 2003). We expect that this assumption would not dramatically influence the reinforcement step, because, once the population has reached the polymorphic equilibrium, males of both cultural traits are abundant (see for example Fig. 2b). However, as we already discussed in Beltman et al. (2004), the step of genetic diversification is likely to become more difficult when mate choice is costly, because at that time the preferred males may not yet be present in high frequencies.

The learning of habitat features occurs in many species. In the case of the brood-parasitic finches the learning of foster species' songs causes a "true" mating and egg laying preference. In most other cases these will be a by-product of feeding preference (e.g., in phytophagous insects). Our assumption that the preference to produce young in a particular habitat and the mating preference are independent traits is then violated. Instead, in such cases there is a single underlying trait that causes the two effects. It is not likely that this would prevent speciation, because as we showed selection on the two effects usually operates in concert toward speciation. Although we did not test this, we thus expect that such a coupling would speed up rather than hamper the speciation process.

We have studied speciation under the assumption that the learning of habitat features is present from the start. However, we assumed that the effect that such learning has on mating behaviour and location where young are produced can change in the course of evolution. Indeed, we included a scenario where there is initially no effect of learning on mating and location where young are produced (this is the case at $p = 0.5$ and $\alpha = 1$). The evolutionary origin of the learning of habitat features, however, is not yet completely understood. It may have evolved for reasons unrelated to the speciation mechanism we study or, alternatively, the evolution of learning and subsequent speciation may be due to adaptation to the environment. For example, brood-parasitic finches use their foster species' songs for mate choice and host searching. Probably, their ancestors were generalist brood parasites and may not have learned the foster species' songs (for a discussion on this topic see Beltman et al., 2003). The learning and use of these songs may have evolved in response to counteradaptations of the hosts against brood parasitism. Learning their songs helps to specialize on the parasitization of a particular foster species. Among brood parasites there is no other group than the Viduidae where the copying of foster species' song occurs (Davies (2000)). However, brown-headed cowbirds are able to discriminate between songs of different host species (Hauber et al. (2002)), although

they are generalist brood parasites. Possibly, the above-described process may occur in this group as well, leading to the specialization of cowbirds' descendants on particular hosts and maybe also to the copying of their songs.

Previous models of speciation have usually ignored the possible role of learning processes, but instead focused on the geographical mode of speciation (see references in Introduction). However, as we discussed previously (Beltman et al., 2004) the learning of habitat features provides an equally powerful, analogous mechanism of generating assortative mating as geographical separation. The possible importance of the learning of habitat features on speciation has been hinted at by several researchers (e.g., Thorpe, 1945; Maynard Smith, 1966; Rice, 1984; Kondrashov and Mina, 1986; West-Eberhard, 2003), but has received relatively little attention so far. The present study (in combination with Beltman et al., 2004) demonstrates the effectiveness of this speciation mechanism theoretically. We think that a stronger experimental and theoretical focus on the role of learning in speciation has much potential for increasing our understanding of the evolution of new species.

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Appendix A. Derivation of recurrence relations (6) and (7)

For notational convenience we define the following matrices:

$$W_A = \begin{pmatrix} w_1 & 0 & 0 \\ 0 & w_2 & 0 \\ 0 & 0 & w_3 \end{pmatrix}, \quad W_B = \begin{pmatrix} w_4 & 0 & 0 \\ 0 & w_5 & 0 \\ 0 & 0 & w_6 \end{pmatrix} \quad (\text{A.1})$$

and

$$M_A = \begin{pmatrix} \beta_A & \frac{1}{2}\beta_A & 0 \\ (1 - \beta_A) & \frac{1}{2} & \beta_A \\ 0 & \frac{1}{2}(1 - \beta_A) & (1 - \beta_A) \end{pmatrix}. \quad (\text{A.2})$$

The matrix M_B is the same as M_A , but with β_B substituted for β_A . If we denote the type densities by a vector $N = (N_1, \dots, N_6)^T$ (as in Table 1), the population dynamics are described by

$$N' = MN, \quad (\text{A.3})$$

where M is a 6×6 matrix with the following structure:

$$M = \begin{pmatrix} (1-p)Q_A W_A M_A & pQ_A W_A M_B \\ pQ_B W_B M_A & (1-p)Q_B W_B M_B \end{pmatrix}. \quad (\text{A.4})$$

Note that the equations given in the Appendix of Belman et al. (2004) can be cast in this form too, with the definitions of $\rho_x(\alpha)$ and Q_x as in Eqs. (2) and (3).

The dimension of the state space can be reduced by considering the following state variables in stead of type densities:

$$\begin{aligned} H_1 &= N_1 + \frac{1}{2}N_2, & H_2 &= N_3 + \frac{1}{2}N_2, \\ H_3 &= N_4 + \frac{1}{2}N_5, & H_4 &= N_6 + \frac{1}{2}N_5, \end{aligned} \quad (\text{A.5})$$

for example $2H_1$ is the density of allele g_A in habitat A .

We will now show that

$$H' = RH, \quad (\text{A.6})$$

where H is the vector $(H_1, \dots, H_4)^T$, and

$$R = \begin{pmatrix} (1-p)Q_A R_{AA} & pQ_A R_{AB} \\ pQ_B R_{BA} & (1-p)Q_B R_{BB} \end{pmatrix}. \quad (\text{A.7})$$

Here,

$$R_{AA} = \begin{pmatrix} w_1\beta_A + \frac{1}{2}w_2(1-\beta_A) & \frac{1}{2}w_2\beta_A \\ \frac{1}{2}w_2(1-\beta_A) & \frac{1}{2}w_2\beta_A + w_3(1-\beta_A) \end{pmatrix}. \quad (\text{A.8})$$

In R_{AB} , β_A is substituted by β_B in this matrix. In R_{BA} and R_{BB} , w_1 , w_2 and w_3 are replaced by respectively w_4 , w_5 and w_6 , and in R_{BB} , moreover, β_B is substituted for β_A .

Let H_A be the vector $(H_1, H_2)^T$, $H_B = (H_3, H_4)^T$, and $F_A = (N_1, N_2, N_3)^T$, $F_B = (N_4, N_5, N_6)^T$ then $H_A = XF_A$, and $H_B = XF_B$ with

$$X = \begin{pmatrix} 1 & \frac{1}{2} & 0 \\ 0 & \frac{1}{2} & 1 \end{pmatrix}. \quad (\text{A.9})$$

From (A.4) it follows that

$$H'_A = (1-p)Q_A XW_A M_A F_A + pQ_A XW_A M_B F_B. \quad (\text{A.10})$$

It is easily verified that

$$XW_A M_A = R_{AA}X \quad \text{and} \quad XW_A M_B = R_{AB}X, \quad (\text{A.11})$$

which implies that

$$H'_A = (1-p)Q_A R_{AA}H_A + pQ_A R_{AB}H_B. \quad (\text{A.12})$$

The relation

$$H'_B = pQ_B R_{BA}H_A + (1-p)Q_B R_{BB}H_B \quad (\text{A.13})$$

is derived analogously.

The relations in (6) can be derived by noting that

$$N_A = H_1 + H_2 = H_A^T \begin{pmatrix} 1 \\ 1 \end{pmatrix} \quad (\text{A.14})$$

and similarly $N_B = H_3 + H_4$. The recurrence equations for g and f follow from $g' = H'_1/N'_A$ and $f' = H'_3/N'_B$.

Appendix B. Proof that $g \geq f$ with equality only when $g = 0$ or 1

From the recurrence equation for g in (7) and (16) it follows that at equilibrium

$$(1-p)N_A\{w_{AA,1} - gw_{AA}\} + pN_B\{w_{AB,1} - gw_{AB}\} = 0. \quad (\text{B.1})$$

Further,

$$\begin{aligned} w_{AA,1} - gw_{AA} &= \beta_A \left\{ \frac{1}{2}w_2 + g(1-g)((w_1 - w_2) - (w_2 - w_3)) \right\} \\ &\quad + (w_2 - w_3)g(1-g) - \frac{1}{2}w_2g, \\ w_{AB,1} - gw_{AB} &= \beta_B \left\{ \frac{1}{2}w_2 + f(1-g)(w_1 - w_2) - g(1-f)(w_2 - w_3) \right\} \\ &\quad + w_2f(1-g) - w_3g(1-f) - \frac{1}{2}w_2f. \end{aligned} \quad (\text{B.2})$$

We will now show that if $f > g$ both these expressions are positive, which contradicts (B.1). First note that $\frac{1}{2}w_2 + g(1-g)((w_1 - w_2) - (w_2 - w_3))$ is positive. This is obviously true when $(w_1 - w_2) > (w_2 - w_3)$. When $(w_1 - w_2) < (w_2 - w_3)$ this function has a global minimum at $g = \frac{1}{2}$, and obviously its value is larger than zero at this point. If $f > g$ then the multiplication factor for β_B in the second equation above is larger than this value, so that value must then be positive too. From (5) it further follows that in this case β_A and β_B are both larger than g . Therefore,

$$\begin{aligned} w_{AA,1} - gw_{AA} &> g \left\{ \frac{1}{2}w_2 + g(1-g)((w_1 - w_2) - (w_2 - w_3)) \right\} \\ &\quad + (w_2 - w_3)g(1-g) - \frac{1}{2}w_2g \\ &= g(1-g)\{g(w_1 - w_2) + (1-g) \times (w_2 - w_3)\} > 0, \end{aligned} \quad (\text{B.3})$$

and

$$\begin{aligned}
 w_{AB,1} - gw_{AB} &> g\left\{\frac{1}{2}w_2 + f(1-g)(w_1 - w_2) - g(1-f)(w_2 - w_3)\right\} \\
 &+ w_2f(1-g) - w_3g(1-f) - \frac{1}{2}w_2f \\
 &= f\left\{g(1-g)(w_1 - w_2) + g^2(w_2 - w_3) + w_2(1-g) + w_3g - \frac{1}{2}w_2\right\} \\
 &- \frac{1}{2}w_2g \\
 &= f\{g(1-g)((w_1 - w_2) + (w_2 - w_3)) + \frac{1}{2}w_2\} - \frac{1}{2}w_2g \\
 &> g\{g(1-g)((w_1 - w_2) + (w_2 - w_3))\} > 0.
 \end{aligned} \tag{B.4}$$

Thus, if $f > g$ both expressions on the left-hand side of (B.1) are positive, which cannot be true. Therefore f must be smaller than or equal to g .

When g is equal to f , it can be seen from (5) that $\beta_A = \beta_B = g$. And from (B.1) and (B.2) we find

$$\begin{aligned}
 g\{g(1-g)((w_1 - w_2) - (w_2 - w_3))\} \\
 + (w_2 - w_3)g(1-g) = 0,
 \end{aligned} \tag{B.5}$$

with solutions $g = 0$ or 1 . The other solution must satisfy

$$g\{((w_1 - w_2) - (w_2 - w_3))\} + (w_2 - w_3) = 0, \tag{B.6}$$

and so

$$g = \frac{(w_2 - w_3)}{(w_2 - w_3) - (w_1 - w_2)}. \tag{B.7}$$

However, there is no g between 0 and 1 that satisfies this equation, which means that there are no polymorphic equilibria with g equal to f .

Appendix C. Proof that when $w_3 = w_6$ the equilibrium with $g = f = 0 \wedge N_A = N_B$ is unstable

A necessary condition for stability of this equilibrium is that the absolute values of all eigenvalues of the Jacobian of the recurrence equations for N_A and N_B in (6) are smaller than one. The partial derivatives are

$$\begin{pmatrix} \frac{\partial Q_A}{\partial N_A}((1-p)w_{AA}N_A + pw_{AB}N_B) & \frac{\partial Q_A}{\partial N_B}((1-p)w_{AA}N_A + pw_{AB}N_B) \\ + (1-p)Q_Aw_{AA} & + pQ_Aw_{AB} \\ \frac{\partial Q_B}{\partial N_A}(pw_{BA}N_A + (1-p)w_{BB}N_B) & \frac{\partial Q_B}{\partial N_B}(pw_{BA}N_A + (1-p)w_{BB}N_B) \\ + pQ_Bw_{BA} & + (1-p)Q_Bw_{BB} \end{pmatrix}. \tag{C.1}$$

In the considered case

$$w_{AA} = w_{AB} = w_{BB} = w_{BA} = w, \tag{C.2}$$

and when $N_A = N_B = N$ the equilibrium conditions lead to

$$Q_Aw_{AA} = Q_Bw_{BB} = 1. \tag{C.3}$$

Furthermore, when density regulation is similar in the two habitats we know that at the equilibrium where $N_A = N_B$, $\partial Q_A / \partial N_A = \partial Q_B / \partial N_B$ and $\partial Q_A / \partial N_B = \partial Q_B / \partial N_A$. Denote these values by respectively γ and η . The Jacobian then becomes

$$\begin{pmatrix} \gamma wN + (1-p) & \eta wN + p \\ \eta wN + p & \gamma wN + (1-p) \end{pmatrix}. \tag{C.4}$$

It is easily shown that the largest eigenvalue of this matrix is larger than one, which implies that the equilibrium is unstable.

Appendix D. Stability conditions for monomorphic equilibria at $p = 0$

From (3) it can be derived that when $p = 0$:

$$\frac{\partial Q_A}{\partial N_B} = \frac{\partial Q_B}{\partial N_A} = 0, \quad \frac{\partial Q_x}{\partial N_x} = -KQ_x^2 \quad (x = A, B). \tag{D.1}$$

Hence, the matrix of partial derivatives for the system $\{N_A, N_B\}$ equals (see (C.1))

$$\begin{pmatrix} -KQ_A^2w_{AA}N_A + Q_Aw_{AA} & 0 \\ 0 & -KQ_B^2w_{BB}N_B + Q_Bw_{BB} \end{pmatrix}. \tag{D.2}$$

D.1. One habitat occupied

We consider the equilibrium with $g = 1, N_A > 0$ and $N_B = 0$. At this equilibrium we see from (2) that $\rho_A(x) = 1, \rho_B(x) = 0$, from (5) that $\beta_A = \beta_B = 1$, and from (8) that $w_{AA,1} = w_{AA} = w_1$ and $w_{BB,1} = w_{BB} = w_4$. Filling in $N_B = 0$ in the second equation in (3) gives $Q_B = E$. From the equilibrium condition for N_A it follows that $Q_A = 1/w_1$. Substituting these values in (D.2) gives the Jacobian for $\{N_A, N_B\}$:

$$\begin{pmatrix} -K\frac{1}{w_1}N_A + 1 & 0 \\ 0 & Ew_4 \end{pmatrix}. \tag{D.3}$$

From $Q_A = 1/w_1$ we can derive that the equilibrium value of N_A equals $\frac{1}{K}(w_1 - \frac{1}{E})$, so the eigenvalues are

$$\lambda_1 = \frac{1}{Ew_1}, \quad \lambda_2 = Ew_4. \tag{D.4}$$

We now turn to the Jacobian for g and f . From (5) we find

$$\begin{aligned} \left(\frac{\partial \beta_A}{\partial g}\right)_{g=1, f=0} &= \rho_A(\alpha) = 1, \\ \left(\frac{\partial \beta_A}{\partial f}\right)_{g=1, f=0} &= 1 - \rho_A(\alpha) = 0, \\ \left(\frac{\partial \beta_B}{\partial g}\right)_{g=1, f=0} &= 1 - \rho_B(\alpha) = 1, \\ \left(\frac{\partial \beta_B}{\partial f}\right)_{g=1, f=0} &= \rho_B(\alpha) = 0, \end{aligned} \quad (\text{D.5})$$

and from (8)

$$\begin{aligned} \left(\frac{\partial w_{AA,1}}{\partial g}\right)_{g=1, f=0} &= 2\left(w_1 - \frac{1}{2}w_2\right), \\ \left(\frac{\partial w_{AA}}{\partial g}\right)_{g=1, f=0} &= 2(w_1 - w_2), \\ \left(\frac{\partial w_{AA,1}}{\partial f}\right)_{g=1, f=0} &= \left(\frac{\partial w_{AA}}{\partial f}\right)_{g=1, f=0} = 0, \\ \left(\frac{\partial w_{BB,1}}{\partial g}\right)_{g=1, f=0} &= \frac{1}{2}w_5, \\ \left(\frac{\partial w_{BB}}{\partial g}\right)_{g=1, f=0} &= w_5, \\ \left(\frac{\partial w_{BB,1}}{\partial f}\right)_{g=1, f=0} &= w_4 - \frac{1}{2}w_5, \\ \left(\frac{\partial w_{BB}}{\partial f}\right)_{g=1, f=0} &= w_4 - w_5. \end{aligned} \quad (\text{D.6})$$

Substituting these values in the partial derivatives of g' and f' gives the Jacobian:

$$\begin{pmatrix} \frac{w_2}{w_1} & 0 \\ -\frac{1}{2}\frac{w_5}{w_4} & \frac{1}{2}\frac{w_5}{w_4} \end{pmatrix} \quad (\text{D.7})$$

with eigenvalues

$$\lambda_3 = \frac{w_2}{w_1}, \quad \lambda_4 = \frac{1}{2}\frac{w_5}{w_4}. \quad (\text{D.8})$$

For an equilibrium to be stable, all eigenvalues should be smaller than one. This is true for λ_3 because $w_2 < w_1$. The stability conditions that follow from the other eigenvalues in (D.4) and (D.8) are summarized in (23) of the main text.

D.2. Both habitats occupied

We consider the equilibrium at which $g = f = 1$. At this equilibrium we have: $\beta_A = \beta_B = 1$, and $w_{AA,1} = w_{AA} = w_1$, $w_{BB,1} = w_{BB} = w_4$. From the equilibrium condition for N_A and N_B it follows that $Q_A = 1/w_1$ and $Q_B = 1/w_4$. From $Q_A = 1/w_1$ we can derive that the

equilibrium value of N_A equals $\frac{1}{K}(w_1 - \frac{1}{E})$. Similarly, the equilibrium value of N_B is $\frac{1}{K}(w_4 - \frac{1}{E})$. Substituting these values in (D.2) gives the eigenvalues:

$$\lambda_1 = \frac{1}{Ew_1}, \quad \lambda_2 = \frac{1}{Ew_4}, \quad (\text{D.9})$$

which gives the first two conditions in (25).

From (5) we find

$$\begin{aligned} \left(\frac{\partial \beta_A}{\partial g}\right)_{g=f=1} &= \rho_A(\alpha), \\ \left(\frac{\partial \beta_A}{\partial f}\right)_{g=f=1} &= 1 - \rho_A(\alpha), \\ \left(\frac{\partial \beta_B}{\partial g}\right)_{g=f=1} &= 1 - \rho_B(\alpha), \\ \left(\frac{\partial \beta_B}{\partial f}\right)_{g=f=1} &= \rho_B(\alpha), \end{aligned} \quad (\text{D.10})$$

and from (8)

$$\begin{aligned} \left(\frac{\partial w_{AA,1}}{\partial g}\right)_{g=f=1} &= (w_1 - \frac{1}{2}w_2)(1 + \rho_A(\alpha)), \\ \left(\frac{\partial w_{AA}}{\partial g}\right)_{g=f=1} &= (w_1 - w_2)(1 + \rho_A(\alpha)), \\ \left(\frac{\partial w_{AA,1}}{\partial f}\right)_{g=f=1} &= (1 - \rho_A(\alpha))(w_1 - \frac{1}{2}w_2), \\ \left(\frac{\partial w_{AA}}{\partial f}\right)_{g=f=1} &= (1 - \rho_A(\alpha))(w_1 - w_2). \end{aligned} \quad (\text{D.11})$$

Substituting these values in the partial derivatives of g' and using symmetry arguments for f' we find the Jacobian matrix

$$\begin{pmatrix} (1 + \rho_A(\alpha))\left(\frac{1}{2}\frac{w_2}{w_1}\right) & (1 - \rho_A(\alpha))\left(\frac{1}{2}\frac{w_2}{w_1}\right) \\ (1 - \rho_B(\alpha))\left(\frac{1}{2}\frac{w_5}{w_4}\right) & (1 + \rho_B(\alpha))\left(\frac{1}{2}\frac{w_5}{w_4}\right) \end{pmatrix}. \quad (\text{D.12})$$

Both $\rho_A(\alpha)$ and $\rho_B(\alpha)$ increase monotonically in α . These functions equal zero when $\alpha = 0$ and tend to one as α becomes infinitely large (see Eq. (2)).

At $\alpha = 1$ the function values equal 0.5, which is of special interest because it represents random mating. When α equals one, the Jacobian becomes

$$\begin{pmatrix} \frac{3}{4}\frac{w_2}{w_1} & \frac{1}{4}\frac{w_2}{w_1} \\ \frac{1}{4}\frac{w_5}{w_4} & \frac{3}{4}\frac{w_5}{w_4} \end{pmatrix}, \quad (\text{D.13})$$

with eigenvalues

$$\lambda_{3,4} = \frac{3(w_2w_4 + w_1w_5) \pm \sqrt{9(w_2^2w_4^2 + w_1^2w_5^2) - 16w_1w_2w_4w_5}}{8w_1w_4}. \quad (\text{D.14})$$

The expression under the root is always positive because $w_1 > w_2$ and $w_5 > w_4$. Hence, the eigenvalues are real numbers. The last stability condition in (25) at $p = 0$ and $\alpha = 1$ then follows from demanding that the eigenvalue with the positive root is smaller than one.

In the limit for $\alpha \rightarrow \infty$ the Jacobian tends to

$$\begin{pmatrix} \frac{w_2}{w_1} & 0 \\ 0 & \frac{w_5}{w_4} \end{pmatrix} \quad (\text{D.15})$$

with eigenvalues

$$\lambda_3 = \frac{w_2}{w_1}, \quad \lambda_4 = \frac{w_5}{w_4}. \quad (\text{D.16})$$

Because $w_2 < w_1$ and $w_5 > w_4$, λ_3 is always smaller than one and λ_4 is always larger than one. Hence, for large values of α , the equilibrium will be unstable.

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