Times needed to evolve mating cues under allopatry and parapatry

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Abstract

The time needed for the evolution of mating cues that distinguish species, such as species-specific songs or plumage coloration in birds, has received little attention. Aiming to gain some understanding of the timing of the evolutionary process we here present models of how mating cues evolve in populations split into subpopulations between which there may (parapatry) or may not (allopatry) be migration. Mating cues can be either neutral or directly selected. In models in which evolution commences with a substitution at a neutral mating-cue locus, under allopatry there is no selection on the mating cue, but under parapatry, selection may be induced on the mating cue by the selective conditions in the subpopulations, and the migration rates between them. We use simulation to calculate how selection pressures on mating cues then depend on selective conditions in subpopulations and migration rates between them. In the second part of the paper, we demonstrate quantitatively how the resulting selection pressures on new mating cues together with mutation rate affect speciation time. Our results suggest that species-specific songs or plumage colorations that are selectively neutral evolve faster under parapatry than under allopatry, and this may explain the short speciation times that are sometimes reported. Although our modelling assumptions are restrictive so that caution is needed in comparing the results to empirical data, we hope that our main results, showing quantitatively how parapatry can reduce speciation times, will encourage further work relaxing model assumptions or studying different models of mate choice.

Keywords: sexual imprinting, phenotype matching, pseudomagic traits, fixation time, fixation probability, nascent speciation

Introduction

Speciation in many species is thought to occur after a period of allopatry, during which a population becomes split into geographically isolated subpopulations that remain separate and diverge over thousands of generations, and eventually can no longer interbreed (see Tobias et al., 2020 for a review of speciation in birds). The times needed for speciation under allopatry are long if mating cues are neutral, as we shall see, but there are many examples in the literature of much more rapid speciation. Noteworthy bird examples occur in the tanagers including southern capuchinos seedeaters (*Sporophila*) and Darwin's finches. The Neotropical southern capuchinos radiated within the last one million years to form 10 predominantly sympatric species that differ primarily in male plumage coloration and song (Campagna et al. 2012, 2017; Turbek et al., 2021). Eight of these species emerged in less than 50,000 generations (Hejase et al., 2020). In Darwin's finches, radiations of ground and tree finches began around 100,000–300,000 years ago (Lamichhaney et al., 2015). Other examples of very fast speciation are found in the fishes (Rabosky et al., 2013), with cichlids having evolved more than 500 variously coloured species in Lake Victoria in 6,000 years (Meier et al., 2023), and European flounders have speciated in the Baltic Sea in 3,000 generations (Momigliano et al., 2017). Examples in other taxa include two sea star species, which have diverged in 6,000 years (Puritz et al., 2012), and Hawaiian Laupala crickets, where species differences are

characterized by differences in male courtship song and the speciation rate has been 4.2 new species per million years (Mendelson & Shaw, 2005).

The evolution of distinctive mating cues is closely associated with speciation because of the importance of choosing a mate of the right species, so rapid speciation is likely to depend on rapid divergence in mating cues. Aiming to gain some understanding of this divergence we here present models of how mating cues evolve in populations split into subpopulations between which there may (parapatry) or may not (allopatry) be migration as shown in Table 1. In our models, selection may (Type 1) or may not (Type 2) act on the mating cue. In Type 2 models, the mating cue is neutral. But although the mating cue is neutral, under Type 2 parapatry selection is induced on mating cues provided the population exists in locally adapted subpopulations, as we will see.

Parapatric speciation is thought to be more likely under phenotype matching than under alternative methods of mate choice (Kopp et al., 2018). Phenotype matching means that individuals with a particular mating cue tend to mate with others with the same mating cue. For certain combinations of migration rates and selection coefficients, with phenotype matching parapatric speciation occurs readily in locally adapted populations (Felsenstein, 1981; Sibly & Curnow, 2022). We consider here two types of parapatric speciation, both of which assume the existence of phenotype matching and migration between subpopulations which differ in

Table 1. Classification of models according to whether the mating cues are adaptive or neutral, and whether or not there is migration between populations. In the models analysed here complete phenotype matching is assumed, meaning that individuals with a particular mating cue only mate with others with the same mating cue.

		Mating cues	
		Adaptive	Neutral
Migration between subpopulations?	No	Type 1 Allopatry	Type 2 Allopatry
	yes	Type 1 Parapatry	Type 2 Parapatry

ecological selection pressures. In the first, which we designate Type 1 parapatric speciation, adaptive traits are used as mating cues, i.e., are "magic traits". The term magic trait refers here to an adaptive trait that is used as a mating cue (see, e.g., Kopp et al., 2018). An example is choosing mates on the basis of having a beak size that is advantageous in the niche in which the population lives. The combination of phenotype matching and a magic trait is known to be particularly favourable for speciation (Smadja and Butlin, 2011). Treating a related case, Servedio & Burger (2020) used a deterministic haploid model to analyse what they term "pseudomagic traits", in which a mating cue locus and an ecological trait locus are separate but linked. Servedio & Burger (2020) show that evolutionary outcomes are similar to Type 1 if the ecological trait locus is tightly linked to the mating cue locus. Alternatively, Sibly & Curnow (2022) used a deterministic diploid model to show quantitatively how local adaptation induces selection on neutral mating cues for the case that a locus controlling mating cues is not linked to a locus controlling local adaptation. We refer to this as Type 2 parapatric speciation. Speciation occurs in Sibly & Curnow's (2022) model because individuals in each niche avoid mating with incomers who predominantly carry disadvantageous alleles. Whether the population will speciate depends in Sibly & Curnow's (2022) model as in Felsenstein's (1981) model on the balance between migration and selection: Some selection at the ecological locus is necessary. Existing models of divergence in mating cues have not calculated speciation times, hence the need for the present paper.

Speciation times in parapatric models depend on mutation and migration rates and the intensity of selection, but the functional relationships between them cannot be derived analytically, because no theory exists of how the intensity of selection on mating cues depends on migration rates between subpopulations and the ecological selective conditions within them. We tackle this latter problem by simulation of a simplified model of Type 2 parapatry in the first part of our paper. This allows the calculation of how effective selection pressures on mating cues depend on selective conditions in subpopulations and migration rates between them. In the second part of the paper, we demonstrate quantitatively how the resulting effective selection pressure on a new mating cue together with mutation rate affects speciation time. Although waiting times for speciation have been considered previously this has been mainly in models where genetic incompatibilities accumulate or populations respond to divergent selection (see, e.g., Gavrilets, 2014). In this paper, the focus is on mating isolation and so the question addressed here is quite new.

Section 1: Dependence of the effective mating-cue selection coefficient on selective regimes within and migration rates between two niches in a Type 2 parapatric population

The objective of this section is to use simulation to calculate how effective selection pressures on mating cues depend on selective conditions in two subpopulations and migration rates between them. This has to be done using a specific model and we use Sibly & Curnow's (2022) two-niche model with phenotype matching in which the loci controlling the mating cues are not linked to the loci controlling local adaptation—i.e., Type 2 parapatric speciation. Sibly & Curnow's (2022) results were based on simulations that assumed complete phenotype matching so that individuals only mate with others who have the same mating cue, an infinite population divided equally between two niches, migration rates the same in both directions and local adaptation the result of two alleles P and Q at a single diploid locus. The mating cue is controlled by a single locus with only D alleles prior to a new mating cue produced by a C allele arising by mutation. C is assumed dominant to D and the CD locus is not linked to the PQ locus. The mating cues on their own are assumed to be neutral so that without local adaptation and migration between niches there is no selection at the mating cue locus. In the presence of local adaptation and migration, however, selection does act at the mating cue locus and leads to speciation. Speciation occurs because eventually there are only two genotypes left in the population, CC and DD, and neither will mate with the other. The strength of selection during the evolutionary process is measured by a selection coefficient which we here term the *effective selection coefficient* on the new mating cue. The analysis presented here is needed because effective selection coefficients on mating cues were not calculated by Sibly & Curnow (2022) but knowledge of their values is needed to see how selection pressures on mating cues relate to migration rates between subpopulations and the ecological selective conditions within them. Knowledge of effective selection coefficients allows us to make links to speciation times in Section 2. In this section, we consider how the effective selection coefficient on the new mating cue relates to migration rates and to the selection coefficients operating on the adaptive trait—positive in one niche and negative the other.

Methods

In Sibly & Curnow's (2022) model generations are discrete and individuals die after mating. At the start of each generation individuals in each niche mate with others of the same mating-cue phenotype, and all mating individuals obtain the same number of offspring. We assume that all individuals irrespective of the frequency of their mating cue do mate. The number of offspring of each genotype that survives in each niche is the product of its initial frequency and its fitness. Population regulation then returns population numbers to their initial values, after which some individuals migrate between niches. Local adaptation is the result of two alleles P and Q at a single locus. PP has fitness 1 in both niches. PQ and QQ have fitness $1 + s_1$ in niche 1 and $1 + s_2$ in niche 2, where s_2 is assumed positive and s_1 negative. Whether or not local adaptation occurs depends not only on the values of s_1 and s_2 and the level of dominance of Q, but also on the migration rates between the two niches. Further details of the model including the recursion equations showing how

genotype frequencies change between generations are given in Supplementary material 1.

For the case that population sizes in the two niches are equal and migration rates in both directions are the same, Sibly & Curnow (2022) used a deterministic simulation of the evolutionary process to map the set of migration and selection rates for which local adaptation occurs and showed that in all analysed cases, the evolutionary outcome is speciation if a C allele coding for a new neutral mating cue arises by mutation. The C allele was originally introduced into the simulation at low frequency (0.05%). As the C allele spread the CD and PQ heterozygotes were eliminated, so that eventually the population consisted only of the CCQQ and DDPP genotypes. The C allele increased in frequency approximately exponentially until close to its final value (example in Figure 1). During the exponential phase the effective selection coefficient on the C allele (s) was calculated as Δ(frequency)/(frequency) when frequency first exceeded 10%, using simulations carried out as in Sibly & Curnow (2022). By repeating this procedure over a range of values of s_1, s_2, and migration rate m, a picture was built up of the dependence of s on s_1, s_2, and m.

Results

Figure 2 shows how the effective selection coefficient on the C allele, s, is affected by migration rate m and the selection coefficient s_2 in niche 2 for two values of s_1, $s_1 = -0.05$ and $s_1 = -0.40$, where s_1 and s_2 represent the strength of selection for the Q allele in niches 1 and 2, respectively. Note first that effective selection for C, i.e., $s > 0$, only occurs within a restricted region in the m s_2 plane. This is the region in which local adaptation at the PQ locus is possible. Outside this region C is not selected or is selected against, so $s \leq 0$. The highest values of the effective selection coefficient are 0.013 in Figure 2A and 0.12 in Figure 2B. They occur on horizontal ridges where the opposing selection conditions in the two niches are close to being equal and opposite. Thus, the ridge occurs at $s_2 \sim 0.05$ in Figure 2A and at $s_2 \sim 0.40$ in Figure 2B. High values of s also occur on vertical ridges at $m \sim 0.05$ in Figure 2A and $m \sim 0.15$ in Figure 2B. Either side of the

ridges, s declines down to zero at the edges of the region in which local adaptation is possible. To the left s declines to zero when $m = 0$, where $m = 0$ corresponds to allopatry since there is no migration between niches. Towards the bottom of Figure 2, s declines steeply and becomes negative as s_2 declines to zero. When s_2 is zero, s is negative because there is no selection for CCQQ in niche 2 and selection against CCQQ in niche 1. s is zero at the upper right of the figure, because local adaptation is not possible there: The region consists entirely of Q alleles, and there is then no selection for C alleles.

In sum, as in Sibly & Curnow (2022), there is no selection for the mating cue outside the region is which local adaptation occurs. Within the region of local adaptation, effective selection on the mating cue seemingly increases with migration rate from zero up to some maximum, and then declines back down to zero at the edge of the adaptive region. Effective selection on the mating cue is also relatively high if the opposing selection conditions in the two niches are approximately equal and opposite, i.e., $s_2 \sim -s_1$.

The cases analysed assume complete phenotype matching, populations divided equally between two niches, migration rates the same in both directions, and local adaptation is the result of two alleles P and Q at a single locus. The effective selection coefficient on the mating cue s is at most 0.12 in the cases analysed in Figure 2, within the range of validity of the assumptions used to derive *Equations 3–5* below. Complete phenotypic matching is assumed in Figure 2, but if some individuals mate with others of a different phenotype then the effective selection coefficient would be reduced. The evolution of choosiness could be explored using the methods and results of Aubier et al. (2023) as a starting point, and theoretical equations with which to investigate this and other parameter variants are available in Sibly & Curnow (2022), though further work is needed to see what happens when key genes are not dominant.

Section 2: Time for a new mating cue to spread to fixation

The time for a new mating cue to spread to fixation depends crucially on the strength of selection acting on the mating cue.
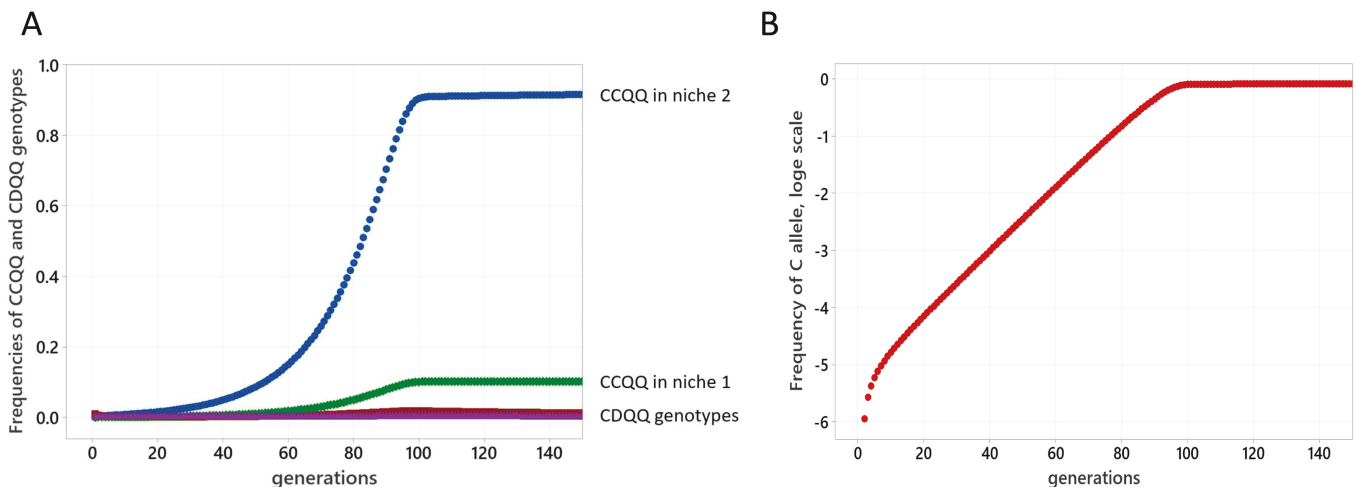
A

B

Figure 1. Example of the exponential increase of the C allele in the Sibly and Curnow (2022) model. (A) The frequency of the CCQQ and CDQQ genotypes in the two niches. The C allele was originally introduced at low frequency (1%) into niche 2 as a CDQQ genotype. The evolutionary outcome is that only two genotypes persist in the two niches, CCQQ and DDPP (DDPP is not shown here). (B) The resulting increase of the C allele is approximately linear on a log scale, indicating that the effective selection coefficient s is constant except for the first few generations, when it is higher. Parameter values were $m = 0.067$, $s_2 = 2.0$, $s_1 = -0.4$. Simulation carried out as in Sibly and Curnow (2022).
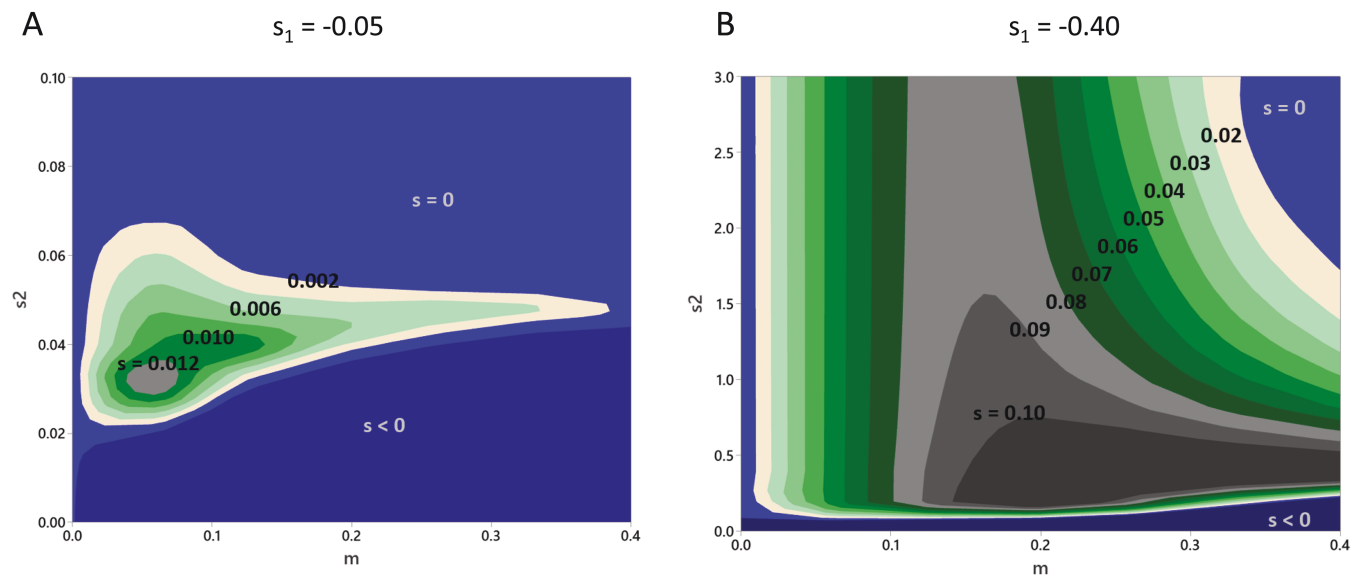
A $s_1 = -0.05$

B $s_1 = -0.40$

Figure 2. The 3D contour plots showing how the effective selection coefficient on the mating cue, s, is affected by migration rate m and s_2, for two values of s_1. Effective selection coefficients s were calculated over grids of points as in Sibly and Curnow's (2022) Figure 2, which showed parameter values for which the evolutionary outcomes are PQ polymorphisms. Our (A) corresponds to Sibly and Curnow's (2022) bottom left panel ($h = 1$, $s_1 = -0.05$); (B) to their bottom right panel ($h = 1$, $s_1 = -0.40$). In these simulations Q was dominant to P and simulations were carried out as in Sibly and Curnow (2022). s was calculated in the phase of exponential increase of C when its frequency first exceeded 10%. The contour plots were obtained by interpolation between grid points using Minitab 21.

There is no selection under Type 2 allopatry because the mating cues are then neutral, but there is selection in the other three cases. Mating cues are adaptive and so by definition subject to selection in both Type 1 models, and in Section 1, we saw that selection is induced on mating cues in Type 2 parapatry if the subpopulations are locally adapted, and we found out how then to calculate the effective selection coefficient.

In this section, we show quantitatively how effective selection pressure together with mutation rate and population size affect speciation time. Speciation times are expected to increase as the strength of selection decreases, here we quantify how the increase depends on mutation rate and population size for populations initially split into two equal subpopulations. This allows us to compare times for a new mating cue to arise and spread to fixation for the four types of model in Table 1.

Methods

Our starting assumption is that mating cues are controlled by a single locus, which is homozygous prior to a new mating cue arising by mutation. The alleles at this locus are labelled D alleles. Any mutation of D can produce a new mating cue. We label C the first such mutation that spreads to fixation, and assume C dominant to D. In Type 1 models, the mating cue is an adaptive trait and so directly subject to natural selection. In Type 2 models mating cues are not subject to selection directly, i.e., they are selectively neutral, but under Type 2 parapatry they may be acted on by selection indirectly, as in Section 1. Our aim in this section is to use standard methods of population genetics to calculate the times for new mating cues to arise and spread to fixation as a result of the mating cue selection coefficient acting directly or indirectly on C. This selection coefficient is zero under Type 2 allopatry, but positive in the other cases.

The time of arising of the first mutated allele C that goes to fixation, here labelled T_a, and the time from this mutation arising to fixation, T_f, are random variables, so the expected time to the fixation of C, E[T], can be calculated from:

$$E[T] = E[T_a] + E[T_f] \tag{1}$$

The time of arising of the first mutated allele that goes to fixation depends on the mutation rate. We let μ be the rate at which new neutral mutations arise per allele per generation. The calculation of E[T] is simpler for neutral than for selected alleles, so we begin by calculating the expected time needed to acquire a new C mating cue under Type 2 allopatry.

Timings under Type 2 allopatry

Under Type 2 allopatry mating cues are selectively neutral. To calculate the expected time of arising of the first C mutation that goes to fixation, $E[T_a]$, we begin by calculating the probability of a neutral mutation arising and going to fixation. This is the product of the probability of a mutation arising, μ, and the probability it goes to fixation. Assuming large N and small μ, the per generation probability of a mutation arising is approximately $2N\mu$, where N is the number of individuals in the population. This is because there are 2N alleles at the focal locus and the chance of each mutating is μ. The probability the arising mutation goes to fixation is 1/(2N) if the mutation is neutral (Kimura & Ohta, 1971; see also Otto & Whitlock, 2013). So the probability of a neutral mutation arising and going to fixation is $2N\mu/(2N) = \mu$ and the expected time of arising of mutations that go to fixation is the reciprocal of this, $1/\mu$.

Assuming the population is split into two subpopulations each of size N/2, then using diffusion approximations with large N and continuous time, the expected time from the arising of a neutral mutation until it reaches fixation is approximately 2N generations, conditional on the allele fixing (Kimura & Ohta, 1971; see also Otto & Whitlock,

2013). The expected time to the fixation of C is now given by *Equation 1* as:

$$\text{Expected time to the fixation of C, } E[T] \approx \frac{1}{\mu} + 2N \quad (2)$$

Timings under Type 1 allopatry and Types 1 and 2 parapatry

In Type 1 speciation—both allopatric and parapatric—the novel mating cue C is adaptive. In this case, completion of local adaptation and speciation coincide. In Type 2 parapatric speciation, local adaptation induces selection on a mating cue that is not linked to an adaptive trait. The strength of selection on the neutral mating cue then depends on how selection operates on the adaptive trait and on the migration rate as described in Section 1 above. In considering the timing of parapatric speciation, what is important is the effective selection pressure, here designated s, that acts on the trait under consideration, which could be either an adaptive trait or a mating cue distinct from the adaptive trait. In this section, s is taken to be constant. This is approximately true in Type 2 parapatry except for the first few generations of the spread of the mating cue, when it is higher (example in Figure 1B). The evolutionary outcomes are speciation in all cases. This is because eventually there are only two genotypes left in the population, CC and DD, and neither will mate with the other. So at the end of the evolutionary process there are two species. C has spread to fixation in one and D in the other.

We now use *Equation 1* to calculate the expected time to the fixation of C, E[T]. The probability of a mutation arising is approximately $2N\mu$, as before. The probability the arising mutation goes to fixation is approximately $2s$ if s is small (Kimura & Ohta, 1971; see also Otto & Whitlock, 2013). So the probability of a selected mutation arising and going to fixation is $4N\mu s$, and the expected time of arising of selected mutations that go to fixation, T_a, is the reciprocal of this, $1/(4N\mu s)$.

The time from C arising to fixation can be obtained from equations given by Charlesworth (2020). These equations apply to cases where the fixation index, F, is constant and known. Under selection, however, as C spreads, mating is increasingly non-random and F increases. This situation has not been modelled, and we therefore, consider two limiting cases: $F = 0$, and F positive and constant. It turns out that the time from C arising to fixation is longer for $F = 0$ than for $F > 0$, so $F = 0$ times represent a limiting case—actual times will be shorter than those for $F = 0$.

With $F = 0$, for a dominant allele at an autosomal locus with weak selection and a large population, Charlesworth (2020) showed that the time from C arising to fixation in units of $2N$, conditional on the allele fixing, is approximately:

$$(2\gamma)^{-1} + \gamma^{-1} \left[p_2^{-1} + \ln\left(p_1 q_2 q_1^{-1} p_2^{-1}\right) - p_1^{-1} \right]$$
$$+ 1.7724\gamma^{-0.5} \quad (3)$$

where $\gamma = 2Ns$, assumed $\gg 1$, p_1 and p_2 are the proportions of the dominant allele at the start and end of its deterministic growth phase satisfying $p_1 = 1 - (2\gamma)^{-1}$, $p_2 = 0.8862\gamma^{-0.5}$; $q_1 = 1 - p_1$, $q_2 = 1 - p_2$, and N_e is taken to be N.

With assortative mating and fixation index F, Charlesworth (2020) showed that the time is approximately:

$$(2\gamma)^{-1} + \gamma^{-1} \left[-\ln\left(q_1 F\right) + F^{-1} \ln\left(F p_2^{-1}\right) \right]$$
$$+ 0.6321(F\gamma)^{-1} \quad (4)$$

In deriving *Equation 4*, it is assumed that $F > O(s)$, and p_2^{-1} is large. Numerical evaluations of *Equations 3 and 4* reported in Supplementary Material 2 show that times from C arising to fixation are always lower if $F > 0$ than if $F = 0$. The expected time to the fixation of a selected mutation for the limiting case of $F = 0$ can now be approximated from *Equation 1* as:

$$E[T] = E[T_a] + E[T_f]$$
$$\approx \frac{1}{4N\mu s} + 2N[(2\gamma)^{-1} + \gamma^{-1} \left[p_2^{-1} + \ln\left(p_1 q_2 q_1^{-1} p_2^{-1}\right) - p_1^{-1} \right]$$
$$+ 1.7724\gamma^{-0.5}] \quad (5)$$

Equations 3–5 hold provided that $s < 0.2$ and Ns is large (Charlesworth, 2020).

Results

The expected times to fixation of a mating cue are shown in relation to the selection coefficient s acting on the mating cue in Figure 3 for various populations sizes N, for the limiting case of $F = 0$. s under Type 2 parapatry is the "effective selection" estimated in Section 1, whereas s for Type 1 models is the selection coefficient acting on the mating cue directly. The case labelled "Neutrality" corresponds to Type 2 allopatry, when $s = 0$. Both T and T_a are plotted in Figure 3A but these overlay if $N < 100,000$ indicating that time from C arising to fixation is then negligible in comparison with the time of arising of the first mutated allele that goes to fixation, T_a. Figure 3A shows that as expected mating cues evolve substantially faster under selection than under neutrality. With $\mu = 10^{-8}$, $s = 0.02$ and a population size of 10,000, cues evolve in 100,000 generations under selection, compared with 100 million generations needed under neutrality. In a population of 100 000, cues evolve in a few thousand generations under selection. Figure 3A shows the situation when the mutation rate $\mu = 10^{-8}$. If the mutation rate is higher, time to fixation is reduced, and the contribution of the time from C arising to fixation is more pronounced. These effects are illustrated in Figure 3B, where $\mu = 10^{-5}$. The colour coding is the same in Figure 3A and B. All times are reduced in Figure 3B in comparison with Figure 3A. Times to fixation under selection are closer together than in Figure 3A because of increases in the contribution of the time from C arising to fixation: these increase with N. Over the ranges of s and N shown in Figure 3B, times to fixation range from under a thousand if $s = 0.2$ and $N = 1,000$, to a little over 100,000 if $s = 0.001$ and $N = 1,000,000$. These are much less than the 2 million generations needed under neutrality with $N = 1,000,000$.

Figure 3 shows quantitatively how much shorter is the time needed for a new mating cue to evolve under selection than under neutrality. If the mutation rate $\mu = 10^{-8}$ per site per generation, the value commonly reported in reptiles, birds, fish, and mammals (Bergeron et al., 2023), then in populations under 100,000 the time needed for a new mating cue to evolve depends almost entirely on the time of arising of the first mutated allele C that goes to fixation, as shown in Figure 3A. The times needed for a new mating cue to evolve under neutrality and selection then simplify to $\frac{1}{\mu}$ and $\frac{1}{4N\mu s}$, respectively. Thus, the time needed under selection is lower than that needed under neutrality by a factor of $4Ns$. On the log–log scales of Figure 3, the relationship for neutrality is $\log(\text{time needed}) = -\log \mu$. The relationship for selection is $\log(\text{time needed}) = -\log \mu - \log 4 - \log N - \log s$. So, *time needed* can be decreased by an order of magnitude by increasing population size N by an order of magnitude, or increasing the effective selection coefficient s by an order of magnitude.
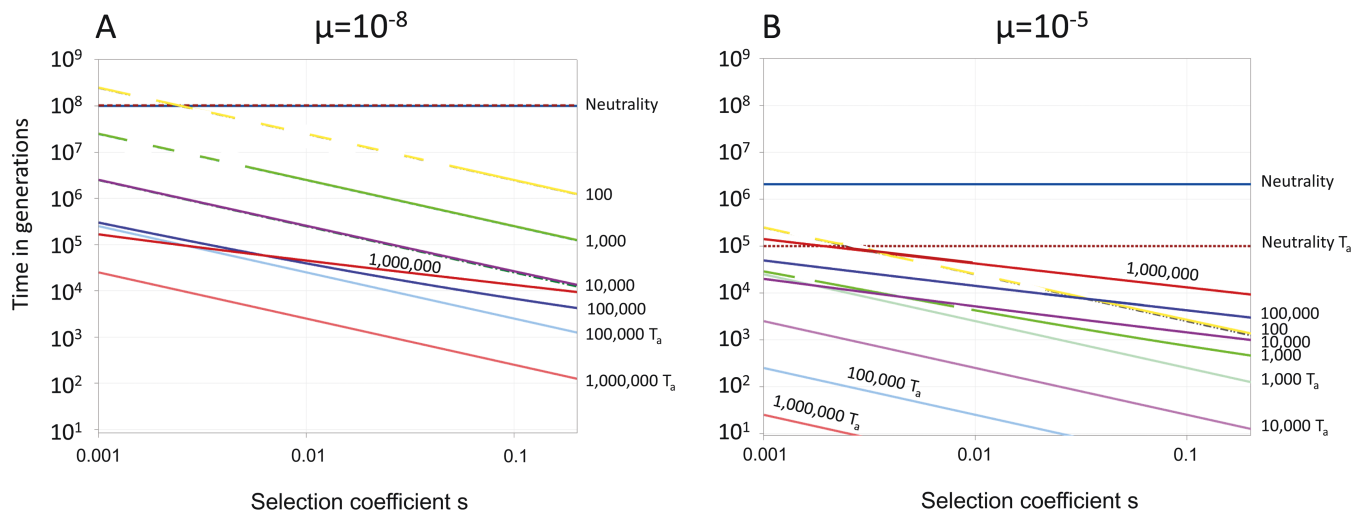
Figure 3. Expected times to fixation of a mating cue under neutrality and selection for the limiting case of $F = 0$. Times to fixation are plotted against the selection coefficient s on log-log scales for two mutation rates: (A) $\mu = 10^{-8}$; (B) $\mu = 10^{-5}$. The lines for neutrality are shown for comparison with those for selection but the selection coefficient under neutrality is zero. The neutrality lines satisfy *Equation 2* with $N = 10^6$. The other lines are for selected populations, for which the numbers in the right-hand columns indicate population size in *Equation 5*. The lines for both E[T] and E[T_a] are plotted and these generally overlay. Where they do not overlay the E[T_a] line has the suffix T_a, the E[T] line has no suffix. The cases in which the lines overlay are in (A) where $N < 100,000$ and neutrality; and in (B) where $N < 1,000$. Portions of lines that are dashed indicate regions where $Ns < 5$, i.e., failure of the assumption Ns large that is used to derive *Equations 3–5*.

If the mutation rate is higher, time to fixation is reduced, and the contribution of the time from C arising to fixation is more pronounced (example in Figure 3B). The net effect is that the time needed for a new mating cue to evolve is still much shorter under selection than under neutrality. Allowing for changes in the *y*-axis scale, results are similar to those shown in Figure 3 as mutation rate is varied from $\mu = 10^{-8}$ to $\mu = 10^{-2}$ (results not shown).

These results assume that phenotypic change can only occur as a result of genetic change at a single locus. Although many genes may be involved in coding for mating cues, the number of possible mutations that could result in phenotypic change is not known. Our initial analysis has therefore been based on calculating times at a single given locus, but times are reduced if there are several loci that can result in phenotypic change. If there are several loci that potentially could code for a new mating cue, the number being given the symbol x, then μ should be replaced by μx throughout the analysis. This is because there are now $2Nx$ alleles at the x focal loci and the chance of each mutating is μ, so the per generation probability of a mutation arising is approximately $2N\mu x$. Considering only the first mutation that goes to fixation, the rest of the analyses follow as before with μ replaced by μx. The effect is identical to that of increasing μ, so that for example in comparison with Figure 3A, Figure 3B could result either from increasing μ by three orders of magnitude or from an equivalent increase in x. So speciation times are reduced the more loci there are that potentially could code for mating cues.

In this section, we have shown quantitatively how effective selection pressure together with mutation rate and population size affect speciation time, for populations made up of two equal-sized subpopulations.

Discussion

Our interest here has been to see how speciation times depend on whether or not there is migration between subpopulations when mating cues are either neutral or directly selected. Our key result is that neutral mating cues, the Type 2 cases, go to fixation faster under parapatry than under allopatry. The results of a quantitative analysis are shown in Figure 3, where the allopatric case is neutral but the parapatric case experiences selection on the mating cue induced by the selective conditions in the subpopulations and the migration rates between them. Selection is also rapid in Type 1 cases in which mating cues are locally adaptive, acted on directly by selection—a prime example in birds is beak size, larger beaks being adaptive in one habitat, smaller beaks in the other—but speciation would not then involve evolution of species-specific songs or plumage coloration unless these were themselves locally adaptive. Our results suggest that species-specific songs or plumage colorations that are selectively neutral evolve faster under parapatry than under allopatry, and this may explain the occurrence of short speciation times such as those described in the Introduction.

Migration between subpopulations is necessary for selection on mating cues in Type 2 models. This is evident on the left-hand side of the plots in Figure 2 where selection on the mating cue is zero at $m = 0$. Under allopatry there is no migration, so there is no selection on the mating cue whether or not there is divergent ecological selection acting on the subpopulations. By contrast in Type 2 parapatry selection is induced despite there being no direct selection on mating cues.

Figure 3 shows quantitatively how much shorter is the time needed for a new mating cue to evolve under selection than under neutrality. The time needed can be reduced by several orders of magnitude, depending on population sizes and the strength of selection. From Figure 3 we conclude that except for very large populations the time needed is approximately $1/4N\mu s$, i.e., scaling as the reciprocal of s. From Figure 2 we know how s depends on migration rate and the strength of selection for the mating cue under Type 2 parapatry. So the relationship between time needed, migration rate and the strength of selection for the mating cue can be visualized as an inverse of Figure 2 replacing the vertical axis of Figure

2, *s*, by its reciprocal. Figures 2 and 3 can also be linked by considering a fictitious example: Suppose an F_{ST} value of 0.31 is recorded for a locus critical to local adaptation, the genotypes varying between two niches. Using the results of Sibly & Curnow (2023), the selection coefficients on one of the alleles would be 0.4 in one niche and –0.4 in the other if the migration rate was 0.01 and the absolute values of the selection coefficients were equal. Figure 2 shows that the mating cue selection coefficient would then be around 0.01, in which case from Figure 3 the expected speciation time would be about 40,000 generations if the population size was 100,000. For smaller populations or lower migration rates, the expected speciation time would be longer. So from measured F_{ST} values for an ecological trait locus, if we have some indication of migration rates we can get an idea of expected speciation times in Sibly & Curnow's (2022) Type 2 parapatry.

The assumptions and approximations used in deriving *Equations 2–5* merit discussion. It has been assumed that mating cues under Type 2 allopatry are selectively neutral, but this might not be true if sexual selection operated on the mating cues during Type 2 allopatry. However, to get differences between the geographic regions it would be necessary for sexual selection to operate differently in the different regions. Sexual selection depends on mate-choosers—often females—having preferences for selected traits, so these preferences also would need to differ between the geographic regions. So while possible in some cases this seems unlikely as a general explanation, and we contend that our assumption of neutrality of mating cues under Type 2 allopatry is an appropriate theoretical starting point. It is also assumed that phenotype matching is complete and that changes in the mating cue sufficient to be imprinted on would be generated by a single nucleotide substitution, and there is scope for further work relaxing these assumptions. Assortative mating is assumed to be cost free, but being choosy may reduce the chance of mating, reducing the mating cue selection coefficient in the parapatric models (Aubier et al., 2023; Kopp & Hermisson, 2008; Schneider & Burger, 2006). The probability of a mutation arising is $1 - (1 - \mu)^{2N}$ and this is approximated as $2N\mu$. This is a good approximation even when $N = 1,000,000$: with $\mu = 10^{-8}$ the approximation then gives 0.0200 compared to the exact value of 0.0198. In deriving *Equations 3–5*, *s* is taken to be constant, though in reality it is higher in Sibly & Curnow's (2022) Type 2 parapatry in the first few generations of the spread of the mating cue, as shown in Figure 1B. The effect of this will be to shorten the time to fixation of a mating cue under Type 2 parapatry. Figure 3 only shows s values up to 0.2 and Ns large, the regions in which Charlesworth's (2020) *Equations 3–5* are valid. In sum, since the values of *s* may often be less than 0.1 (Figure 2), our conclusions are unlikely to be affected by the approximations used in deriving *Equations 2–5*, though there is scope for further work relaxing our other assumptions.

Our results encourage further research on species that are in the process of speciating or have very recently speciated. A key question is how phenotype matching is achieved. A likely candidate in birds is sexual imprinting, a process whereby individuals choose mates that resemble other individuals, usually one of their parents. Sexual imprinting seems to be a general feature of birds, shown to exist in over 100 species belonging to 15 different orders, and in both sexes (ten Cate & Vos, 1999), and has also been found in mammals, fish (cichlids and stickleback), and frogs (Verzijden et al., 2012;

Yang et al., 2019). Phenotype matching could alternatively be achieved if the gene(s) determining mating cues were either identical to or close to loci determining mate preferences (Ritchie & Butlin, 2024).

Finally, we offer the thought that with phenotype matching of mating cues, Type 2 parapatric speciation is a means of enhancing local adaptation, increasing the frequency of P in the habitat in which it is adaptive and Q where it is adaptive. Although our modelling assumptions are restrictive so that caution is needed in comparing the results to empirical data, we hope that our main results, showing quantitatively how Type 2 parapatry can reduce speciation times, will encourage further work relaxing model assumptions or studying different models of mate choice.

Supplementary material

Supplementary material is available at *Journal of Evolutionary Biology* online.

Data availability

No new data were generated or analysed in support of this research.

Author contributions

Richard Sibly (Conceptualization [Lead], Formal analysis [Lead], Software [Lead], Writing—original draft [Lead], Writing—review & editing [Lead]), and Robert Curnow (Formal analysis [Supporting], Writing—original draft [Supporting], Writing—review & editing [Supporting])

Conflicts of interest

None.

References

Aubier, T. G., Buerger, R., & Servedio, M. R. (2023). The effectiveness of pseudomagic traits in promoting premating isolation. *Proceedings of the Royal Society B-Biological Sciences*, *290*. https://doi.org/10.1098/rspb.2022.2108

Bergeron, L. A., Besenbacher, S., Zheng, J., … Zhang, G. (2023). Evolution of the germline mutation rate across vertebrates. *Nature*, *615*(7951), 285–291. https://doi.org/10.1038/s41586-023-05752-y

Campagna, L., Benites, P., Lougheed, S. C., … Tubaro, P. L. (2012). Rapid phenotypic evolution during incipient speciation in a continental avian radiation. *Proceedings of the Royal Society B-Biological Sciences*, *279*, 1847–1856. https://doi.org/10.1098/rspb.2011.2170

Campagna, L., Repenning, M., Silveira, L. F., … Lovette, I. J. (2017). Repeated divergent selection on pigmentation genes in a rapid finch radiation. *Science Advances*, *3*(5). https://doi.org/10.1126/sciadv.1602404

Charlesworth, B. (2020). How long does it take to fix a favorable mutation, and why should we care? *American Naturalist*, *195*(5), 753–771. https://doi.org/10.1086/708187

Felsenstein, J. (1981). Skepticism towards Santa Rosalia, or why are there so few kinds of animals. *Evolution*, *35*(1), 124–138. https://doi.org/10.2307/2407946

Gavrilets, S. (2014). Models of speciation: where are we now? *Journal of Heredity*, *105*(S1), 743–755. https://doi.org/10.1093/jhered/esu045

Hejase, H. A., Salman-Minkov, A., Campagna, L., … Siepel, A. (2020). Genomic islands of differentiation in a rapid avian radiation have been driven by recent selective sweeps. *Proceedings of the National Academy of Sciences of the United States of America*, *117*(30554), 30565. https://doi.org/10.1073/pnas.2015987117

Kimura, M., Ohta, T., 1971. *Theoretical aspects of population genetics*. Princeton University Press.

Kopp, M., & Hermisson, J. (2008). Competitive speciation and costs of choosiness. *Journal of Evolutionary Biology*, *21*(4), 1005–1023. https://doi.org/10.1111/j.1420-9101.2008.01547.x

Kopp, M., Servedio, M. R., Mendelson, T. C., … van Doorn, G. S. (2018). Mechanisms of assortative mating in speciation with gene flow: Connecting theory and empirical research. *American Naturalist*, *191*(1), 1–20. https://doi.org/10.1086/694889

Lamichhaney, S., Berglund, J., Almen, M. S., … Andersson, L. (2015). Evolution of Darwin's finches and their beaks revealed by genome sequencing. *Nature*, *518*(7539), 371–375. https://doi.org/10.1038/nature14181

Meier, J. I., McGee, M. D., Marques, D. A., … Seehausen, O. (2023). Cycles of fusion and fission enabled rapid parallel adaptive radiations in African cichlids. *Science*, *381*(6665), 1428. https://doi.org/10.1126/science.ade2833

Mendelson, T. C., & Shaw, K. L. (2005). Sexual behaviour: Rapid speciation in an arthropod. *Nature*, *433*(7024), 375–376. https://doi.org/10.1038/433375a

Momigliano, P., Jokinen, H., Fraimout, A., … Merila, J. (2017). Extraordinarily rapid speciation in a marine fish. *Proceedings of the National Academy of Sciences of the United States of America*, *114*(6074), 6079. https://doi.org/10.1073/pnas.1615109114

Otto, S. P., & Whitlock, M. C. (2013). Fixation probabilities and times. *eLS*. https://doi.org/10.1002/9780470015902.a0005464.pub3

Puritz, J. B., Keever, C. C., Addison, J. A., … Toonen, R. J. (2012). Extraordinarily rapid life-history divergence between *Cryptasterina* sea star species. *Proceedings of the Royal Society B: Biological Sciences*, *279*, 3914–3922. https://doi.org/10.1098/rspb.2012.1343

Rabosky, D. L., Santini, F., Eastman, J., … Alfaro, M. E. (2013). Rates of speciation and morphological evolution are correlated across the largest vertebrate radiation. *Nature Communications*, *4*(1). https://doi.org/10.1038/ncomms2958

Ritchie, M. G., & Butlin, R. K. (2024). Genetic coupling of mate recognition systems in the genomic era. *Cold Spring Harbor Perspectives in Biology*, *16*. https://doi.org/10.1101/cshperspect.a041437

Schneider, K. A., & Burger, R. (2006). Does competitive divergence occur if assortative mating is costly? *Journal of Evolutionary Biology*, *19*(2), 570–588. https://doi.org/10.1111/j.1420-9101.2005.01001.x

Servedio, M. R., & Burger, R. (2020). The effectiveness of pseudomagic traits in promoting divergence and enhancing local adaptation. *Evolution*, *74*(11), 2438–2450. https://doi.org/10.1111/evo.14056

Sibly, R. M., & Curnow, R. N. (2022). Sexual imprinting leads to speciation in locally adapted populations. *Ecology and Evolution*, *12*(11). https://doi.org/10.1002/ece3.9479

Sibly, R. M., & Curnow, R. N. (2023). Allele frequencies and selection coefficients in locally adapted populations. *Journal of Theoretical Biology*, *565*, 111463. https://doi.org/10.1016/j.jtbi.2023.111463

Smadja, C. M., & Butlin, R. K. (2011). A framework for comparing processes of speciation in the presence of gene flow. *Molecular Ecology*, *20*(24), 5123–5140. https://doi.org/10.1111/j.1365-294x.2011.05350.x

ten Cate, C., Vos, D. R., 1999. Sexual imprinting and evolutionary processes in birds: A reassessment. In: P. J. B. Slater, et al., (Eds.), *Advances in the study of behavior*, Vol. 28, (pp. 1–31). Academic Press.

Tobias, J. A., Ottenburghs, J., & Pigot, A. L. (2020). Avian diversity: Speciation, macroevolution, and ecological function. *Annual Review of Ecology, Evolution, and Systematics*, *51*(1), 533–560. https://doi.org/10.1146/annurev-ecolsys-110218-025023

Turbek, S. P., Semenov, G. A., Enbody, E. D., … Taylor, S. A. (2021). Variable signatures of selection despite conserved recombination landscapes early in speciation. *Journal of Heredity*, *112*(6), 485–496. https://doi.org/10.1093/jhered/esab054

Verzijden, M. N., ten Cate, C., Servedio, M. R., … Svensson, E. I. (2012). The impact of learning on sexual selection and speciation. *Trends in Ecology & Evolution*, *27*(511), 519. https://doi.org/10.1016/j.tree.2012.05.007

Yang, Y. S., Servedio, M. R., & Richards-Zawacki, C. L. (2019). Imprinting sets the stage for speciation. *Nature*, *574*, 99. https://doi.org/10.1038/s41586-019-1599-z