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Song learning as an indicator mechanism: Modelling the developmental stress hypothesis

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Abstract

The 'developmental stress hypothesis' attempts to provide a functional explanation of the evolutionary maintenance of song learning in songbirds. It argues that song learning can be viewed as an indicator mechanism that allows females to use learned features of song as a window on a male's early development, a potentially stressful period that may have long-term phenotypic effects. In this paper we formally model this hypothesis for the first time, presenting a population genetic model that takes into account both the evolution of genetic learning preferences and cultural transmission of song. The models demonstrate that a preference for song types that reveal developmental stress can evolve in a population, and that cultural transmission of these song types can be stable, lending more support to the hypothesis.

Keywords: Developmental stress; Vocal learning; Bird song

1. Introduction

Bird song is a classic example of a sexually selected trait, and is also one of the best studied examples of non-human animal cultural transmission (reviewed in Catchpole and Slater, 1995; Marler and Slabbekoorn, 2004). Despite the wealth of studies and data on song function and development the evolutionary function of song *learning* remains unclear (Slater, 2003). There have been several proposed functions, such as the acquisition of a large and varied repertoire, habitat matching and neighbour matching (see, e.g. Marler and Slabbekoorn, 2004, for a review), but it seems that none of these apply widely to more than a few song learning species.

On the other hand, song learning appears to incur some costs, which suggests that the trait must have been positively maintained by selection (Lachlan and Slater, 1999). These costs include the development and maintenance of the complex system of brain nuclei which underlie song learning, and the substantial investment in time required to develop normal conspecific song. Learning also introduces the risk that a bird will fail to acquire a normal song due to a lack of suitable models; birds may acquire heterospecific song, or simply fail to find a tutor at all. Both of these will result in adult song that is unlikely to function as well as normal song. The 'cultural trap hypothesis', which argues that species that have developed cultural transmission of song are unlikely to lose the trait because of the interaction of genetic predispositions and processes of cultural evolution, is the only current hypothesis that can apply to a wide range of species (Lachlan and Slater, 1999; Lachlan and Feldman, 2003).

Recently, a more adaptive evolutionary function for song learning has been suggested which is in accord with several empirical studies. The 'developmental stress hypothesis' (DSH) proposes that song learning may serve as an indicator mechanism that allows females to judge a potential mate's quality according to how well he has learned conspecific song (Nowicki et al., 1998; Buchanan et al., 2003; Nowicki and Searcy, 2004). Songbirds are altricial and infancy is fraught with potential stresses, including parasites and undernutrition (see, e.g. O'Connor, 1984). If developmental stress of a male bird has long-term effects, such as affecting the number of viable offspring

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a pairing can produce, it is plausible that selection would favour any mechanism that would allow females to accurately judge the degree of developmental stress of a potential mate. Various studies have shown that the brain structures mediating song learning develop in infancy, late compared to the rest of the avian nervous system, and so adult song behaviour may be irreparably affected by stresses that affect this development (discussed in Nowicki and Searcy, 2004). It seems plausible that females could evolve a preference for features of song that are acquired during this period as this would enable them to identify males affected by developmental stress.

The DSH has been supported by a range of empirical studies. A number of possible stressors have been studied in several species, for example; undernutrition has an effect on accuracy of song note copying in male swamp sparrows (*Melospiza georgiana*) (Nowicki et al., 2002a), social rank has an effect on acquired repertoire size in the European starling (*Sturnus vulgaris*) (Spencer et al., 2004) and food restriction and corticosterone administration selectively affect growth of the HVC (an important song control nucleus) in zebra finches (*Taeniopygia guttata*) (Buchanan et al., 2004). Nowicki et al. (2000) also provide support for a key prediction of the hypothesis, demonstrating that at least one measure of nestling growth correlates with adult repertoire size in the great reed warbler (*Acrocephalus arundinaceus*). Another prediction of the hypothesis is that females attend to these effects, and studies have shown that female song sparrows (*Melospiza melodia*) respond more to males that have copied the notes of their tutors more accurately (Nowicki et al., 2002b), and that female zebra finches significantly prefer the songs of control males to those of males stressed by either food restriction or corticosterone administration (Spencer et al., 2005).

These data suggest that several features of male song are affected by developmental stress and that females attend to these features, supporting some of the key predictions of the hypothesis. However, a number of issues raised remain unresolved; these include the effect of developmental stress on female preference and the cultural stability of a song type that is not acquirable by all members of the population. In this paper we attempt to address some of these issues and to add further support to this hypothesis using a population genetic model of the evolution of song preferences. With the model we investigate two important questions raised by the hypothesis: firstly, can a preference for culturally transmitted features of song affected by developmental stress evolve in a population, even when stress affects both female preference and male production? Secondly, can cultural transmission of songs with such features be stable, despite the fact that those members of the population suffering developmental stress cannot acquire or produce them?

2. The models

The models presented here are population genetic models in which we assume an infinite population with discrete generations and a 1:1 sex ratio. We also assume haploid genetics to simplify the analysis, as has been used in related models (e.g. Kirkpatrick, 1982; Aoki, 1989; Lachlan and Feldman, 2003).

We model developmental stress simply as resulting in either a high or low quality bird, whereby a low quality bird may be thought of as undernourished or parasitised. The probability of an individual bird of either sex being high quality is defined as δ. The factors affecting a bird's quality are assumed to be determined by the environment. Quality is therefore not inherited and is assigned to individuals independently of their genetic constitution and the quality of their parents. This is similar to Heywood's (1989) 'good' and 'bad' environments in his model of the handicap mechanism. We assume that it would be beneficial to females to be able to identify a potential mate's quality, but that a bird's quality is not directly observable. Instead we assume that the quality of a bird affects its ability to learn some song types. In the model, 'type 2' songs are only learnable by high quality birds, while 'type 1' songs are learnable by both high and low quality birds. Although we make no further assumptions about the song types other than this difference in learnability, it is useful to think of type 2 song as being more complex in some way than type 1 song, e.g. it may have more complex phrase or note structure. Considered in this way, we are therefore assuming that high quality birds are able to learn more complex songs than low quality birds. We also assume that only high quality birds are able to distinguish between the two song types. The proportion of type 2 songs in the cultural environment is denoted as t_2 and the proportion of type 1 songs $t_1 = 1 - t_2$. Importantly, we assume that both males and females are affected by developmental stress and that this stress can affect both sexes' adult behaviour.

A bird's ability to acquire a particular song type is also affected by a genetic component, we model this as a single autosomal locus A for which two alleles exist, A_1 and A_2.[1] This gene may be considered as coding for a learning bias and we assume (as did Lachlan and Feldman, 2003) that the same gene controls song learning bias in both males and females. This assumption seems plausible as studies have shown (reviewed in Riebel, 2003) that, in many species, both sexes are born with a preference for conspecific song which is affected by early song exposure (e.g. in zebra finches, Lauay et al., 2004), that females share many of the song system nuclei with males, and that females can produce song under abnormal hormonal conditions (Riebel, 2003). Birds with allele A_1 can only learn type 1 songs. Birds with allele A_2 are able to learn

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[1] Although we only present results for a single locus here we have also modelled the case when song production and preference are controlled by genes at two separate loci. This makes algebraic analysis considerably harder (as we then have 16 different types of birds and also need to track the linkage disequilibrium between the two loci), but numerical iterations of the recursion equations indicate that the model's behaviour is qualitatively similar to the one locus case.

Table 1
The effect of the three factors on the adult phenotype

Quality (δ)	Allele (a_2)	Model song (P_{T_2})	Adult song	Adult preference	Label (X_i)	Frequency (x_i)
L	A_1	1	1	Either	X_1	$(1-\delta)(1-a_2)(1-P_{T_2}) = x_1$
H	A_1	1	1	Either	X_2	$\delta(1-a_2)(1-P_{T_2}) = x_2$
L	A_2	1	1	Either	X_3	$(1-\delta)a_2(1-P_{T_2}) = x_3$
H	A_2	1	1	Either	X_4	$\delta a_2(1-P_{T_2}) = x_4$
L	A_1	2	1	Either	X_5	$(1-\delta)(1-a_2)P_{T_2} = x_5$
H	A_1	2	1	Either	X_6	$\delta(1-a_2)P_{T_2} = x_6$
L	A_2	2	1	Either	X_7	$(1-\delta)a_2P_{T_2} = x_7$
H	A_2	2	2	2 (if $s>0$)	X_8	$\delta a_2P_{T_2} = x_8$

song types 1 and 2, but are biased to acquiring type 2 song. This bias will, however, only be expressed if a bird hears type 2 song as an infant. The proportion of the population with allele A_2 is denoted as a_2, with the proportion of birds with allele A_1, $a_1 = 1 - a_2$.

This gene affects adult song behaviour in both sexes in the following way. A high quality female with allele A_2 has a bias to acquiring type 2 song, and if she is exposed to this song type as an infant, she will memorise it and later will preferentially mate with a male singing a type 2 song. The strength of this mating preference is represented by the parameter s, with $s = 1$ implying such a female will exclusively mate with males singing type 2 song, and $s = 0$ meaning such a female mates indiscriminately, with intermediate values implying intermediate preference for type 2 song. All other females are unable to differentiate type 1 song from type 2 song and so will mate indiscriminately with a male singing either type. A high quality male with allele A_2 that is exposed to type 2 song is assumed to memorise this song and then go on to learn to produce it as an adult, i.e. we are assuming that the males follow the auditory template model of song development (see Catchpole and Slater, 1995, for a discussion of this model). Other males are only able to develop a type 1 song.

To model song acquisition, we assume that each infant bird is exposed to a set of m songs, randomly sampled from all the songs of the previous generation (this is thus a model of oblique cultural transmission as used in Lachlan and Feldman, 2003). They then pick a single model song to learn from. If the set contains at least one instance of type 2 song a high quality bird with allele A_2 will learn type 2 song. All other birds are unable to learn type 2 song, and will acquire type 1. The probability, P_{T_2}, of any bird hearing at least one instance of type 2 song is given by the following equation:

$$P_{T_2} = 1 - (1 - t_2)^m. \tag{2.1}$$

The following three factors thus contribute to an adult bird's phenotype:

- The bird's environmentally specified quality, either *high* (denoted as H) or *low* (denoted as L).
- The allele it inherits from its parents, either A_1 or A_2.
- The set of songs the bird hears as an infant.

The effects of these factors on the adult song and song preference behaviour is shown in Table 1. There are eight possible combinations of quality, allele and model song, giving eight types of individual of each sex in the model which we label $X_1, \ldots, X_8$. The frequencies of these types are given by the values of δ, a_2 and t_2 in each generation, as shown in the table, which we denote as x_i. In summary, only high quality individuals bearing allele A_2 who are exposed to type 2 song, identified as type X_8 in the table, will develop a mating preference for type 2 song (as females) and are able to produce type 2 song (as males). All other individuals show no adult mating preference and can only produce type 1 song. Type 2 song is thus a reliable indicator of male quality; only high quality males are able to acquire and later produce it.

With this model we are interested in the conditions under which allele A_2, which governs the ability to acquire type 2 song, can spread in a population even when it has no effect on some carriers of the allele (namely types X_3, X_4 and X_7), and reduces the number of potential mates for the choosy X_8 females (assuming that $s>0$). We are also interested in whether cultural transmission of the type 2 song can be stable despite the fact that it cannot be acquired or produced by every individual in the population.

2.1. Polygyny

For the first full model, we assume a polygynous mating system. We are aware that many songbird species are largely monogamous and we model this in Section 2.2, but as these models can be seen as mathematical variations on the polygynous model, for clarity we first present the polygynous case. This also allows comparison with other models of the evolution of culturally transmitted song which also assume polygyny (e.g. Aoki, 1989; Lachlan and Feldman, 2003).

We assume that each time a female chooses a mate she samples n males and will mate with the male whose song she prefers the most.[2] The X_8 females prefer to mate with

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[2] This is thus modelling a 'best of n' mate selection strategy, which is one of a number of possible mate selection strategies. While we have not formally incorporated any other strategies into the model, we feel that as long as the key property that the choosy X_8 females are not guaranteed to find a preferred mate remains, the results would be qualitatively similar.

Table 2
Frequencies of matings for the polygynous model

Females	Males			
	X_1	…	X_7	X_8
X_1				$x_1 \cdot x_8$
$\vdots$		$x_i \cdot x_j$		$\vdots$
X_7				$x_7 \cdot x_8$
X_8	$(1-s) \cdot x_8 \cdot x_1$	…	$(1-s) \cdot x_8 \cdot x_7$	$((1-s) \cdot x_8 \cdot x_8) + (s \cdot x_8 \cdot P_{X_8})$

X_8 males, and a proportion s of the time such a female will exclusively pick an X_8 male from their set of n, if there is not an X_8 male in this set they will not mate. The probability, P_{X_8}, that at least one X_8 male is in the sample of n males is given by the following equation:

$$P_{X_8} = 1 - (1 - x_8)^n. \tag{2.2}$$

A proportion $1-s$ of the time the X_8 females, as well as all other females, mate indiscriminately, but will always find a mate. The frequencies of matings between the different types of birds under these assumptions is given in Table 2. As we are assuming polygyny, each male is able to mate multiple times.

In the model, we assume that the effect of quality on fitness is to affect the number of viable offspring a mated pair produce. This seems like a plausible assumption, as a parasitised or undernourished male is likely to be a less effective parent than a high quality male. Unfortunately we are not aware of any direct empirical investigation of the effect of developmental stress on male parental abilities, but Naguib et al. (2006) show that the developmental stress (in their study, brood size) of mother zebra finches has an effect on the hatching and fledgling success of their daughters one generation later. We do, however, have some indirect evidence for the effect on male parental abilities. Hasselquist (1998) shows that male syllable repertoire size is positively correlated with harem size and fledging success in great reed warblers, and, as mentioned earlier, Nowicki et al. (2000) show that at least one measure of nestling developmental stress has an effect on syllable repertoire size in this species, so it seems that developmentally stressed males may fare worse as parents. In reality, developmental stress is also likely to affect an individual's chance of survival until reproductive age. However, with this model we are only concerned with the effect of quality on reproductive success, and so we assume that birds of high and low quality are equally viable until reproductive age.

We define the fitness of mated pairs as a function of the qualities of both the female and her chosen mating partner. The fitness of a bird that does not mate is assumed to be 0. There are four classes of possible matings, a high or low quality female mating with a high or low quality male. The relative fitnesses of each of these classes of pairings are defined in Table 3. This value can be considered a measure of the relative number of viable offspring that a mated pair will produce, and we assume here that these values will take a value between 0 and 1. Alleles A_1 and A_2 are equally likely to be transmitted from an $A_1 \times A_2$ mating.

Table 3
The relative fitness of each of the four possible classes of mated pairs as a function of individual quality

Female	Male	
	H	L
H	1	f_{HL}
L	f_{LH}	f_{LL}

According to these assumptions we can now write recursion equations for the value of a_2 in the next generation, a_2', and the value of t_2 in the next generation, t_2', which is simply the proportion of X_8 males in the current generation. These recursions therefore include both genetic and cultural transmission. The equations demonstrate that for allele A_2 to spread, the average fitness of birds with this allele (w_{A_2}) must be greater than the average fitness of birds with allele A_1 (w_{A_1}):

$$t_2' = x_8, \tag{2.3}$$

$$a_2' = \frac{w_{A_2}}{w_{A_1} + w_{A_2}}, \tag{2.4}$$

where

$$\begin{aligned} w_{A_2} = {} & f_{LL} \cdot [(x_3 + x_7)(x_1 + x_3 + x_5 + x_7)] \\ & + f_{LH} \cdot \left[(x_3 + x_7)(x_4 + x_8) \right. \\ & \left. + \frac{(x_1 + x_5)(x_4 + x_8) + (x_3 + x_7)(x_2 + x_6)}{2} \right] \\ & + f_{HL} \cdot \left[((1-s) \cdot x_8 + x_4)(x_3 + x_7) \right. \\ & \left. + \frac{(x_2 + x_6)(x_3 + x_7) + ((1-s) \cdot x_8 + x_4)(x_1 + x_5)}{2} \right] \\ & + 1 \cdot \left[s \cdot x_8 \cdot P_{X_8} + (1-s) \cdot x_8 \cdot (x_4 + x_8) \right. \\ & + x_4 \cdot (x_2 + x_4 + x_6 + x_8) \\ & \left. + \frac{(1-s) \cdot x_8 \cdot (x_2 + x_6) + (x_2 + x_6) \cdot x_8}{2} \right], \end{aligned}$$

$$\begin{aligned} w_{A_1} = {}& f_{LL}\cdot[(x_1+x_5)(x_1+x_3+x_5+x_7)] \\ &+ f_{LH}\cdot\left[(x_1+x_5)(x_2+x_6) \right. \\ &\left. + \frac{(x_1+x_5)(x_4+x_8)+(x_3+x_7)(x_2+x_6)}{2}\right] \\ &+ f_{HL}\cdot\left[(x_2+x_6)(x_1+x_5) \right. \\ &\left. + \frac{(x_2+x_6)(x_3+x_7)+((1-s)\cdot x_8+x_4)(x_1+x_5)}{2}\right] \\ &+ 1\cdot\left[(x_2+x_6)(x_2+x_4+x_6) \right. \\ &\left. + \frac{(1-s)\cdot x_8\cdot(x_2+x_6)+(x_2+x_6)\cdot x_8}{2}\right]. \end{aligned}$$

We can graphically represent the co-evolution of the A_2 allele and type 2 song with a vector-field plot in two dimensions which shows how a_2 and t_2 change from a range of possible values, this is shown in Fig. 1. This figure demonstrates that for all values of a_2 when $t_2 \neq 0$ there is frequency-dependent selection for or against allele A_2, except for an internal equilibrium. While the precise value of a_2 above which allele A_2 invades depends on the value of t_2, the vector plots show that it is approximately true that when a_2 is above the value at the internal equilibrium, A_2 invades. When a_2 is below this value, generally A_2 is selected against. Thus we use the value of a_2 at the internal equilibrium as an indicator of the value of a_2 above which A_2 will invade.

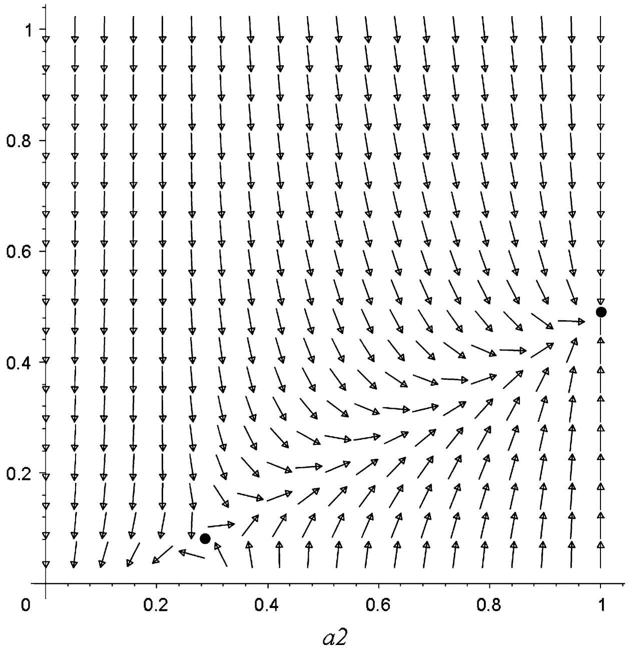

Fig. 1. Vector-field plot showing how the frequency of the type 2 song preference allele, a_2, and the frequency of type 2 song in the cultural environment, t_2, change from a range of possible values in the polygynous model. The equilibrium points are marked with a circle. The parameter values used here are: $\delta = 0.5$, $m = 10$, $n = 5$, $f_{LH} = 0.75$, $f_{HL} = 0.5$, $f_{LL} = 0.25$, $s = 0.75$. Note that the maximum possible value of t_2 is given by δ so at the $\hat{a}_2 = 1$ equilibrium in this graph $t_2 = 0.5$.

At equilibrium $a_2' = a_2$ and $t_2' = t_2$. The recursion equations (2.3) and (2.4) can be solved to give the values at which these conditions hold. The equilibrium equations do not have a general analytic solution (because of terms raised to the powers of the parameters m and n), but we can look at extremes of the model to get some understanding of the general behaviour. If we assume that $t_2 > 0$ and that m is large then the probability of hearing a type 2 song, $P_{T_2} \approx 1$. Substituting this into the equations means we find two equilibria where A_2 is either at fixation in the population or is extinct. The equilibrium values for a_2 and t_2 at these points are; $\{\hat{a}_2 = 0, \hat{t}_2 = 0\}$, $\{\hat{a}_2 = 1, \hat{t}_2 = \delta\}$. As the vector-field plot suggests, there is no stable equilibrium where alleles A_1 and A_2 coexist and $t_2 \neq 0$. The expression for the unstable polymorphic equilibrium is rather complicated and so is included in Appendices A–C.

The equilibrium we have found when $\hat{a}_2 = 0$ is not actually a valid equilibrium of the full model, as when $a_2 = 0$, $t_2 = 0$, so our assumption that $P_{T_2} \approx 1$ no longer holds. In fact solving the full model finds one solution when $t_2 = 0$, $\{\hat{a}_2 = a_2, \hat{t}_2 = 0\}$. This means that when $t_2 = 0$ the value of a_2 will not change. This is an intuitive result as when there are no type 2 songs in the environment the birds carrying A_2 behave in exactly the same way as the A_1 carrying birds, and so selection cannot act on the frequency of A_2.

A full stability analysis of these three equilibria is included in Appendices A–C, and this shows that the A_2 fixation equilibrium is the only generally stable equilibrium when $s > 0$. The polymorphic equilibrium is unstable for a wide range of the parameter values, and the equilibrium where $t_2 = 0$ is stable to perturbations in t_2 for some values of a_2 and the parameters, but perturbations in a_2 will persist. This has some interesting consequences for a finite population.

When $t_2 = 0$ selection cannot act on a_2. This means that in a finite population the value of a_2 will be controlled by effects such as pleiotropy and drift. If a_2 were to drift to a value greater than the polymorphic equilibrium value and there was then some cultural invention or mutation event which created some type 2 songs, allele A_2 could then invade the population and remain stable.[3] As the stability analysis shows, invasion of allele A_2 is the only globally stable equilibrium value, but the likelihood of invasion in a finite population will increase as the polymorphic equilibrium value of a_2 decreases, i.e. as the basin of attraction for the invasion of A_2 gets larger.

The polymorphic equilibrium value of a_2 depends on only four of the model parameters (m, n, δ and f_{HL}, for

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[3] As noted earlier, this is not a completely rigorous analysis as there are some values of a_2 larger than the equilibrium value that will be selected against for low values of t_2, but the value of a_2 at the polymorphic equilibrium gives us a reasonable numerical proxy for values above which A_2 will be positively selected for.

details of this expression see Appendices A–C). To demonstrate the effects of these parameters on the polymorphic equilibrium value of a_2, and hence the opportunity for invasion of A_2, we varied one parameter at a time while holding the others constant. The effects of each of these parameters are shown in Fig. 2. These graphs demonstrate that as the number of songs heard in infancy (m), the number of males each female chooses a mate from (n), and the proportion of high quality individuals (δ) increase, the value of a_2 above which A_2 is selected for decreases. As the relative fitness of high quality females who mate with low quality males (f_{HL}) increases it becomes harder for allele A_2 to invade. These results bear out the intuition that as factors increasing the chance that an X_8 female finds an X_8 mate increases, invasion by A_2 is easier. When the relative fitness of high quality females who mate with low quality males increases, the advantage of the X_8 females over other high quality females decreases and so the opportunity for invasion of A_2 decreases.

Some of the model parameters do not affect the equilibrium values but do have an effect on the stability of the equilibria. These parameters thus affect the likelihood of finding the system at a given equilibrium and the speed at which the system evolves to an equilibrium. As Appendices A–C demonstrate in detail, increasing the relative fitness of a low quality female mating with a low quality male (f_{LL}) and that of a low quality female mating with a high quality male (f_{LH}) reduces the advantage of X_8 females and so decreases the stability of invasion by A_2. Increasing the strength of the X_8 female's preference for type 2 song singing males (s) increases the disparity in behaviour between the X_8 females and the other types and so will speed up the invasion or extinction of allele A_2. When $s = 0$ there are no stable equilibria and there is no selection for or against A_2.

2.2. Monogamy

Many songbird species are largely monogamous and, as our model assumes that males only provide direct benefits to females (e.g. food, parental care), our assumption in the previous section that high quality males may mate an unlimited number of times may be misleading. It is unlikely that a high quality male would be able to provide such benefits to several females at once. In this section we therefore incorporate monogamy into the model.

To model monogamy we need to assume that as a female chooses a mate this male is no longer available for mating with any other female. When $s>0$, a proportion s of the X_8 females (henceforth referred to as the 'choosy' X_8 females) preferentially choose X_8 males and when they make their choices they will skew the distribution of available X_8 males in the population. All other females choose at random and so they will not change the distribution of males. We have been unable to deal with this mathematically in general and instead we have made two simplifying assumptions to allow us to calculate the mating frequencies. Firstly we follow O'Donald (1980) in that we only consider the two cases when either the choosy proportion of the X_8 females get to pick their mates *before* all the other females, or when these females choose *after* all the other

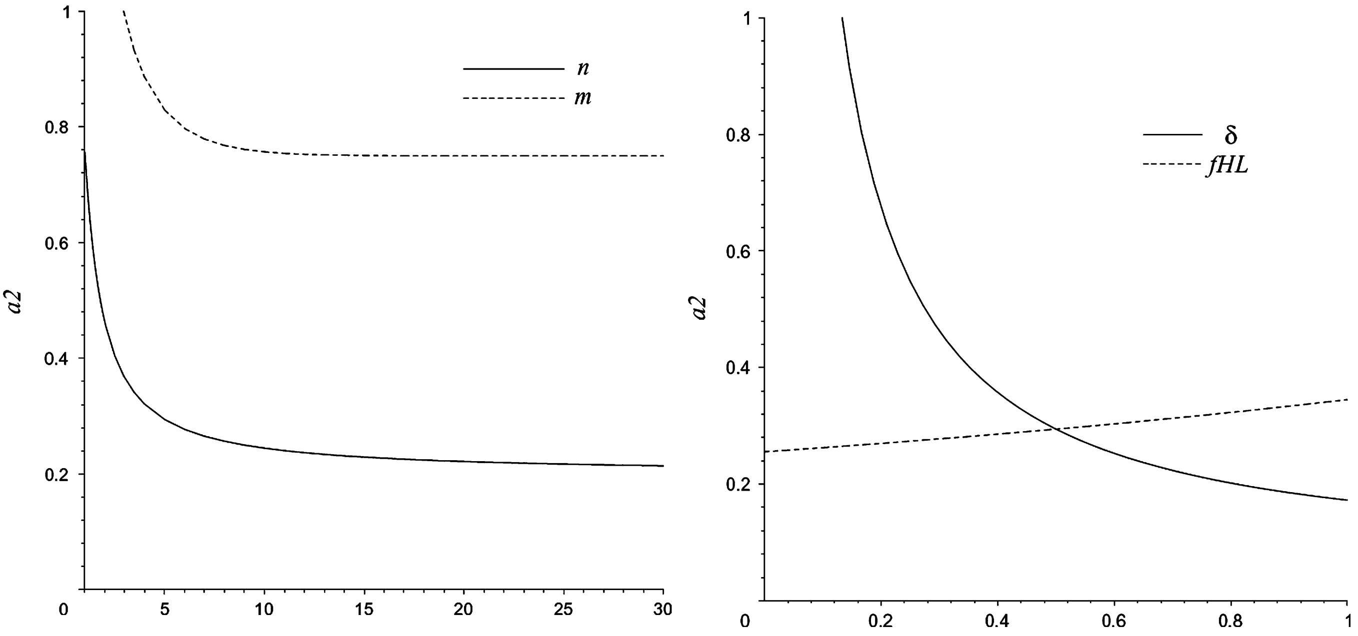

Fig. 2. Graphs showing the effect of the number of songs heard as an infant (m), the number of males a female chooses a mate from (n), the proportion of high quality birds (δ), and the relative fitness of a high quality female mating with a low quality male (f_{HL}) on the polymorphic equilibrium value of a_2 in the polygynous model. The default parameter values used are: $\delta = 0.5$, $m = 10$, $n = 5$, $f_{HL} = 0.5$. Note that increasing m, n and δ decreases the equilibrium value, making invasion by A_2 more likely, while increasing f_{HL} makes invasion less likely.

Table 4
Frequencies of matings for the monogamous model when the choosy $s \cdot x_8$ proportion of the X_8 females choose before the other females

Females	Males			
	X_1	$\ldots$	X_7	X_8
X_1				$\frac{x_1 \cdot (1-s) \cdot x_8}{1-(s \cdot x_8)}$
$\vdots$		$\frac{x_i \cdot x_j}{1-(s \cdot x_8)}$		$\vdots$
X_7				$\frac{x_7 \cdot (1-s) \cdot x_8}{1-(s \cdot x_8)}$
X_8	$\frac{(1-s) \cdot x_8 \cdot x_1}{1-(s \cdot x_8)}$	$\ldots$	$\frac{(1-s) \cdot x_8 \cdot x_7}{1-(s \cdot x_8)}$	$\frac{((1-s) \cdot x_8)^2}{1-(s \cdot x_8)} + (s \cdot x_8)$

Table 5
Frequencies of matings for the monogamous model when the choosy $s \cdot x_8$ proportion of the X_8 females choose after the other females

Females	Males			
	X_1	$\ldots$	X_7	X_8
X_1				$x_1 \cdot x_8$
$\vdots$		$x_i \cdot x_j$		$\vdots$
X_7				$x_7 \cdot x_8$
X_8	$(1-s) \cdot x_8 \cdot x_1$	$\ldots$	$(1-s) \cdot x_8 \cdot x_7$	$((1-s) \cdot x_8 \cdot x_8) + (s \cdot x_8 \cdot x_8)$

females.[4] The former approach is the one taken by some previous models of monogamy (e.g. Andersson, 1986), but we model both extremes as these represent the highest and lowest possible number of matings involving X_8 females. These extremes therefore give us an upper and lower bound on the case where the X_8 females choices are intermixed with the other females. The second simplification we make is that the number of mates females choose from, $n = \infty$ so that a choosy X_8 female is guaranteed to find an X_8 male if there are any left in the population (as again otherwise we would have to deal with a changing distribution of male types). We realise that both of these assumptions are biologically implausible, but we hope that these extremes of the model will provide some insight on the full behaviour that we could not otherwise obtain.

The frequencies of matings between all eight phenogenotypes when the X_8 females choose first is given in Table 4, and the frequencies when the X_8 females choose last is given in Table 5.

For the case where the choosy X_8 females choose after the other females, a proportion $(1-x_8)+(1-s) \cdot x_8$ of the X_8 males will have paired off with other females. This will leave a proportion $s \cdot x_8$ of the X_8 males, so the frequency of choosy $X_8 \times X_8$ matings will be $s \cdot x_8 \cdot x_8$ and the remaining proportion $1-x_8$ of the choosy X_8 females will not find a mate. This means that this model is in fact a special case of the polygynous model for $P_{X_8} = x_8$ (which is mathematically equivalent to setting $n = 1$) and so the recursion equations (2.3) and (2.4) and the equilibria found earlier are the same for this model, but with n set to 1.

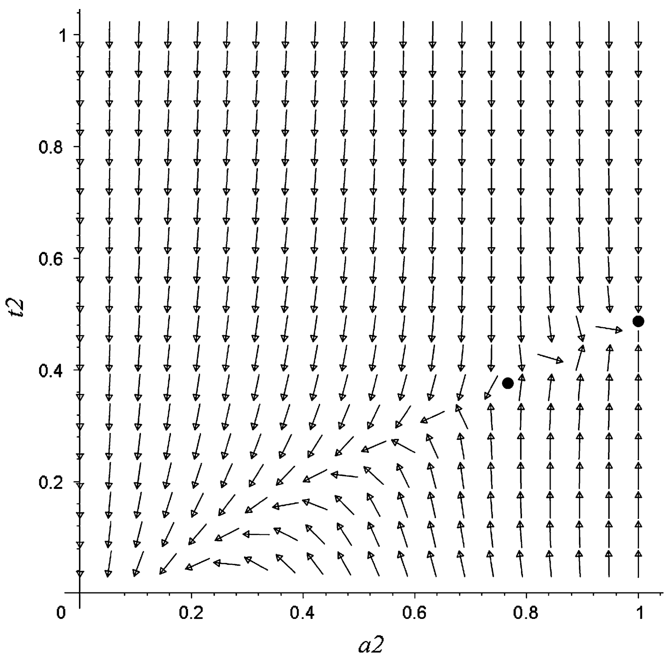

Fig. 3. Vector-field plot for the monogamous model when the X_8 females choose after the other females. The equilibrium points are marked with a circle. The parameter values used here are: $\delta = 0.5$, $m = 10$, $f_{LH} = 0.75$, $f_{HL} = 0.5$, $f_{LL} = 0.25$.

---

[4] We do not consider the proportion $(1-s)$ of the X_8 females as they choose indiscriminately and therefore do not affect the distribution of males.

A vector-field plot for this model is shown in Fig. 3. We see that the internal equilibrium for this model (with the same values of m, δ and f_{HL} as used in the polygynous model) requires a higher value of a_2 and so we would expect that allele A_2 would be less likely to invade this population than for the polygynous model. Fig. 5 shows the effect of m, δ and f_{HL} on the polymorphic equilibrium value of a_2, again demonstrating that higher values of m and δ increase the chance of invasion of A_2. Increasing f_{HL} again decreases the chance of invasion by A_2 but it has a rather stronger effect here than in the polygynous model. We can see that when $f_{HL} = 1$ there is no region of selection for A_2 and so it would be very unlikely to invade. In other words, as expected, there needs to be some advantage for high quality females to mate with high quality males.

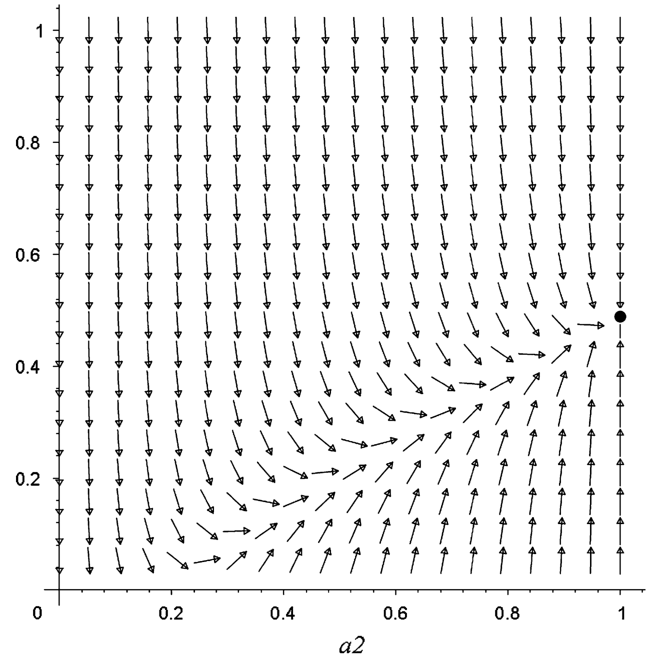

Fig. 4. Vector-field plot for the monogamous model when the X_8 females choose before the other females. The equilibrium point is marked with a circle. Note that there is no polymorphic equilibrium in this model. The parameter values used here are: $\delta = 0.5$, $m = 10$, $f_{LH} = 0.75$, $f_{HL} = 0.5$, $f_{LL} = 0.25$.

For the case where the choosy X_8 females choose before the other females we note that, by definition, there will always be as many X_8 males as X_8 females. As we assume here that $n = \infty$, this means that the choosy proportion s of the X_8 females are guaranteed to be paired with an X_8 male so there remains only a proportion $1 - s$ of the X_8 males remaining for the other females to select. We therefore need to redefine the recursion equations slightly for this model. Essentially we reduce the frequency of any mating event that includes an X_8 male mating with any female type other than a choosy X_8 female by $1 - s$, and we then divide each of the remaining mating event frequencies by $1 - (s \cdot x_8)$ to allow for the reduced frequency of X_8 males. The full recursions for this model are given in Appendices A–C and a vector-field plot for this model is shown in Fig. 4. This model also has a stable equilibrium with A_2 at fixation, and again, if $t_2 = 0$ any value of a_2 is stable. Unlike the other two models there is no polymorphic equilibrium and there is no region of selection against A_2, this is a consequence of the guarantee that a choosy X_8 female will find a high quality X_8 mate; i.e. unlike the previous models there is no risk for being choosy (Fig. 5).

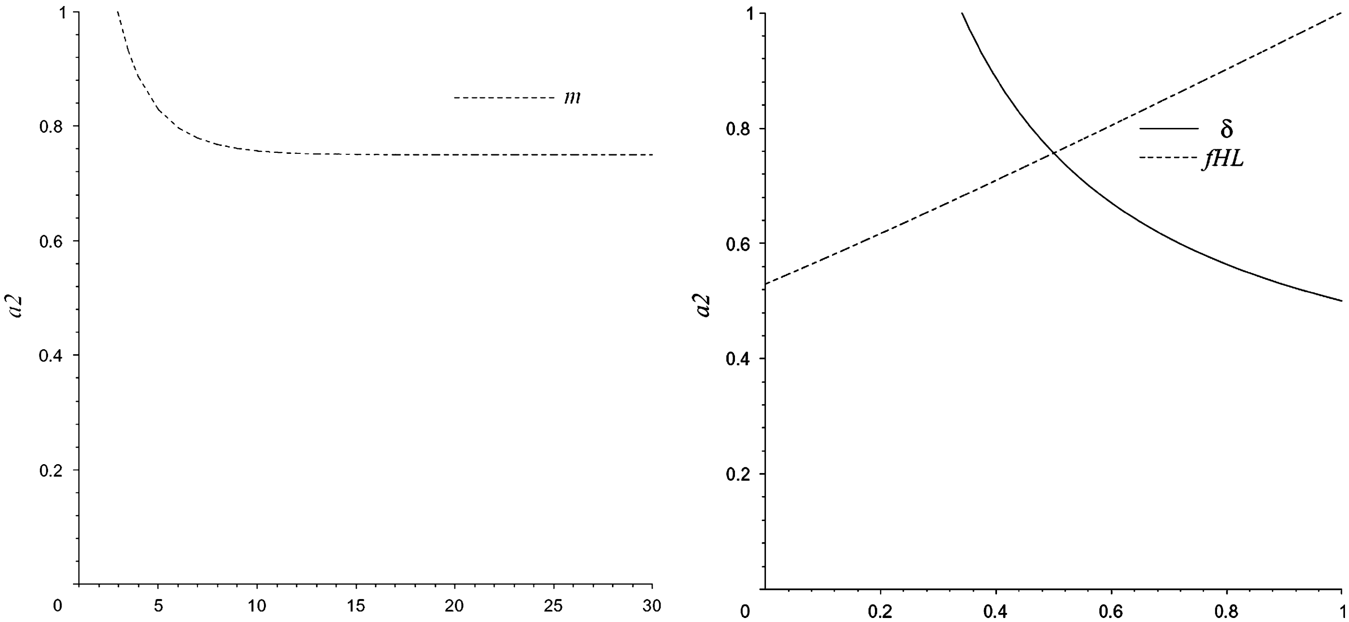

Fig. 5. Graphs showing the effect of the number of songs heard as an infant (m), the proportion of high quality birds (δ), and the relative fitness of a high quality female mating with a low quality male (f_{HL}) on the polymorphic equilibrium value of a_2 in the monogamous model when the X_8 females choose after the other females. The default parameter values used are: $\delta = 0.5$, $m = 10$, $f_{HL} = 0.5$. Note that increasing m and δ decreases the equilibrium value, making invasion by A_2 more likely, while increasing f_{HL} makes invasion less likely.

Although there is no region of selection against A_2 in this model there is a region where there is no selection for A_2. As the stability analysis included in Appendices A–C demonstrate, A_2 will be subject to selection when $a_2 > 1/\delta m$. When this condition is satisfied a small perturbation to t_2 will allow A_2 to be positively selected for. Overall in this model then, we would expect allele A_2 to be able to invade this population more easily than in the previous two models but the likelihood of invasion is again dependent on the values of δ and m, with larger values making invasion more likely.

As demonstrated in Appendices A–C, for both of these models, the parameters f_{LL}, f_{LH} and s have the same qualitative effect on the stability of the equilibria as we found for the monogamous model.

These models thus provide the first theoretical support for the DSH, showing that a preference for less learnable 'complex' song can evolve, and that cultural transmission of this song type is stable.

3. Discussion

The DSH proposes that learned features of male song can be used as an indicator of early developmental stress. The models we present demonstrate that, in a range of conditions, selection can favour a genetic learning bias for culturally transmitted song types which reveal a potential mate's level of developmental stress. They also show that there can be stable cultural transmission of these less learnable song types. The opportunity for invasion of such an allele in a finite population depends; however, on several biologically relevant parameters, including the prevalence of stressors, the number of unique songs heard as an infant and the number of potential mates available to females to choose from. Assumptions about the mating system also have an important effect. The models also incorporate some considerations that have yet to be investigated empirically, such as the effect of early song exposure and developmental stress on female preferences.

We make very few assumptions about the nature of the song types, so any feature of song whose acquisition is affected by developmental stress may be used as an indicator. This seems consistent with the biological data, because, as we discussed earlier, it appears that females of several different species attend to different features of song, but importantly all of which seem to be particularly affected by developmental stress.

The models presented here are admittedly simple, and there are a number of modifications we could make to make them more biologically plausible, such as working with a finite population and modelling the cultural transmission of song in a more realistic way than the panmictic cultural environment we assume here. Making such modifications would, however, make the mathematical analysis of the interactions of the parameters considerably harder and less clear. Nevertheless, we feel that these simple models incorporate some of the key features of the DSH and, while we hope to relax some of these assumptions in future work, as they stand, the models suggest a number of predictions which may be testable empirically and we present some here.

Firstly, if there are a low proportion of high quality birds, i.e. the average level of developmental stress in the population is high, the model predicts that we will be less likely to see such a system evolve. This is because it will be harder for the few high quality birds to overcome the frequency-dependent selection against them below the threshold value (which we discuss further below). The model also predicts that we are more likely to see such a system evolve in species where the females are able to pick mates from a relatively large pool of males, and, in monogamous species, where the high quality females are able to pick mates earlier in the breeding season than low quality females (as originally suggested by Darwin, 1879). A final, rather intuitive, prediction is that if the fitness detriment of mating with a low quality male is small then there is little advantage to finding a high quality male and such a system is much less likely to evolve.

Unlike other models of sexual selection, we do not include an explicit cost difference for birds singing or preferring either of the two song types. This was a deliberate decision, as it appears that many of the features of male song that female birds have been shown to prefer appear to be relatively cheap to produce (Nowicki and Searcy, 2004). As an example, it is not clear that a bird singing a song with a larger range of acquired syllables will, for example, expend more time or energy, or be more likely to be predated upon, than a bird singing a simpler song. Yet, as mentioned earlier, female great reed warblers appear to prefer males singing songs with more syllable variation, and males singing in this way appear to be more successful parents (Hasselquist, 1998). It is generally accepted that in order to be reliable a signal must be costly in some way (e.g. Grafen, 1990) and so this appears to be something of a quandary. The original intention of Nowicki et al. (1998) in proposing the DSH was to resolve this problem. They suggested that learned features of song can be reliable indicators of male quality as a result of the *developmental* cost of acquiring the song. Our models include this developmental cost implicitly by assuming that high quality individuals are able to learn some song types that low quality individuals cannot. In assuming that the X_8 females will sometimes fail to find a mate, we also impose a cost on choosiness.

In the first two models we found a strong threshold effect, due to the frequency-dependent selection for or against X_8 individuals. We found that the frequency of the A_2 allele must rise above a threshold value, by some mechanism such as random drift, before it can stably invade the population. How likely this situation is to arise is therefore significant in our analysis of the model. All we require of such an allele is that it makes the bearer predisposed to learning some song types rather than others; this might be as a result of some form of auditory bias that occurred by mutation or drift, or by selection on auditory capacities not related to song preference. We feel that such mutations are likely to have occurred fairly frequently in the evolution of the songbirds to give rise to the great variety of song types and preferences we find today. The only special property we require of this bias is that the ability to learn a song that satisfies the bias is correlated in some way with the level of developmental stress. As we discussed in Section 2.1, once an allele encoding this sort of bias is present in a finite population, it will be subject to forces such as drift until some cultural invention or mutation event occurs which produces a song type with the appropriate features. High quality bearers of the allele are then able to reliably find a high quality mate and, in sufficient numbers, the allele can stably invade the population.

Previous theoretical work on the evolution of cultural communication systems, especially human language, (e.g. Brighton et al., 2005; Oudeyer, 2005) has argued that there is often a cultural evolutionary pressure in such systems for the signals to become increasingly learnable. This seems an intuitive result as culturally transmitted communication systems must be able to be acquired by each new generation of learners if they are to persist, and so less learnable forms are likely to be selected against. It is a surprising result of our models that selection can favour a preference for a song type that is, by definition, less learnable, and that such types can be stably culturally transmitted. This is a result of the fact that less learnable song types allow female birds to differentiate males according to their learning ability. The idea that songs that are less learnable might be more attractive to females is supported by recent work showing that both female swamp sparrows (Ballentine et al., 2004) and canaries (*Serinus canaria*) (Draganoiu et al., 2002) prefer songs that are closer to the physical performance limit of males (in these cases of the trill rate and frequency bandwidth), and therefore hardest to produce and, plausibly, to acquire.

The models synthesise the available biological data and verbal arguments and provide the first theoretical support for a novel role for cultural transmission in sexual selection (though see also Laland, 1994). This may have implications for other species that rely on cultural transmission, for example humans are also altricial and acquire language early in life. It is possible that an effect similar to the one we investigate here may have played a role at some stage in the evolution of the human language faculty.

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Appendix A. The expression for the polymorphic equilibrium for the polygynous model

$$\hat{a}_2 = \frac{e^{(Y/n)} - 1}{\delta \cdot (e^{(Ym/n)} - 1)}, \tag{A.1}$$

$$\hat{t}_2 = 1 - e^{(Y/n)}, \tag{A.2}$$

where

$$Y = \ln\left(1 + \frac{f_{HL} \cdot \delta - f_{HL} - \delta}{2}\right).$$

Appendix B. Recursion equations for the monogamous model when the X_8 females choose before the other females

$$t_2' = x_8, \tag{B.1}$$

$$a_2' = \frac{w_{A_2}}{w_{A_1} + w_{A_2}}, \tag{B.2}$$

where

$$\begin{aligned} w_{A_2} = {} & f_{LL} \cdot \left[\frac{(x_3 + x_7)(x_1 + x_3 + x_5 + x_7)}{1 - (s \cdot x_8)}\right] \\ & + f_{LH} \cdot \left[\frac{(x_3 + x_7)(x_4 + (1 - s) \cdot x_8)}{1 - (s \cdot x_8)} + \frac{(x_1 + x_5)(x_4 + (1 - s) \cdot x_8) + (x_3 + x_7)(x_2 + x_6)}{2 \cdot (1 - (s \cdot x_8))}\right] \end{aligned}$$

$$
\begin{aligned}
&+f_{HL}\cdot\left[\frac{((1-s)\cdot x_8+x_4)(x_3+x_7)}{1-(s\cdot x_8)}+\frac{(x_2+x_6)(x_3+x_7)+((1-s)\cdot x_8+x_4)(x_1+x_5)}{2\cdot(1-(s\cdot x_8))}\right]\\
&+1\cdot\left[s\cdot x_8+\frac{(1-s)\cdot x_8\cdot(x_4+(1-s)\cdot x_8)+x_4\cdot(x_2+x_4+x_6+(1-s)\cdot x_8)}{1-(s\cdot x_8)}\right.\\
&\left.+\frac{(1-s)\cdot x_8\cdot(x_2+x_6)+(x_2+x_6)\cdot(1-s)\cdot x_8}{2\cdot(1-(s\cdot x_8))}\right],
\end{aligned}
$$

$$
\begin{aligned}
w_{A_1}=&f_{LL}\cdot\left[\frac{(x_1+x_5)(x_1+x_3+x_5+x_7)}{1-(s\cdot x_8)}\right]\\
&+f_{LH}\cdot\left[\frac{(x_1+x_5)(x_2+x_6)}{1-(s\cdot x_8)}+\frac{(x_1+x_5)(x_4+(1-s)\cdot x_8)+(x_3+x_7)(x_2+x_6)}{2\cdot(1-(s\cdot x_8))}\right]\\
&+f_{HL}\cdot\left[\frac{(x_2+x_6)(x_1+x_5)}{1-(s\cdot x_8)}+\frac{(x_2+x_6)(x_3+x_7)+((1-s)\cdot x_8+x_4)\cdot(x_1+x_5)}{2\cdot(1-(s\cdot x_8))}\right]\\
&+1\cdot\left[\frac{(x_2+x_6)(x_2+x_4+x_6)}{1-(s\cdot x_8)}+\frac{(1-s)\cdot x_8\cdot(x_2+x_6)+(x_2+x_6)\cdot(1-s)\cdot x_8}{2\cdot(1-(s\cdot x_8))}\right].
\end{aligned}
$$

Appendix C. Stability analysis

The local stability of the equilibria we have found can be investigated by finding the leading eigenvalue of the (Jacobian) stability matrix of the model evaluated at each of the equilibrium values (for details of this technique see, e.g., Otto and Day, 2006). This tells us the effect that a small perturbation, ε, will have on the equilibrium values of a_2 and t_2 (ε is assumed to be small enough to ignore in second and higher order terms). If the leading eigenvalue is greater than 1 then the perturbation will grow over time and so the equilibrium is unstable, while if the leading eigenvalue is less than 1 the perturbation will shrink over time and the equilibrium is locally stable.

C.1. Polygynous model

To make algebraic analysis possible we again make the simplifying assumption that $t_2 > 0$ and that m is large, so that $P_{T_2} = 1$. In this case for the A_2 fixation equilibrium, where $\{\hat{a}_2 = 1, \hat{t}_2 = \delta\}$, the only non-zero eigenvalue is given by the following equation:

$$
\lambda=\frac{f_{LL}\cdot(2-4\delta+2\delta^2)+f_{LH}\cdot(2\delta-2\delta^2)+f_{HL}\cdot(2\delta-s\delta-2\delta^2-s\delta^2)+2\delta^2-s\delta^2}{2\cdot[f_{LL}\cdot(1-2\delta+\delta^2)+f_{LH}\cdot(\delta-\delta^2)+f_{HL}\cdot(\delta-\delta^2-s\delta+s\delta^2)+s\delta-s\delta(1-\delta)^n+\delta^2-s\delta^2]}. \tag{C.1}
$$

Eq. (C.1) is a rather complicated expression and we have been unable to find simple expressions of the parameters which allow us to see when the equilibrium will be stable. Instead, to investigate the effect of the various parameters on the eigenvalue we have varied one parameter at a time while holding the others constant, the results of this analysis are shown in Fig. 6. This figure demonstrates that $\lambda < 1$ for a wide range of parameter values, the only time that $\lambda \geqslant 1$ is when δ is very low or when $s = 0$, i.e. when the X_8 females show no preference for type 2 song. This suggests that this equilibrium is generally stable for plausible parameter values.

For the polymorphic equilibrium the only non-zero eigenvalue is a very complicated expression, but using a computer algebra system we have been able to perform the same graphical analysis as used above. The effects of each of the parameters is shown in Fig. 7. We see that the $\lambda > 1$ for a wide range of parameter values which suggests that this equilibrium is generally unstable.

For the final equilibrium of the model where $\{\hat{a}_2 = a_2, \hat{t}_2 = 0\}$ and we no longer assume that $P_{T_2} = 1$, there are two non-zero eigenvalues: $\lambda_1 = 1$ and $\lambda_2 = \delta a_2 m$. The first eigenvalue reflects the fact that when $t_2 = 0$ any perturbation in a_2 will persist over time but will neither shrink nor grow. The second eigenvalue characterises the stability of a perturbation in t_2. $\lambda_2 > 1$ when $a_2 > 1/\delta m$, so if a_2 drifts to a value larger than this a perturbation to t_2 will grow and A_2 will become subject to frequency-dependent selection.

C.2. Monogamous models

For the monogamous model where the X_8 females choose after the other females, the equilibria are the same as for the polygynous model and so the same stability analysis applies here, except that the parameter n is fixed at 1.

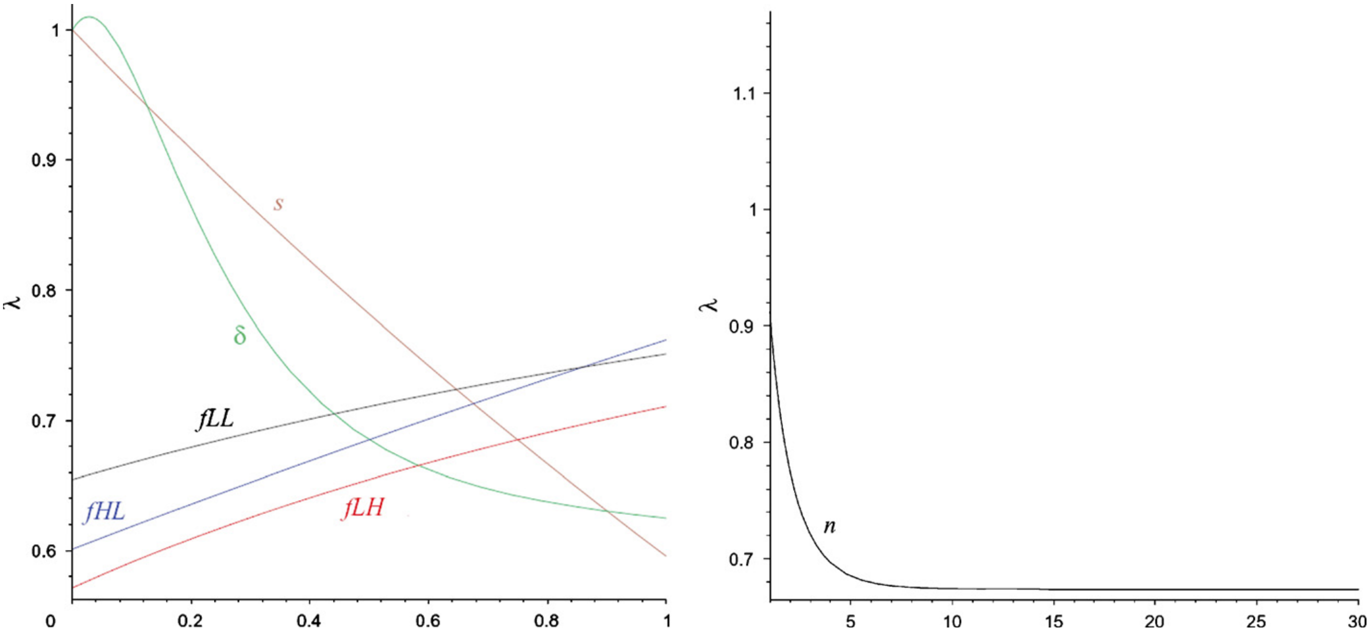

Fig. 6. Graphs showing the effect of the parameters on the leading eigenvalue of the A_2 fixation equilibrium for the polygynous model. The default parameter values used here are: $\delta = 0.5, m = 10, n = 5, f_{LH} = 0.75, f_{HL} = 0.5, f_{LL} = 0.25, s = 0.75$. Note that $\lambda < 1$ for all parameter values (except when $\delta < \sim 0.05$ and $s = 0$).

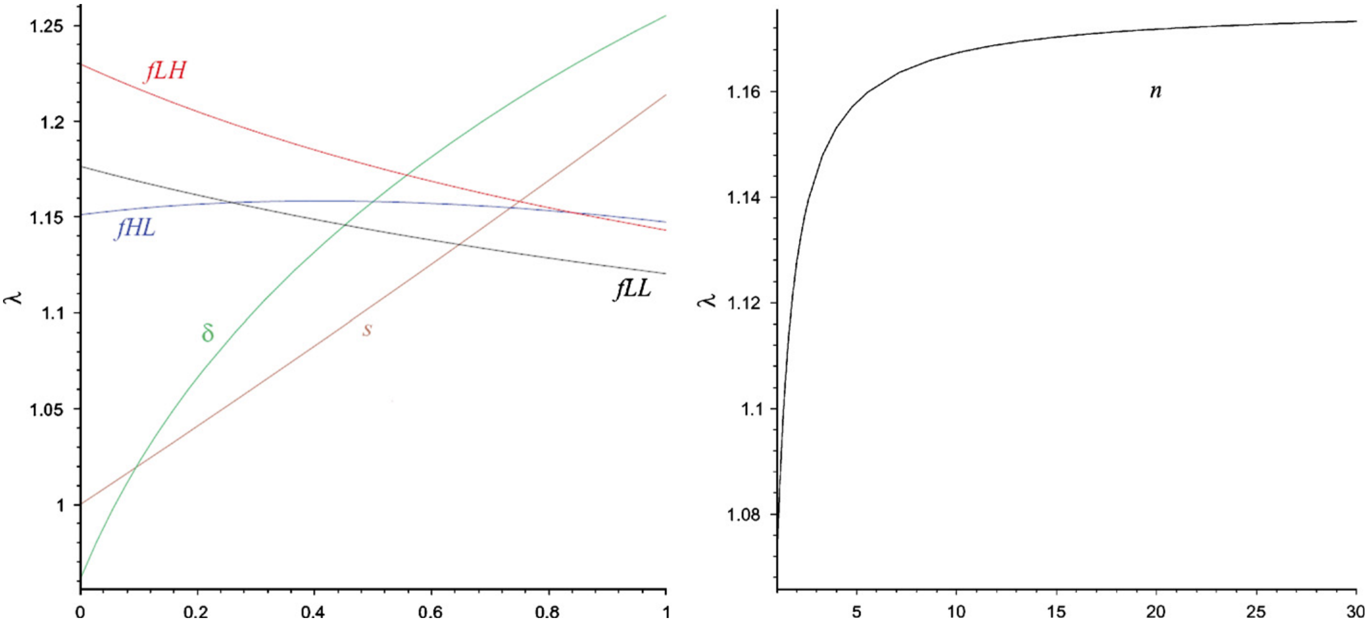

Fig. 7. Graphs showing the effect of the parameters on the leading eigenvalue of the polymorphic equilibrium for the polygynous model. The default parameter values used here are: $\delta = 0.5, m = 10, n = 5, f_{LH} = 0.75, s = 0.75, f_{HL} = 0.5, f_{LL} = 0.25$. Note that $\lambda > 1$ for a wide range of parameter values except when $\delta < \sim 0.05$ and $s = 0$.

For the case where the X_8 females choose before the other females there is no polymorphic equilibrium, but there is a fixation equilibrium where, again, $\{\hat{a}_2 = 1, \hat{t}_2 = \delta\}$. The only non-zero eigenvalue of this equilibrium is given by Eq. (C.2). This is again a rather complicated expression and so we provide a graphical analysis of the effect of different parameter values in Fig. 8. We see again that this equilibrium appears to be stable over a broad range of parameter values:

$$\lambda = \frac{f_{LL} \cdot (2 - 4\delta + 2\delta^2) + f_{LH} \cdot (2\delta - s\delta - 2\delta^2 + s\delta^2) + f_{HL} \cdot (2\delta - s\delta - 2\delta^2 - s\delta^2) + 2\delta^2 - 2s\delta^2}{2 \cdot [f_{LL} \cdot (1 - 2\delta + \delta^2) + f_{LH} \cdot (\delta - s\delta - \delta^2 + s\delta^2) + f_{HL} \cdot (\delta - s\delta - \delta^2 + s\delta^2) + s\delta + \delta^2 - 2s\delta^2]}. \tag{C.2}$$

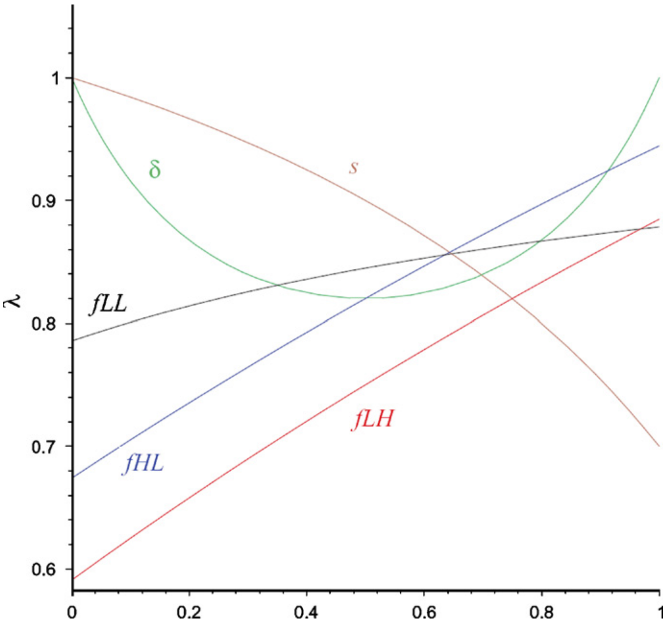

Fig. 8. Graph showing the effect of the parameters on the leading eigenvalue of the A_2 fixation equilibrium for the monogamous model when the X_8 females choose before the other females. The default parameter values used here are: $\delta = 0.5$, $m = 10$, $f_{LH} = 0.75$, $f_{HL} = 0.5$, $f_{LL} = 0.25$, $s = 0.75$. Note that $\lambda < 1$ for all parameter values tested here (except when $\delta = 0$ or 1 and when $s = 0$).

The eigenvalues for the $\{\hat{a}_2 = a_2, \hat{t}_2 = 0\}$ equilibrium of this model are the same as for the polygynous case and so the same analysis applies here. However, as there is no region of selection against A_2 in this model the result that $\lambda_2 > 1$ when $a_2 > 1/\delta m$ gives us the value of a_2 above which A_2 is positively selected for. Therefore, as δ and m increase this threshold value decreases and so the likelihood of invasion by A_2 increases.

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