Table 1: Summary of choices made in previous models	
	Lachlan and Servedio [2]
♂trait(s)	allele A / a: song predisposition
	song
How ♂trait is learned	
Inherited	
♀trait(s)	
How ♀trait is learned	
Inherited	
Errors	
Population structure	
Mating structure	
♀preference	
Selection	

1 Question

1. H1 Song learning can decelerate speciation by allowing for genetically diverse birds to mate with each other, maintaining gene flow between subpopulations that might either begin to diverge

2. H2 Song learning can accelerate speciation by increasing standing genetic variation, which would allow for quicker divergence once new selection pressures arise [2]

3. H3 Song learning can accelerate speciation because culturally inherited traits can evolve more quickly than genetically inherited ones [1]

2 Goals

3 Model

3.1 Continuous traits Each male has a song and each female has preference for a particular song. She will mate with males with songs other than her preferred song, but the probability of her doing so decreases as the potential mate's song gets less similar to her preferred song. Each female mates once and chooses a male according to her preferences and the distribution of songs present in the population. Each male, therefore, may breed multiple times or not at all. We assume that generations are non-overlapping, so once the adults breed they die and we can shift our focus to the new generation. To begin with, we

assume that males acquire their songs from their fathers at birth and females acquire their preferences from their mothers at birth. We further assume an unbiased sex ratio. Before the new generation mates, each male has a small probability of "mutating" its song. This can be interpreted as a learning error or as innovation. After mutation, the new males and females mate.

Mathematically, each male has a song $x \in \mathbb{R}$ and each female has a preference $y \in \mathbb{R}$. The probability density of the male songs will be written $P_{\mathrm{m}}(x)$ and the probability density of female preferences will be written $P_{\mathrm{f}}(y)$. The preference of a female with preference y mates for a male with song x is

$$f_y(x) = \frac{1}{\sqrt{2\pi\sigma^2}} \exp\left(-\frac{(x-y)^2}{2\sigma^2}\right),$$

which is maximal when $x = y$ and decreases as $|x-y|$ increases. The probability that a female with preference y choose a male with song x is

$$\frac{P_{\mathrm{m}}(x)f_y(x)}{\int_{\mathbb{R}} P_{\mathrm{m}}(x')f_y(x')dx'},$$

so the probability of a (x, y) pair mating is then

$$P(x, y) = \frac{P_{\mathrm{f}}(y)P_{\mathrm{m}}(x)f_y(x)}{\int_{\mathbb{R}} P_{\mathrm{m}}(x')f_y(x')dx'}.$$

Each such pair will produce a male with song x and a female with preference y. Before mating, the male's song changes to $x - \delta_{\mathrm{mut}}$ with probability $p_{\mathrm{mut}}/2$ and to $x + \delta_{\mathrm{mut}}$ with probability $p_{\mathrm{mut}}/2$. Under these assumptions, the probability density of female preferences does not change over time:

$$P_{\mathrm{f}}(y, t+1) = P_{\mathrm{f}}(y, t).$$

The probability density of male songs in the next generation, before mutating and after mutating, follows

$$P_{\mathrm{m}}(x, t+1/2) = \int_{\mathbb{R}} P(x, y)dy$$

$$P_{\mathrm{m}}(x, t+1) = (1 - p_{\mathrm{mut}})P_{\mathrm{m}}(x, t+1/2) + p_{\mathrm{mut}}/2P_{\mathrm{m}}(x - \delta_{\mathrm{mut}}, t+1/2) + p_{\mathrm{mut}}/2P_{\mathrm{m}}(x + \delta_{\mathrm{mut}}, t+1/2)$$

The last thing we need to specify is the initial distributions of male songs and female preferences.

CODE FOR THE POPULATION DYNAMICS:

```
dynamics <-function(){
Pm = matrix(0,Nm,Tsteps+1) #probability of male songs over time
Pm[,1] = m_init

Pf = matrix(0,Nf,Tsteps+1) #probability of female preferences over time
```

```
Pf[,1] = f_init

# t = 1
for(t in 1:Tsteps){
        Pm_adults = Pm[,t]
        Pf_adults = Pf[,t]
        pxy = matrix(0,Nm,Nf) #probability of a (x,y) pair
        ### should I round Pm_adults?!? how?!? is that why I'm getting bumps?!?
        for(j in 1:Nf){
                y = frange[j]
                # weight = 1/sqrt(2*pi*sigma2)*exp(-(mrange-y)^2/(2*sigma2))
                weight = dnorm(mrange,mean=y,sd=sqrt(sigma2)) #female preference function
                # weight = matrix (0,Nf,1)
                # weight[c(f0,x1)] = 1
                # weight[j] = 1+alpha
                z = int(weight*Pm_adults) #normalization factor
                if(z!=0){
                        pxy[,j] = Pf_adults[j]*weight*Pm_adults/z
                        }
        }
        Pm_beforemut = matrix(0,Nm)
        for(i in 1:Nm){
                Pm_beforemut[i] = int(pxy[i,]) #probability of males being born
        }
        Pm_aftermut = matrix(0,Nm)
        Pm_aftermut = (1-mut_prob)*Pm_beforemut + mut_prob/2*c(Pm_beforemut[2:Nm],0)
                + mut_prob/2*c(0,Pm_beforemut[1:Nm-1]) #and then they change their songs
        Pm[,t+1] = Pm_aftermut
        Pf[,t+1] = Pf_adults
}
pop_dens = list(Pm=Pm,Pf=Pf)
return(pop_dens)
}
```

GLOBAL / NEEDED PARAMETERS:

```
step = 0.01 #step size of trait space
int_step = step #step to use for integration function
# alpha = 0.5 #if preference function is a step fx, strength of preference
# sigma2 = #variance of female preference function
# mut_prob =  #probability a male changes song to one on either side
# mut_delta = #how to implement mutations of different sizes?
# fmix_sigma2 = #variance of female distribution(s)
# mmix_sigma2 = 0.1 #variance of male distribution(s)
# Tsteps = #how many generations
```

```
mrange = seq(-10,10,by=step) #range of male songs
Nm = length(mrange)
mmin = -1
mmax = 1
m0 = which(mrange==mmin)
m1 = which(mrange==mmax)
mrange_orig = seq(mmin,mmax,by=step)
frange = seq(-10,10,by=step) #range of female preferences
Nf = length(frange)
fmin = -1
fmax = 1
f0 = which(frange==fmin)
f1 = which(frange==fmax)
frange_orig = seq(fmin,fmax,by=step)
```

INTERESTING PARAMETERS:

```
sigma2 = 0.1
mut_prob = 0.01
fmix_sigma2 = 1
Tsteps = 60

m_init = array(0, dim = c(Nm,1))
m_init[m0] = 0.6
m_init[m1] = 0.4
m_init[,1] = m_init[,1]/int(m_init[,1])


p = .4
f_init = p*dnorm(frange,-1,fmix_sigma2)+(1-p)*dnorm(frange,1,fmix_sigma2)

pop_dens = dynamics()
Pm = pop_dens$Pm
Pf = pop_dens$Pf
```

Even with a continuous distribution of female preferences, we find that after several generations, the male song distribution is concentrated in several discrete peaks (Figure 1).

```
v = Pm[,1]
Tsteps = 1
m_init = v
m_init = m_init/int(m_init)

p = .4
f_init = p*dnorm(frange,-1,fmix_sigma2)+(1-p)*dnorm(frange,1,fmix_sigma2)
```
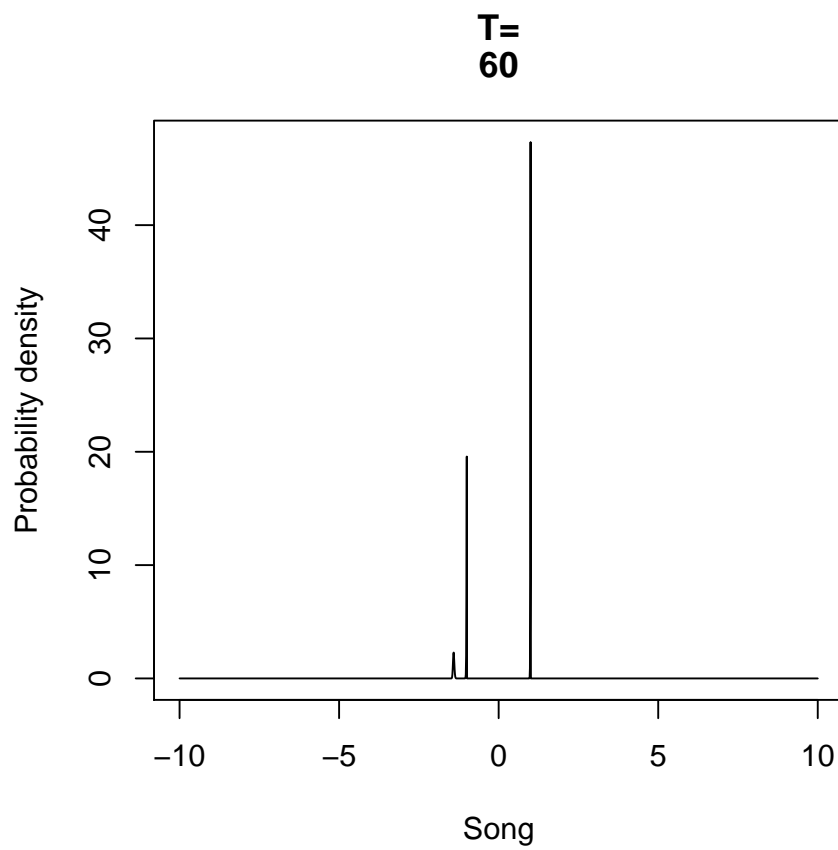
T=
60

Figure 1: Probability density of male songs. Notice the discrete peaks.

```
# f_init = .3*dnorm(frange,-1,fmix_sigma2)+.3*dnorm(frange,0,fmix_sigma2)+.4*dnorm(frange,1,

Pm2 = matrix(0,Nm,Tsteps+1)
Pm2[,1] = m_init

Pf2 = matrix(0,Nf,Tsteps+1)
Pf2[,1] = f_init

pop_dens2 = dynamics()
Pm2 = pop_dens2$Pm
Pf2 = pop_dens2$Pf

# break down the mating and preference probabilities
c = 1e-10 #recognition cutoff
d = sqrt(-2*sigma2*log(sqrt(2*pi*sigma2)*c))
#^distance / difference at which a female can recognize a male
recognized = array(0,dim=c(Nm,1))

for(i in 1:Nm){
        x = mrange[i]
        y1 = x - d
        y2 = x + d
        w1 = which(frange>=x-d)
        w2 = which(frange<=x+d)
        recognized[i] = int(Pf2[intersect(w1,w2),1]
        *dnorm(x-frange[intersect(w1,w2)],mean=0,sd=sqrt(sigma2)))
        #^how many females recognize each male, weighted by their preferences
}

preferences = array(0,dim=c(Nm,Nf))
female_tots = matrix(0,Nf)

for(j in 1:Nf){
        y = frange[j]
        # weight = 1/sqrt(2*pi*sigma2)*exp(-(mrange-y)^2/(2*sigma2))
        weight = dnorm(mrange,mean=y,sd=sqrt(sigma2))
        # weight = matrix (0,Nf,1)
        # weight[c(f0,x1)] = 1
        # weight[j] = 1+alpha
        z = int(weight*Pm2[,Tsteps])
        # if(z!=0){
                # pxy[,j] = Pf2[j,1]*weight*Pm2[,Tsteps]/z
                # }
        preferences[,j] = weight #preference given by each female to each male
        female_tots[j] = z #total preferences given by each female
```
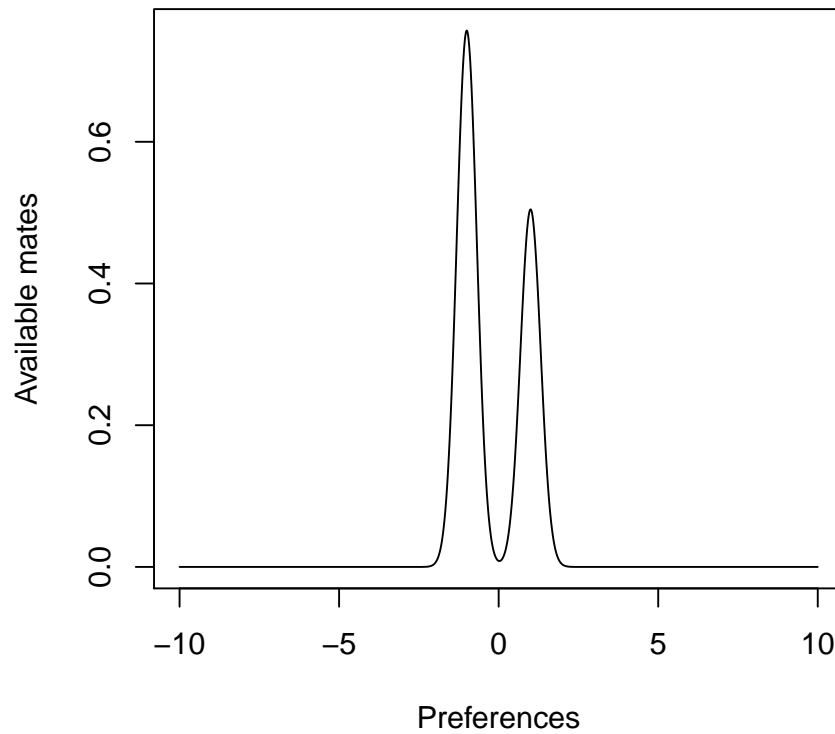
Figure 2: Available mates as a function of female preference.

```
}
```

```
plot(frange, female_tots, type='l', xlab = 'Preferences',ylab = 'Available mates')
```

References

[1] D.E. Irwin. Culture in songbirds and its contribution toward the evolution of new species. In E. Slingerland and M. Collard, editors, *Creating Consilience: Integrating the Sciences and the Humanities*, pages 163–178. Oxford University Press, 2012.

[2] R. Lachlan and M. Servedio. Song learning accelerates allopatric speciation. *Evolution*, 58(9):2049–2063, 2004.