"Skepticism Towards Santa Rosalia, or Why are There so Few Kinds of Animals?"

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Introduction

- In attempts to understand speciation and the forces that drive it, past speciation models have focused on the ecological explanations.
  - For example, species diversity was often explained through the lens of competitive exclusion.
- Because of this, previous population genetic models of speciation have shown sympatric speciation to be achievable under conditions that are not difficult to achieve.
  - This led Felenstein to propose the overarching question: why do we not see more species?
- This paper explores the possibility that there may be genetic constraints to speciation, which could explain the lack of speciation we see in the real world.

Basic Model

- The basic model consisted of 3 loci: A, B, and C (each with two alleles)
  - Locus B and Locus C affect natural selection
  - Locus A controls assortative mating through mate preference

- Parameters
  - S = fitness/selection coefficient
  - D = Mating Preference
  - M = Migration - Initial model sets migration to 0.5 for complete mixing.
  - r = recombination factor - initial model sets recombination to 0.5 which doesn't effect the initial outcome and provides a baseline.

- Considers an infinite large population with one set of chromosomes(Haploidy) and discrete generations.

- Island migration between two populations is assumed.

Natural Selection		
Allele Combinations	Group 1	Group 2
BC	(1+s)^2	1
Bc	1+s	1+s
bC	1+s	1+s
bc	1	(1+s)^2

↓

Assortative Mating		
	A	a
A	p2(1-d)+pd	p(1-p)(1-d)
a	p(1-p)(1-d)	(1-p)^2*(1-d)+(1-p)d

Basic Model and Results

The basic model shows how speciation can occur in a case where there are two alleles that affect environmental adaptation at loci B and C, through assortative mating
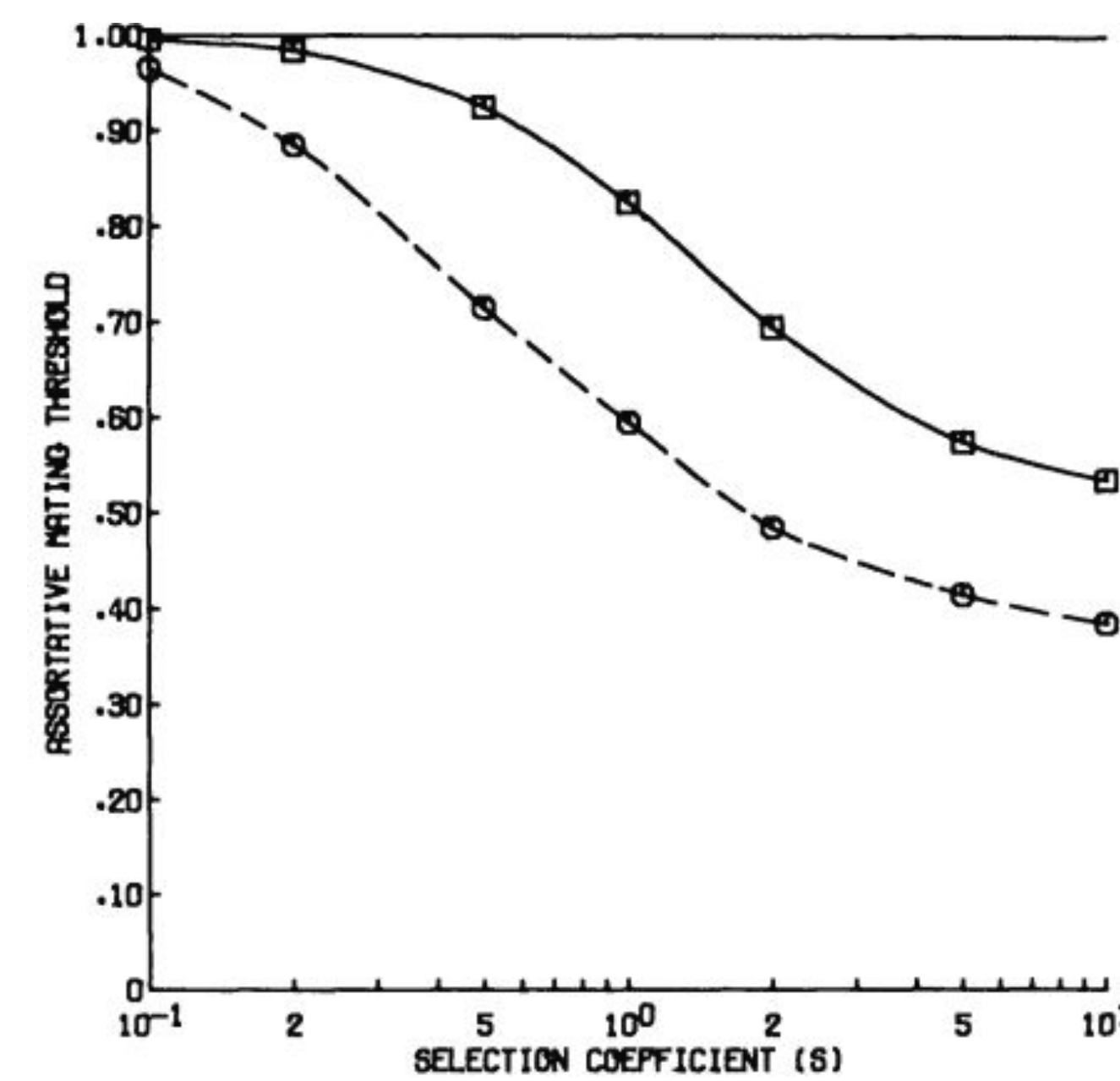

Figure 1a.

s	r_{12}	r_{23}	m	SMR	SRM
					d
1.0	.5	.5	.5	.82−.83	.81−.82
1.0	.5	.5	.1	.59−.60	.57−.58
1.0	.5	.5	.01	.51−.55	.53−.54
1.0	.1	.5	.1	.28−.29	.27−.28
1.0	.5	.1	.1	.86−.87	.86−.87

Figure 1b. This table shows threshold amounts for assortative mating required to induce speciation within each combination of model factors, as well as the order of selection, recombination, and migration that must occur.

Figure 1a. The model allows a graphical representation of factors including migration (M), selection coefficient (S), and the mating threshold/preference (D). The x-axis highlights the selection coefficient (S), while the y-axis highlights the assortative mating threshold. The solid line represents a plot where m=0.5, whereas the dotted line represents a plot where m=0.1.

- The region above the curve is where the disequilibrium between A and B/C can become established, and speciation can occur. No disequilibrium can become established below the curve, due to insufficient assortative mating that is unable to overcome gene flow.
- It is possible to create a sympatric speciation model that occasionally does not speciate. Speciation requires strong selection and a strong isolating mechanism.
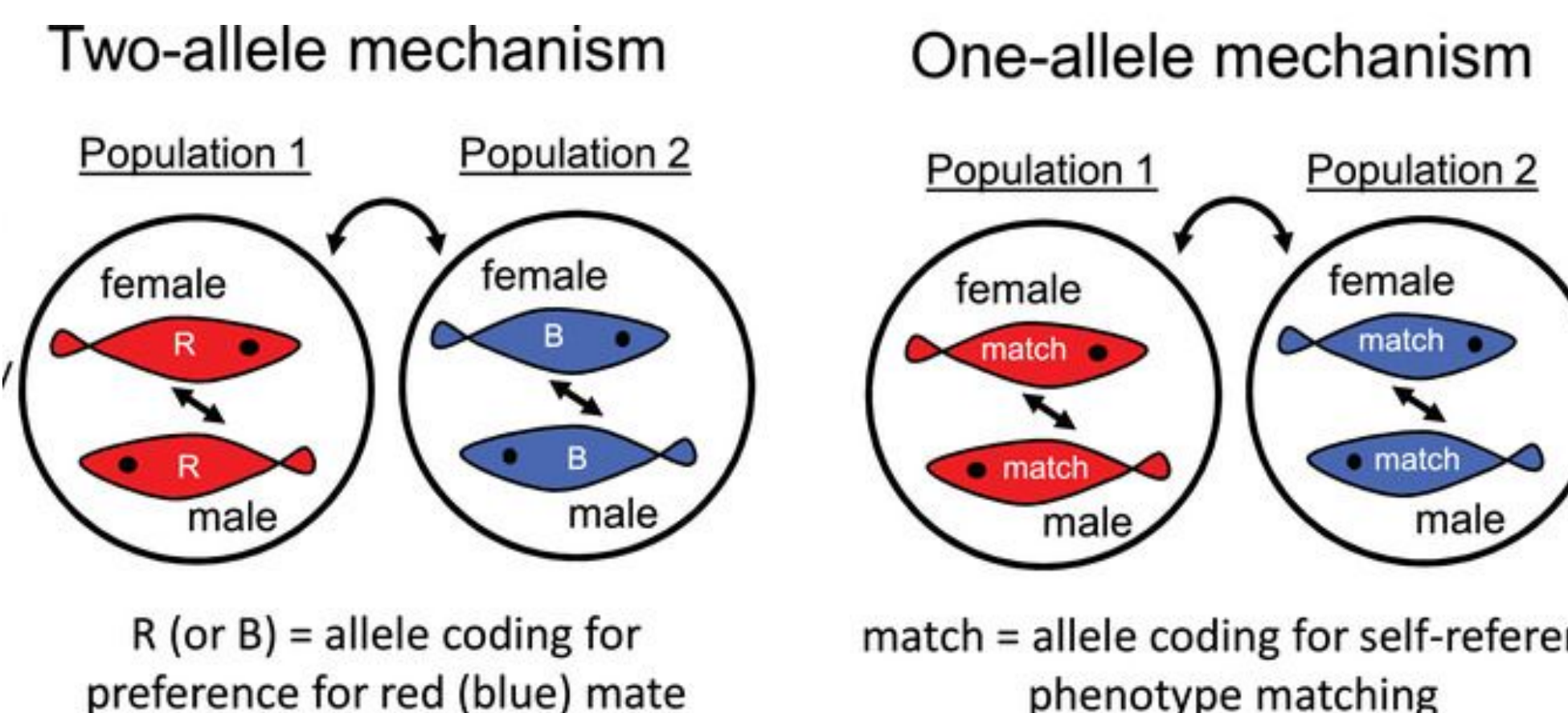- Recombination: high amounts of recombination lead to lower chances of speciation as seen in Figure 1b.

Figure 2 (cited from Butlin et al.; see citations)

Figure 2. highlights both one- and two-allele mechanisms inherently expressed through assortative mating and its relationship to speciation. A one-allele mechanism is when a single allele amplifies the rate at which assortative mating occurs. This single allele will spread across both populations. Whereas the one-allele model can be altered to have two outcome comparisons. This is relevant when different or separate alleles code for two different phenotypes, which amplifies assortative mating. In other words, R will code for one phenotype, and B will code a different phenotype.

- Speciation CAN occur under a two allele mechanism.

Model Variants

Timing of Migration:
- *Assumption*: Instead of event order of Selection - Migration - Recombination (SMR), speciation can occur if recombination is prior to migration (SRM)
- *Result:* (Haploid) To prevent linkage disequilibrium, d was smaller in SRM order than SMR order - as expected; (Diploid) In some cases, success of speciation was harder to find in SRM order than SMR order

Interaction between Loci:

$$1 + 2s + ks^2$$

- *Assumption:* the association of prezygotic and postzygotic isolation mechanisms depends mostly on minute changes in additive (k=1) and multiplicative (k=0) fitness combinations
- *Result:* At a value of m=0.1, speciation occurred at k=-0.5; thus the smaller mean fitness values of the Bc and bC genotypes is only a requirement for the Levene Model (m=0.5), changing values can make speciation easier

Diploidy
- *Assumption*: Whether the mating scheme is a haploid or diploid case, the probability of mating is dependent on the Locus A genotype

	AA $(1 + d)/2$	Aa $1/2$	aa $(1 − d)/2$
Genotypes			Fitness in subpopulation I / II
BBCC	$(1 + s)^4$		1
BbCC, BBCc	$(1 + s)^3$		$1 + s$
BBcc, BbCc, bbCC	$(1 + s)^2$		$(1 + s)^2$
Bbcc, bbCc	$1 + s$		$(1 + s)^3$
bbcc	1		$(1 + s)^4$

- *Result*: The qualitative results are similar between the haploid and diploid models; the exception being that increasing linkage between loci B and C does not increase speciation restriction as much in the diploid model

Implications, Further Exploration, and Conclusions

Implications:
➢ In sympatric speciation, there will be less genetic differentiation in genes that contribute to isolation after speciation, than in allopatric speciation.
➢ If genetic variation in both one-allele and two-allele isolation is high, then there will be no block to speciation.

Ideas for Expanding the Felsenstein Model:
➢ Make the genetic profile of the reproductively isolating and adaptive traits polygenic to explore whether results from this study can be extrapolated to traits with different numbers of genes controlling a trait.
➢ Explore the effects of unequal population sizes in the subpopulations.
➢ Examine situations where a novel species arises in a nearby population.

Conclusion:
➢ The model:
  ○ Two loci under natural selection in two subpopulations.
  ○ Different alleles adapted to the different subpopulations.
  ○ A third locus in which there is assortative mating that affects the proportions of the other two loci.
➢ What acts against sympatric speciation?
  ○ Recombination, which randomizes the association between assortative mating and natural selection!
➢ Recombination opposes speciation only in cases where there is substitution of different alleles, instead of substitution of the same alleles.

Citations

Felsenstein, Joseph. "Skepticism Towards Santa Rosalia, or Why are There so Few Kinds of Animals?" *Evolution*, vol. 35, no. 1, 1981, pp. 124-38. JSTOR, https://doi.org/10.2307/2407946. Accessed 6 Mar. 2024.
Butlin, Roger K. & Servedio, Maria R. et al. "Homage to Felsenstein 1981, or why are there so few/many species?" *Evolution*, vol. 75, no. 5, 2021.. pp. 978-88. Wiley Online Library, https://doi.org/10.1111/evo.14235. Accessed 6 Mar. 2024.