Effects of Evolution of Species Discrimination on Population Viability

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Methods

0.1 Model Assumptions

We model a scenario where recently diverged species come into secondary contact. The two species are present in sympatry, and there is ecological competition between them. (Interspecific competition > intraspecifc competition hence, unstable ecological equilibrium)

Tom: the model concerns a secondary contact zone, where members of the two species (or should we call these populations...) frequently interact...

Initially, males of both species are completely indiscriminate - i.e. they court conspecific and heterospecific males with equal probability.

The Model

Species and Mating Consider species 1 and 2. There are F_1 and F_2 females and M_1 and M_2 males. Females mate just once but they might reject some males that approach them before mating.

Female Acceptance A female of species i accepts an approaching heterospecific male $1 - y_i$

Male Discrimination Consider a male that discriminates with strength z_i. This impacts both the rate at which he approaches heterospecific females (the more he discriminates, the less he approaches them), but it might also impact the rate at which he approaches conspecific ones. This is the idea behind many Servedio papers: if you reject wrong type of mates, you might have more of a 'budget' to approach conspecifics.

Approach Rates For this reason, we could model his rate of approaching conspecifics as $1 + \alpha z_i$, while his rate of approaching heterospecifics is $1-z_i$. The relevant range for both $1 - s$ and z is from 0 to 1.

Female Perspective From the perspective of a focal female of species 1, matings with conspecifics occur at a rate $M_1(1 + \alpha z_1)$ while matings with heterospecifics occur at a rate $M_2(1 - y_1)(1–z_2)$. She is assumed to mate just once, thus this one mating is with a conspecific with a probability

$$\frac{M_1(1 + \alpha z_1)}{M_1(1 + \alpha z_1) + M_2(1 - y_1)(1–z_2)} \tag{1}$$

The complementary probability is 1 minus that, and is (in the simplest case) assumed to lead to no offspring.
The other species' female perspective is derived similarly.

0.2 Male Fitness

Now, for males. What is male fitness? Heterospecific matings do not lead to anything (in the simplest case), conspecific matings do.

The number of offspring in a breeding season, considering conspecific matings, can be represented by the equation:

$$N_{t+1} = \frac{F_1 M_1(1 + \alpha \bar{z}_1)}{M_1(1 + \alpha \bar{z}_1) + M_2(1 - y_1)(1 - \bar{z}_2)} \tag{2}$$

Number of offspring produced per unit male rating rate is:

$$\frac{N_{t+1}}{(1 + \alpha \bar{z}_1)} = \frac{F_1 M_1}{M_1(1 + \alpha \bar{z}_1) + M_2(1 - y_1)(1 - \bar{z}_2)} \tag{3}$$

Thus, the focal male is responsible for a portion of the total number of offsprings produced, proportional to its own mating rate

$$N_{focal_{(t+1)}} = \frac{F_1(1 + \alpha z_1)}{M_1(1 + \alpha \bar{z}_1) + M_2(1 - y_1)(1 - \bar{z}_2)} \tag{4}$$

The average male fitness is $\frac{N_{t+1}}{M_1}$:

$$\bar{W} = \frac{F_1(1 + \alpha z_1)}{M_1(1 + \alpha z_1) + M_2(1 - y_1)(1 - z_2)} \tag{5}$$

0.2.1 Breeder's Equation

We make use of the breeder's equation $\Delta \bar{z} = h^2 S$ to model the evolution of a trait (z), in response to selection within a single generation. h^2 is the narrow-sense heritability of the trait, or the proportion of phenotypic variance (V_P) in the trait made up by additive genetic variance (V_A) across the population.

0.2.2 Evaluating Selection Differential for Male Discrimination from Fitness function

$$\bar{z_{t+1}} - \bar{z}_t = S_{diff}$$

Where $\bar{z}_{t+1}$, the mean value of the phenotypic trait in the next generation is

$$\bar{z}_{t+1} = (\frac{1}{\bar{W}_m} \int W_m(z) z p(z)\, dz)$$

For derivation of the above equation see **??**

W_{z_1} (fitness) of the male with trait z_1 is

$$\frac{F_1(1+\alpha_1 z_1)}{M_1(1+\alpha_1 \bar{z}_1) + M_2(1-s_1)(1-\bar{z}_2)} \tag{6}$$

$$\frac{W_{z_1}}{\bar{W}_z} = \frac{(1+\alpha_1 z_1)}{(1+\alpha_1 \bar{z}_1)} \tag{7}$$

Assume that the traits follow a Gaussian distribution centered on $\bar{z}_1$ with variance σ_p^2 (phenotypic variance). (Note: Strictly, this is not true - (the traits should be between 0 and 1). But it can be an approximation if we assume that the variance is low)

$$p(z_1) = \frac{1}{\sqrt{2\pi\sigma_p^2}} \exp\left(-\frac{(z_1 - \bar{z}_1)^2}{2\sigma_p^2}\right)$$

$$\int_{-\infty}^{\infty} \frac{W_{z_1}}{\bar{W}_z} p(z_1) dz_1 = \frac{(z_1 + \alpha_1 {z_1}^2)}{(1+\alpha_1 \bar{z}_1)} p(z_1) dz_1 \tag{8}$$

$$\int_{-\infty}^{\infty} \frac{W_{z_i}}{W_z} p(z_1) dz_1 - \bar{z}_1 = \frac{\alpha_1 \sigma_p^2}{1+\alpha_1 \bar{z}_1}. \tag{9}$$

The above selection differential is multiplied with h which is $\frac{\sigma_a^2}{\sigma_p^2}$ to obtrain $\Delta\bar{z}$

Thus,

$$\Delta\bar{z} = \frac{\alpha\sigma_a^2}{(1+\alpha\bar{z})} \tag{10}$$

0.3 Evolution of Female permissivness to heterospecific courtship

Assumptions: There is no linkage between y_i of females and z_i of males. Both of these traits are autosomal and there is no sex-linkage

The female permissiveness $1 - y_i$ can be an evolving trait.

Previously, we described that from the female perspective, the number of offspring produced is equivalent to the probability of mating with a conspecifc Under the assumption that females can mate only once. We computed the conspecifc mating probabilty as follows: :

$$P_{conspecific} = \frac{M_1(1+\alpha z_1)}{M_1(1+\alpha z_1) + M_2(1-y_1)(1-z_2)}$$

This is equivalent to the expected number of offspring produced by a female with resistance trait value $1 - y_i$

$$W_f(y_i) = P_{conspecific} = \frac{M_1(1+\alpha z_1)}{M_1(1+\alpha z_1) + M_2(1-y_i)(1-z_2)}$$

0.3.1 Average Female Fitness

To compute the average fitness of females in the population, $\bar{W_f}$, we take the average over the distribution of y in the population. Since there is variation in y, the average fitness across all females can be written as:

$$\bar{W_f} = \frac{M_1(1+\alpha \bar{z_1})}{M_1(1+\alpha z_1) + M_2(1-\bar{y})(1-\bar{z_2})}$$

where $\bar{y}$ is the average value of y_i across all females in the population.

0.3.2 Calculating Trait Change using Selection Differential

Let's now derive the selection differential equation for females, using a similar approach as we did for males but with the trait y instead of z. We'll calculate the expected change in the female trait y over one generation due to selection.

The selection differential equation, but now applied to the female trait y is as follows:

$$\bar{y}_{t+1} - \bar{y}_t = S_{diff}$$

Where $\bar{y}_{t+1}$ is the mean value of the female phenotypic trait y in the next generation, and $\bar{y}_t$ is the current generation's average. The selection differential S_{diff} is the difference between the trait mean in the next generation and the current one.

In analogy to the male case, the mean trait in the next generation is given by:

$$\bar{y}_{t+1} = \frac{1}{\bar{W_f}} \int W_f(y) y p(y) \, dy$$

Where: - $\bar{W_f}$ is the average female fitness in the population. - $W_f(y)$ is the fitness of a female with trait y. - $p(y)$ is the probability distribution of the female trait y.

As derived earlier, $\bar{W_f}$ and $W_f(y)$ is:

$$W_f(y_i) = \frac{M_1(1+\alpha z_1)}{M_1(1+\alpha z_1) + M_2(1-y_i)(1-z_2)}$$

And for the average trait value $\bar{y}$:

$$\bar{W}_f = \frac{M_1(1+\alpha z_1)}{M_1(1+\alpha z_1) + M_2(1-\bar{y})(1-z_2)}$$

The ratio of the individual fitness $W_f(y_i)$ to the average fitness $\bar{W}_f$ (selection gradient) is:

$$\frac{W_f(y_i)}{\bar{W}_f} = \frac{M_1(1+\alpha z_1)}{M_1(1+\alpha z_1) + M_2(1-y_i)(1-z_2)} \cdot \frac{M_1(1+\alpha z_1) + M_2(1-\bar{y})(1-z_2)}{M_1(1+\alpha z_1)}$$

Simplifying this:

$$\frac{W_f(y_i)}{\bar{W}_f} = \frac{M_1(1+\alpha z_1) + M_2(1-\bar{y})(1-z_2)}{M_1(1+\alpha z_1) + M_2(1-y_i)(1-z_2)}$$

For small variations in y_i, i.e. (variance of y is small or $y_i - \bar{y} << 1$) this ratio can be approximated by a linear expansion around $\bar{y}$: (For explanation see **??**

$$\frac{W_f(y_i)}{\bar{W}_f} \approx 1 + \frac{M_2(1-z_2)(y_i-\bar{y})}{M_1(1+\alpha z_1) + M_2(1-\bar{y})(1-z_2)}$$

Probability distribution assumption for Female Heterospecific Mating Resistance Trait Assume that the trait y_i follows a Gaussian distribution centered on $\bar{y}$ with variance σ_p^2 (the phenotypic variance):

(Assumption $\sigma_p^2 <<< 1$)

$$p(y_i) = \frac{1}{\sqrt{2\pi\sigma_p^2}} \exp\left(-\frac{(y_i-\bar{y})^2}{2\sigma_p^2}\right)$$

Evaluating the Selection Differential Now we need to compute the integral for the next generation's mean trait $\bar{y}_{t+1}$:

$$\bar{y}_{t+1} = \frac{1}{\bar{W}_f} \int_{-\infty}^{\infty} W_f(y_i) y_i p(y_i)\, dy_i$$

Using the approximation for $W_f(y_i)$, we get:

$$\bar{y}_{t+1} \approx \frac{1}{\bar{W}_f} \int_{-\infty}^{\infty} \left(1 + \frac{M_2(1-z_2)(y_i-\bar{y})}{M_1(1+\alpha z_1) + M_2(1-\bar{y})(1-z_2)}\right) y_i p(y_i)\, dy_i$$

This splits into two integrals:

$$\bar{y}_{t+1} \approx \frac{1}{\bar{W}_f} \left(\int_{-\infty}^{\infty} y_i p(y_i)\, dy_i + \frac{M_2(1-z_2)}{M_1(1+\alpha z_1) + M_2(1-\bar{y})(1-z_2)} \int_{-\infty}^{\infty} (y_i-\bar{y}) y_i p(y_i)\, dy_i \right)$$

Solving the Integrals

The first integral is just the mean $\bar{y}$, as $p(y_i)$ is centered at $\bar{y}$:

$$\int_{-\infty}^{\infty} y_i p(y_i)\, dy_i = \bar{y}$$

The second integral, involving $(y_i - \bar{y})y_i$, is related to the variance σ_p^2:

$$\int_{-\infty}^{\infty} (y_i - \bar{y}) y_i p(y_i)\, dy_i = \sigma_p^2$$

Final Expression for the Selection Differential Substituting these results into the expression for $\bar{y}_{t+1}$, we obtain:

$$\bar{y}_{t+1} \approx \bar{y} + \frac{M_2(1 - z_2)\sigma_p^2}{M_1(1 + \alpha z_1) + M_2(1 - \bar{y})(1 - z_2)}$$

Thus, the selection differential is:

$$S_{diff} = \bar{y}_{t+1} - \bar{y} = \frac{M_2(1 - z_2)\sigma_p^2}{M_1(1 + \alpha z_1) + M_2(1 - \bar{y})(1 - z_2)}$$

The above selection differential is multiplied with h which is $\frac{\sigma_a^2}{\sigma_p^2}$ to obtrain $\Delta\bar{z}$

Thus,

$$\Delta\bar{\bar{y}} = \frac{M_2(1 - z_2)\sigma_a^2}{M_1(1 + \alpha z_1) + M_2(1 - \bar{y})(1 - z_2)} \tag{11}$$

Thus, resistance y_i increases with each generation. The selection differential S_{diff} is proportional to the phenotypic variance σ_p^2. There is stronger selection when the heterospecifics are less discriminatory, and the heterospecfic : conspecific number is higher

Ecological Model

Previously, we derived the number of offsprings in the next generation in this model. This turned out to be

$$N_{off_{(t+1)}} = \frac{F_1 M_1 (1 + \alpha\bar{z}_1)}{M_1(1 + \alpha\bar{z}_1) + M_2(1 - y_1)(1 - \bar{z}_2)} \tag{12}$$

Assume both species have 1:1 sex ratio at all generations. Thus, $F = M$

$$N_{off_{(t+1)}} = \frac{\left(\frac{N_1}{2}\right)\left(\frac{N_1}{2}\right)(1 + \alpha\bar{z}_1)}{\left(\frac{N_1}{2}\right)(1 + \alpha\bar{z}_1) + \left(\frac{N_2}{2}\right)(1 - y_1)(1 - \bar{z}_2)} \tag{13}$$

This simplifies to...

$$N_{off_{(t+1)}} = \frac{\left(\frac{N_1}{2}\right)(N_1)(1 + \alpha\bar{z}_1)}{(N_1)(1 + \alpha\bar{z}_1) + (N_2)(1 - y_1)(1 - \bar{z}_2)} \tag{14}$$

Offspring Competition Note that the above equation gives the production of offspring from a single mating season; one also needs to include the intraspecific and interspecfic competition which will regulate the population.

For this purpose, one can use the Leslie-Grover Discrete competition equation

To sum it up, $N(t+1)$ depends on To sum it up, $N(t+1)$ depends on a) Resource Competition b)Mating Rates when there is incomplete species discrimination (Reproductive Interference)

$$N_1(t+1) = \left(\frac{b_1'}{1+\alpha_{11}N_1(t)+\alpha_{12}N_2(t)}\right) \cdot \frac{\left(\frac{N_1}{2}\right)(N_1)(1+\alpha\bar{z}_1)}{(N_1)(1+\alpha\bar{z}_1)+(N_2)(1-y_1)(1-\bar{z}_2)} \tag{15}$$

Let $\frac{b_1'}{2}$ be b_1, then:

$$N_1(t+1) = \left(\frac{b_1 N_1(t)}{1+\alpha_{11}N_1(t)+\alpha_{12}N_2(t)}\right) \cdot \left(\frac{N_1(1+\alpha_1\bar{z}_1)}{N_1(1+\alpha_1\bar{z}_1)+N_2(1-y_1)(1-\bar{z}_2)}\right) \tag{16}$$

Likewise, for species 2 the equation will become :

$$N_2(t+1) = \left(\frac{b_2 N_2(t)}{1+\alpha_{22}N_2(t)+\alpha_{21}N_1(t)}\right) \cdot \left(\frac{N_2(1+\alpha_2\bar{z}_2)}{N_2(1+\alpha_2\bar{z}_2)+N_1(1-y_2)(1-\bar{z}_1)}\right) \tag{17}$$

1 Results and Analysis

1.1 Evolution of Male Discrimination Example Simulation

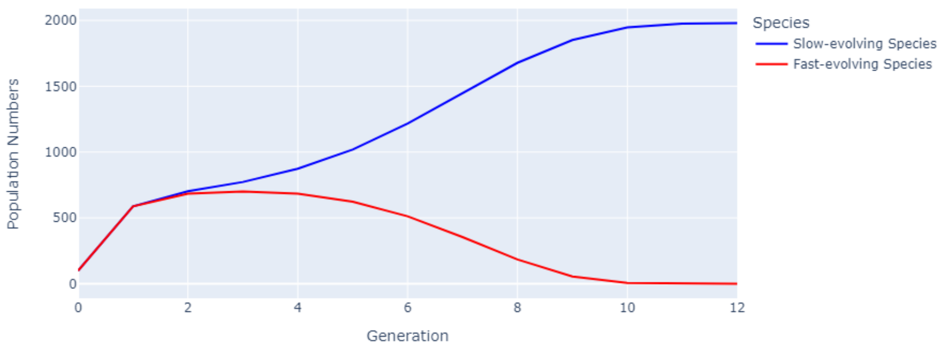


Figure 1:Population Number Change of Both Species

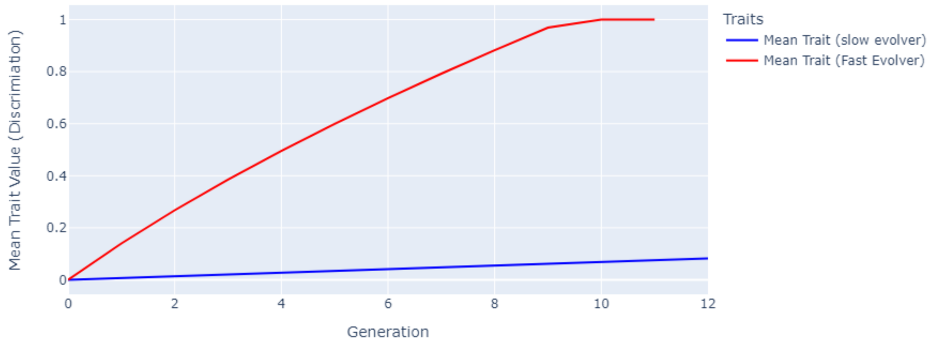


Figure 2:Mean Male Discrimination Trait Change of Both Species

2 References

1. Kuno, E. (1992). Competitive exclusion through reproductive interference. Researches on Population Ecology, 34, 275-284.

2. Takafuji, A., Kuno, E., & Fujimoto, H. (1997). Reproductive interference and its consequences for the competitive interactions between two closely related Panonychus spider mites. Experimental & Applied Acarology, 21, 379-391.

3. Morita, K., & Yamamichi, M. (2023). How does the magnitude of genetic variation affect ecological and reproductive character displacement?. Population Ecology, 65(4), 220-230.

4. Gómez-Llano, M., Germain, R. M., Kyogoku, D., McPeek, M. A., & Siepielski, A. M. (2021). When ecology fails: how reproductive interactions promote species coexistence. Trends in Ecology & Evolution, 36(7), 610-622.

5. Kyogoku, D., & Wheatcroft, D. (2020). Heterospecific mating interactions as an interface between ecology and evolution. Journal of Evolutionary Biology, 33(10), 1330-1344.

6. Servedio, Maria R., and Russell Lande. "Population genetic models of male and mutual mate choice." Evolution 60.4 (2006): 674-685.

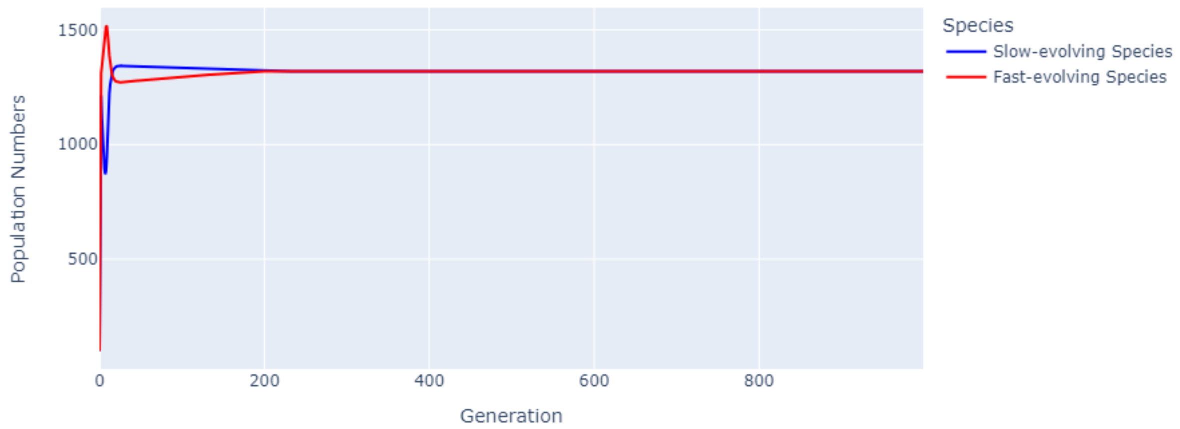
3 Acknowledgements

I acknowledge the Kishore Vaigyanik Protsahan Yojana (KVPY) for the scholarship. I express my gratitude to Professor Hanna Kokko and Dr. Tom Keaney for their invaluable

guidance. I also extend my thanks to the members of the Kokkonuts group for their constructive discussions. Illustrations were created using BioRender. I occasionally utilized ChatGPT for coding simulations.

4 Supplementary

Example simulation in which both male discrimination and female resistance evolves



Example simulation in which onlyl female resistance evolves