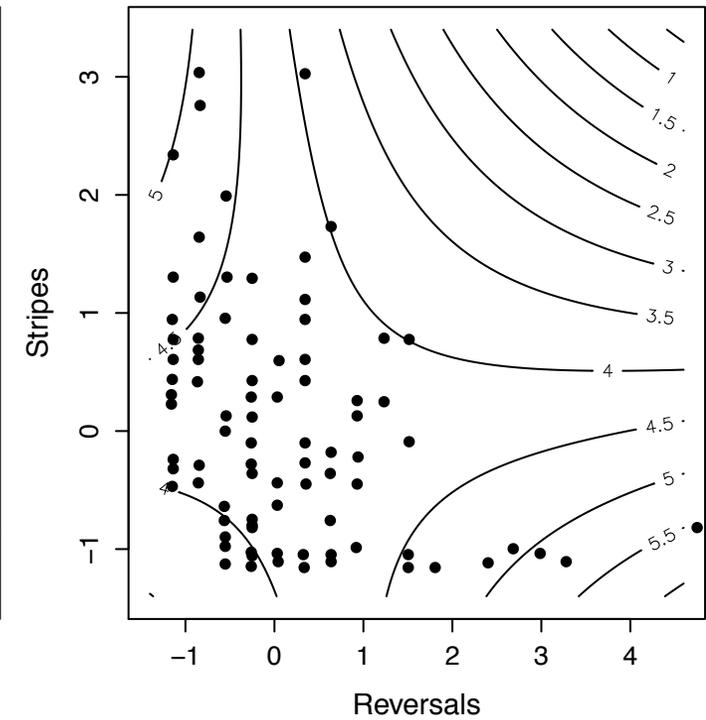
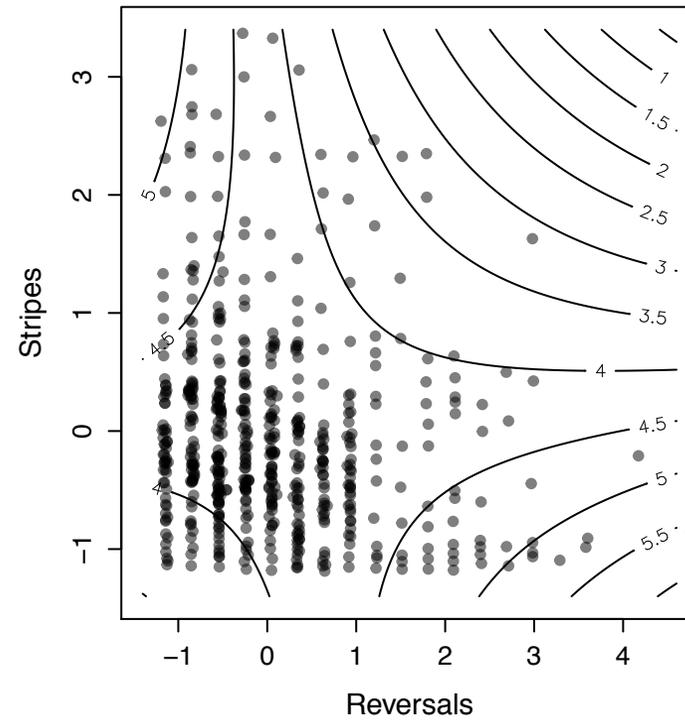
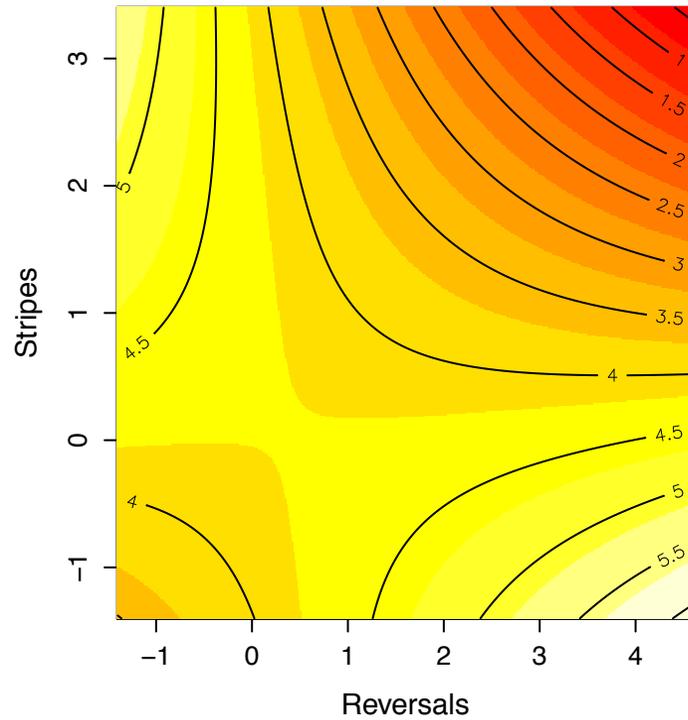


Coop, Chapter 9

The Response of Multiple Traits to Selection



Introduction

- The fitness of an organism is the outcome of many, many physiological processes and phenotypes
- Natural selection is therefore acting on multiple phenotypes at a time
- Selection for the optimum phenotype of one trait may pull another genetically correlated trait away from its optimum
- In this situation we have what are known as “fitness trade-offs” across traits



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Introduction

- To understand short-term selection on multiple phenotypes we can use the Breeder's equation:

$$\begin{aligned}R_1 &= V_{A,1}\beta_1 + V_{A,1,2}\beta_2 \\R_2 &= V_{A,2}\beta_2 + V_{A,1,2}\beta_1\end{aligned}\tag{9.1}$$

- The first term (e.g., $V_{A,1}\beta_1$) is the additive genetic variance multiplied by the selection gradient for each trait and is no different than when we focused on a single trait
- The second term ($V_{A,1,2}\beta_2$) reflects the additive covariance between traits, since our response in one phenotype is modified by selection on other traits that genetically covary

Introduction

- These equations can also be written in matrix form for any number of traits
- The change in the mean of multiple phenotypes within a generation can be written in a vector \mathbf{S} and response across multiple generations as vector \mathbf{R} which can be related by:

$$\mathbf{R} = \mathbf{G}\mathbf{V}^{-1}\mathbf{S} = \mathbf{G}\boldsymbol{\beta} \quad (9.2)$$

- Where \mathbf{V} and \mathbf{G} are our matrices of variance-covariance of phenotypes and additive genetic values respectively and $\boldsymbol{\beta}$ is a vector of selection gradients on traits accounting for phenotypic covariances with other traits

Introduction

- We can return to the work of Grant and Grant in the Medium ground-finch for an example of selection on multiple traits
- After a strong bout of selection from 1976-77, only 15% of individuals survived and there were significant changes in multiple phenotypes



Trait	Mean before Selection (1976)	S	β	Mean next gen.
Weight	16.06	0.74	0.477	17.13
Bill Length	10.63	0.54	-0.144	10.95
Bill Depth	9.21	0.36	0.528	9.70

Introduction

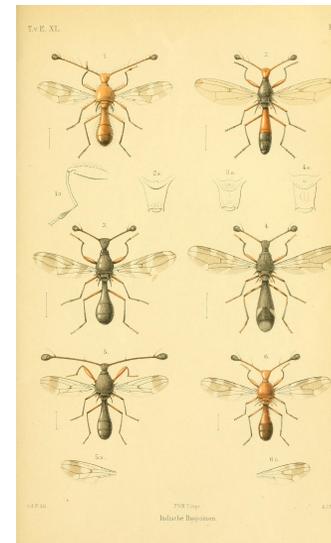
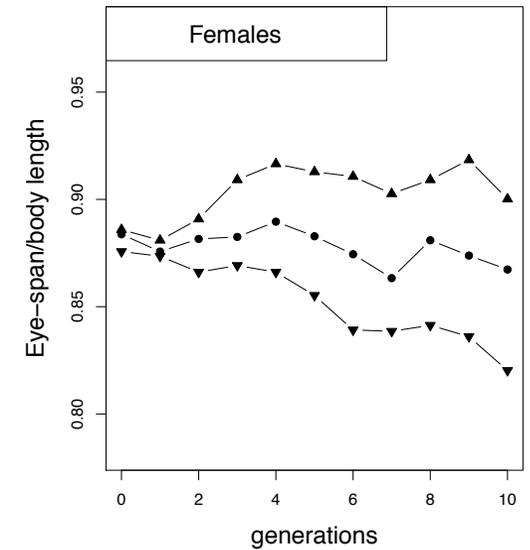
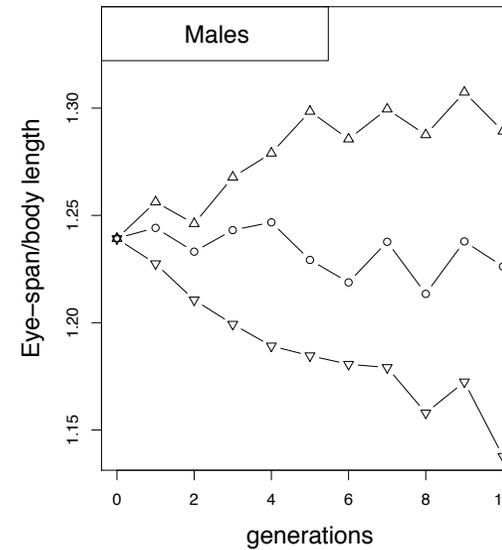
Trait	Mean before Selection (1976)	S	β	Mean next gen.
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Bill Length	10.63	0.54	-0.144	10.95
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- After accounting for phenotypic covariances, the Grants found that both weight and bill depth experienced directional selection toward larger values
- Weak selection occurred for shorter bills (a negative value for β)
- However, bill length actually increased due to genetic covariance with weight and bill depth which were under strong selection for larger values



Introduction

- Another example of correlated response to selection across traits can be found in the stalk-eyed flies
- Wilkinson (1993) conducted an experiment in which he selected up and down on eye-stalk-to-body-size ratio for 10 generations in males
- While no selection was applied in females, a response was also seen in females because of the correlation in male and female body proportions



Introduction

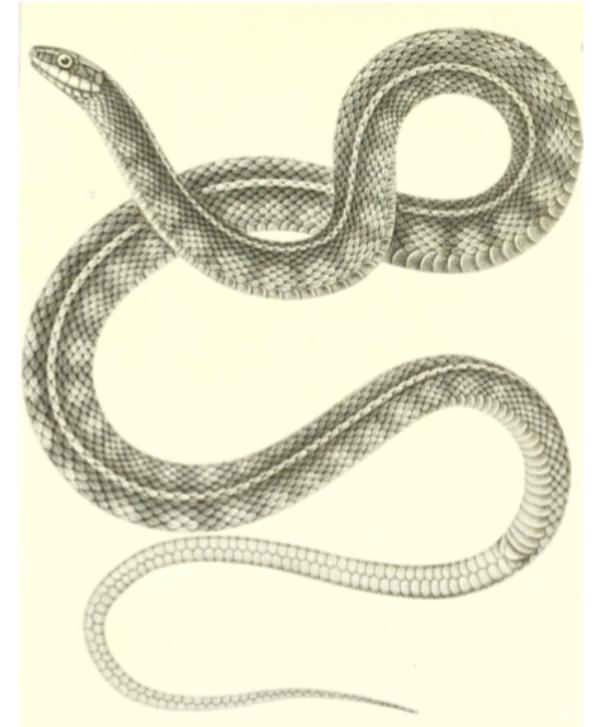
- Another approach to looking at selection across multiple traits is what is known as the “Lande-Arnold” regression
- This approach is capable of looking at both linear/directional (β) and quadratic/stabilizing-disruptive (γ) gradients of selection

$$w_i \sim \beta_1 x_{1,i} + 1/2\gamma_1 x_{1,i}^2 + \beta_2 x_{2,i} + 1/2\gamma_2 x_{2,i}^2 + \gamma_{1,2} x_{1,i} x_{2,i} + \bar{w} \quad (9.3)$$

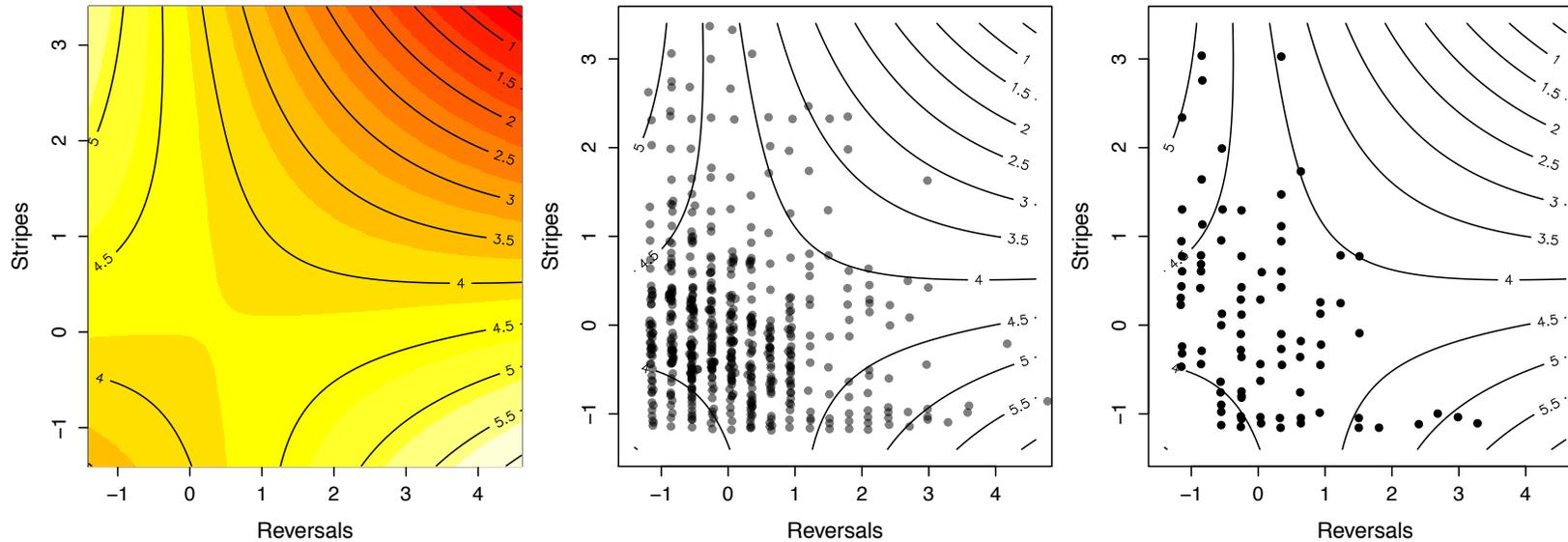
- The covariance selection gradient between traits in this approach is $\gamma_{1,2}$ and will tell us if there appears to be interaction as selection is acting on multiple traits

Introduction

- An example application of the Lande-Arnold regression approach can be found in a study by Brodie III (1992)
- Hundreds of garter snakes born in the lab were released into the wild and their fate was monitored using a mark-recapture approach
- Before release, the snakes were assessed for the amount of stripes they had and for their behavior when being pursued by a predator—did they have an inclination to switch directions while fleeing?



Introduction



- Brodie III found that neither trait (stripes nor direction switch) was under selection purely on its own but that there was a significant negative covariance between them; individuals with many stripes and few reversals or few stripes and many reversals were more likely to survive

9.1.1 Hamilton's rule and the evolution of altruistic and selfish behaviors

- Methods to look at selection in multiple traits have been applied to many evolutionary questions and kin and sexual selection are two excellent examples
- First off, kin selection: a shift in thinking that occurred due to Darwin's work was the realization that species do not exist for the benefit of other species
- Bees did not evolve to pollinate flowers nor to make honey for bears
- Their reason to exist is to leave offspring for the next generation



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9.1.1 Hamilton's rule and the evolution of altruistic and selfish behaviors

- However, there is a bit of a wrinkle in this broad conclusion when considering species like honey bees
- Worker honey bees are sterile and do not care for their own offspring, but rather for their Queen's offspring
- In this way, they are sacrificing their own fitness for the benefit of others, an example of altruism
- Hamilton, in 1964, provided the first evolutionary explanation of this puzzling behavior



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9.1.1 Hamilton's rule and the evolution of altruistic and selfish behaviors

- Hamilton's thinking, which led to what is known as "Hamilton's Rule", was that, while an individual may be compromising its own fitness by giving resources to or foregoing reproduction for a relative, there may be a benefit if shared alleles have a higher likelihood of making it to the next generation
- For example, let's imagine two related individuals, i and j , who have two phenotypes ($X = 1$ or 0) for whether they do or don't provide altruistic help to the other
- These could be, for example, siblings that share food or resources with their brother or sister or a child that foregoes reproduction to care for its parents' offspring

9.1.1 Hamilton's rule and the evolution of altruistic and selfish behaviors

- Providing the altruistic behavior incurs a cost C on the donor; whereas receiving the altruistic behavior confers a benefit B .
- Hamilton's Rule indicates that the altruistic trait will spread if:

$$2FB > C \quad (9.4)$$

- Where F is the kinship coefficient between interacting individuals i and j
- Essentially, a costly altruistic behavior will spread if it is sufficiently beneficial to a related individual

9.1.1 Hamilton's rule and the evolution of altruistic and selfish behaviors

- We can relate altruism and Hamilton's rule to the quantitative genetic framework we have set up for selection on multiple traits if we think of the phenotypes of related individuals (i and j) as genetically correlated phenotypes.
- Using the multivariate form of the Breeder's equation, we can write the expected change in our altruistic behavior across generations as:

$$R = \beta_i V_A + \beta_j V_{A,i,j}, \quad (9.6)$$

- Where the slope of our altruistic individual's regression of behavioral phenotype on fitness (β_i) is proportional to $-C$ and the slope of our interacting partner's phenotype on our focal individual's fitness (β_j) is proportional to B

9.1.1 Hamilton's rule and the evolution of altruistic and selfish behaviors

$$R = \beta_i V_A + \beta_j V_{A,i,j}, \quad (9.6)$$

- Our altruistic behavior will then increase ($R > 0$) if:

$$\begin{aligned} \beta_i V_A + \beta_j V_{A,i,j} &> 0 \\ B \frac{V_{A,i,j}}{V_A} &> C \end{aligned} \quad (9.8)$$

- The genetic covariance between individual i and j 's altruistic phenotype, assuming they are related, is $2F_{i,j}V_A$ so the altruistic phenotype will increase if:

$$\begin{aligned} B \frac{2F_{i,j}V_A}{V_A} &> C \\ 2F_{i,j}B &> C \end{aligned} \quad (9.9)$$

9.1.1 Hamilton's rule and the evolution of altruistic and selfish behaviors

$$B \frac{2F_{i,j} V_A}{V_A} > C$$
$$2F_{i,j} B > C \quad (9.9)$$

- The take-home here is that altruism will spread through kin selection if the cost to the individual (i) displaying the altruistic behavior is paid back due to the benefit of interacting with a related individual (j)

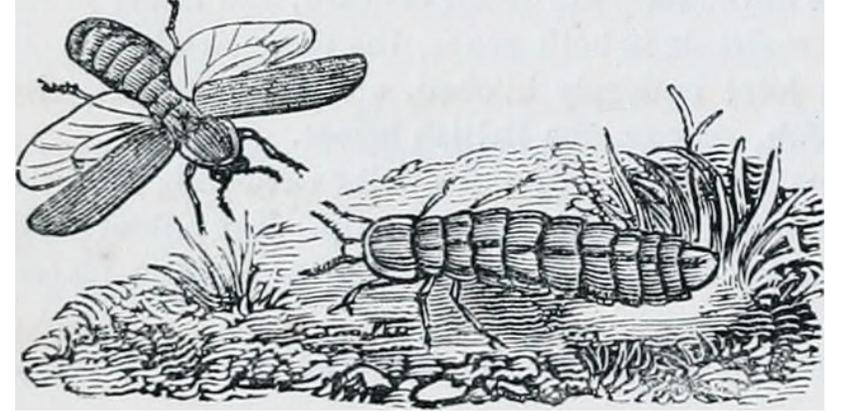
9.1.1 Hamilton's rule and the evolution of altruistic and selfish behaviors

- One of the clearest examples of altruism is the repeated evolution of eusociality where sterile castes help rear their siblings rather than have offspring of their own
- Eusociality has evolved at least 8 times in the Hymenoptera (ants, bees, wasps, etc...), where monandry (females mating with a single male) is common and relatedness is maximized among siblings



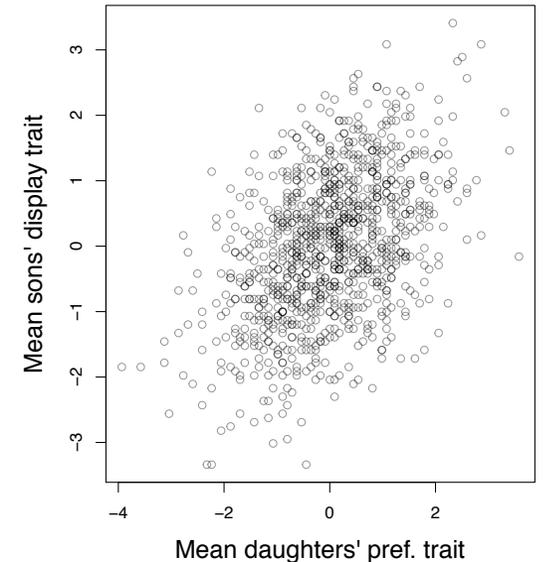
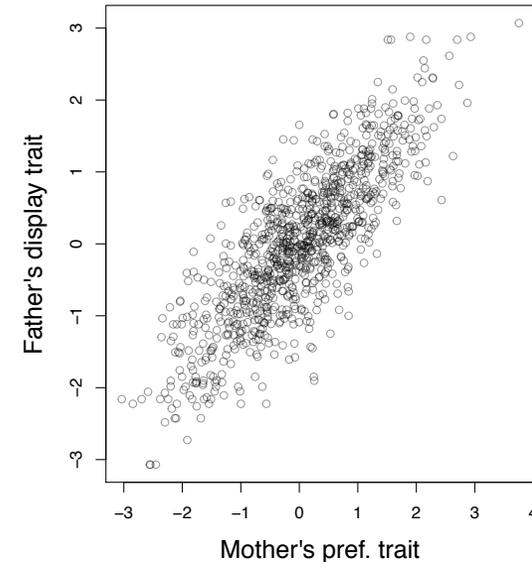
9.1.2 Sexual selection and the evolution of mate preference by indirect benefits

- Organisms often put enormous effort into finding and attracting mates, sometimes at a cost to survival
- This choosiness may ultimately increase their fitness, though, through the gain of parental care for offspring, avoidance of parasites, or increased fertility of chosen mates
- For example, male glow worms choose females that glow brighter and this phenotype is positively correlated with fecundity



9.1.2 Sexual selection and the evolution of mate preference by indirect benefits

- Benefits of mate choice may not be realized until the next generation when, for example, they result in higher fitness (“good genes” hypothesis) or attractiveness (“runaway” or “sexy sons” hypotheses) of offspring
- For example, a mother’s choice of a father based on display trait may result in sons with similarly attractive display traits who will have a higher likelihood of finding mates and reproducing



9.1.2 Sexual selection and the evolution of mate preference by indirect benefits

- Let's consider a male display trait such as tail length and a preference trait for tail length in females
- Male tail length is under direct selection with a response across generations of:

$$R_{\sigma} = \beta_{\sigma} V_{A,\sigma} \quad (9.13)$$

- If we assume that the female preference trait is not under direct selection ($\beta_{\text{♀}} = 0$), then response to selection for the preference trait is:

$$R_{\text{♀}} = \beta_{\text{♀}} V_{A,\text{♀}} + \beta_{\sigma} V_{A,\text{♀}\sigma} = \beta_{\sigma} V_{A,\text{♀}\sigma} \quad (9.14)$$

- Meaning the female preference trait responds to selection if it is genetically correlated with the male display trait

9.1.2 Sexual selection and the evolution of mate preference by indirect benefits

- Correlation between male display and female preference traits could happen if:
 1. There is a single locus underlying both traits (pleiotropy)
 2. Assortative mating (female preference for long tails mate with long-tailed males, female preference for short tails mate with short-tailed males)
 - For example, consider that males with long tails will carry the long-tailed preference gene because their long-tailed dad mated with a long-tail preferring mom

9.1.2 Sexual selection and the evolution of mate preference by indirect benefits

- As an example of display and mate preference, let's consider an experiment in guppies (*Poecilia reticulata*)
- Female guppies often prefer males with orange coloration
- Houde (1994) established four replicate population pairs and selected for increased and decreased orange coloration in males
- Females were chosen randomly each generation so preference was not selected directly



9.1.2 Sexual selection and the evolution of mate preference by indirect benefits

- Houde measured response to selection for both male display and female preference
- In populations selected for increased male orange coloration, females had a stronger preference for orange males, while the opposite was true in populations selected for decreased orange coloration

