Overview of lecture 14

1. Epistasis for fitness generates Linkage Disequilibrium, D

2. Linkage Disequilibrium, D, is a crummy term. It refers to a statistical association between alleles at different loci, which may or may not be on the same chromosome (i.e., physically linked). Write your own, more-descriptive term below:

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My term is B-LAC: Between-Locus Allelic Covariance.

Indeed, D is equal to cov(a, b). See Hartl and Clark (2nd ed. pages 53-54)

Similarly, we could think of correlations between alleles at the same locus as W-LAC: within-locus allelic covariance.

3. Recombination reduces D.

One major effect of recombination is to reduce the covariance between alleles, thus making the genotypes closer to that expected based simply on the frequencies of the alleles contained in the genotytpe. See the worksheet on the web. Or better yet, write your own excel worksheet.

Now we want to relate linkage disequilibrium to another problem in sexual selection.

4. Female choice can generate linkage disequilibrium between the alleles for female choice and the alleles for male traits.

A. First we need to demonstrate female choice. Malte Andersson's experiment {Andersson, M. 1982 Female choice selects for extreme tail length in a widowbird. *Nature* 299, 818–820.}

Experimental evidence for female choice

Long-tailed widow birds (Andersson 1982)

Male tails: up to 50 cm long

Female tails: 7 cm long

Males defend large territories

Males show off their tails in advertising flights to females visiting their territories

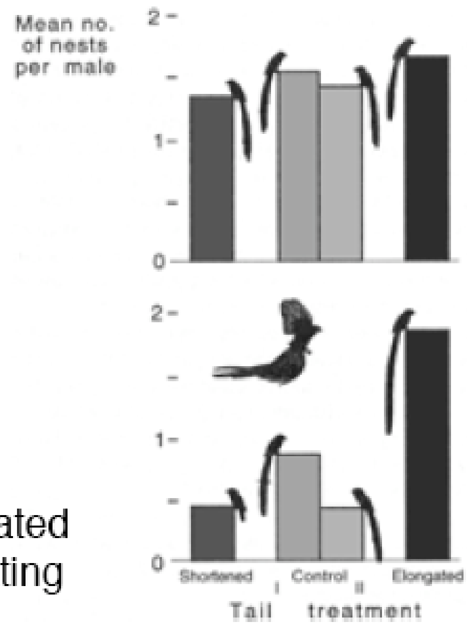
Up to 9 females may nest in a male's territory

Male helps build nest frame, but after that provides little parental care

Experimental evidence for female choice

Andersson's (1982) experiment:

1) Shortened tails to 14 cm
2) Control I: unmanipulated
3) Control II: cut tail and glued it back on
4) Elongated tail by adding 25 cm



Reproductive success in the 4 treatment groups before manipulation

Reproductive success in the 4 treatment groups after manipulation

→ males with elongated tails had highest mating success

Thus, Andersson's experiment demonstrates a preference by females for males with longer tails. Why are the male's tails not longer in the wild? Many other experiments also show female choice.

Now we want to see how linkage disequilibrium affects the outcome of sexual selection. Here is the thing in words.

Step 1. There is variation in the male trait. Here we will assume only two types: males with long tails and males with short tails. We also assume a haploid model. Males with long tails have allele T, and males with short tails have allele t.

Step 2. There is natural selection against the long tales. Under natural selection alone, the relative fitness of males with allele T (long tails) is (1 – s). The relative fitness of males with allele t is one.

Step 3. Males with long tales are preferred by choosy females. Hence sexual selection is a possible countervailing force to natural selection. The strength of the force depends on the frequency of choosy females.

Step 4. There is no direct selection on female choice. Females with the preference allele P produce the same number of offspring as females with the no-preference allele, p. Any selection on female choice has to be indirect.

Step 5. What if the p allele is fixed (no choosy females in the pop)? Selection will clearly be for short tails. Allele t will become fixed.

Step 6. What if the p allele is not fixed (some choosy females in the pop)? It depends. If there are enough choosy females that show a strong enough preference for long-tailed males, then the T allele will increase when rare if the advantage under sexual selection outweighs the disadvantage under sexual selection.

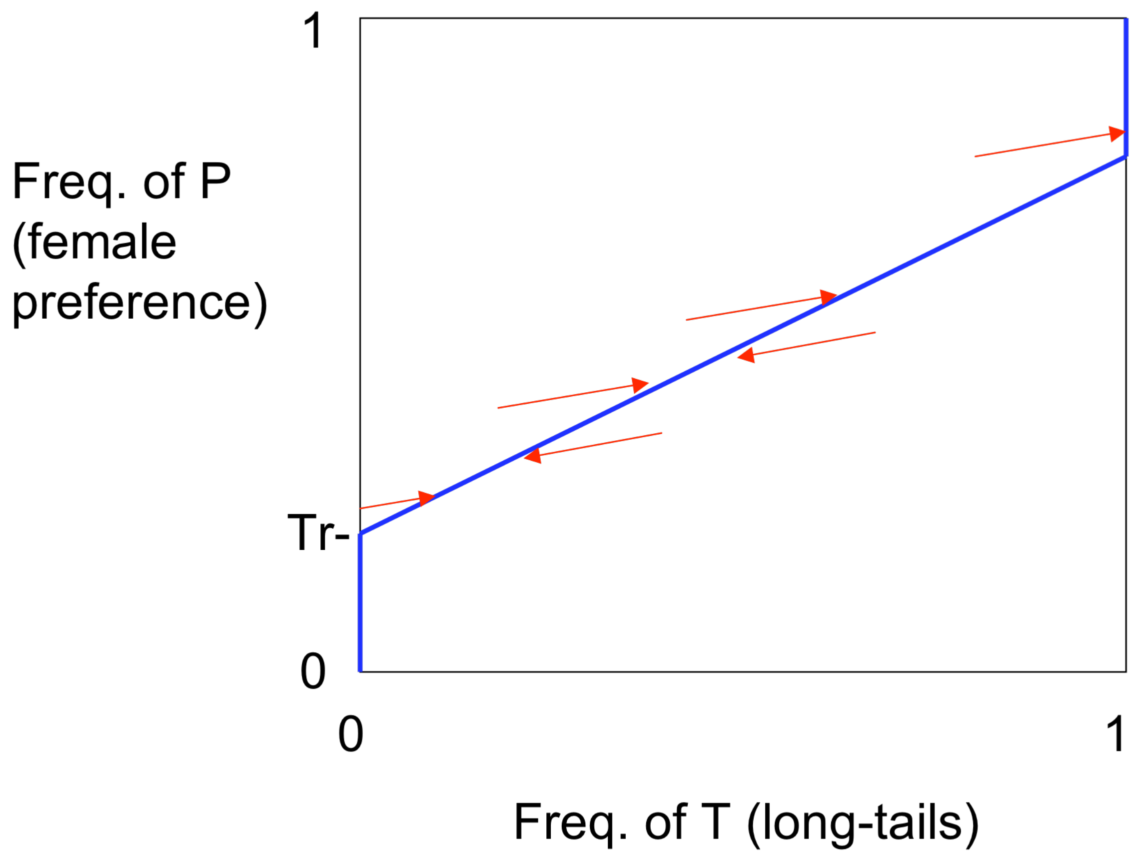
Step 7. Assuming the T alleles spreads, what can we say about the offspring of choosy females? Both the male and female offspring of choosy females will have genes for both long tails and for choosiness. But the long tails will only be expressed in their sons (sex-limited expression is assumed here), and the choosiness will only be expressed in their daughters. Hence there is a kind of covariance between alleles at the two loci (the locus for tail length and the locus for choice). In other words, there is linkage disequilibrium. The choice allele becomes associated with the long-tail allele more often than expected by chance.

Step 8. Now what can we say about the spread of the choice allele? Well, the sons of choosy females tend to have long tails as well as the allele for female choice (even though it is not expressed). If these long-tailed sons are preferred by the females in the next generation, then the allele for female choice is also indirectly selected, because it is in linkage Disequilibrium with the long-tail allele. So selection by choosy females for males with long tails causes in increase in the choosiness of females. As you can see, choosiness and long-tails can get into a kind of positive feedback loop. This positive feedback, if it happens, was called run away sexual selection by R.A. Fisher. Here, that would mean that the T allele and the P allele become fixed. However in Kirkpatrick's model, there can be a line of neutral equilibria in which the male trait and the female choice are both polymorphic.

B. Mark Kirkpatrick's haploid model. Kirkpatrick's model makes the assumptions made above. He was one of the first to assume that there is no direct selection on the female choice. If you look at the equation for delta P (p2 in his model), you will see that it depends explicitly on D (linkage disequilbrium), and that if D=0, delta P = 0 (equation 1b in Kirkpatrick 1982). Hence the preference will not evolve if linkage disequilibrium is not generated. (Insert drawing on chalkboard of Kirkpatrick's model below. Explain how it works. What is meant by the "line of equilibria." What is the effect of drift away from points on the line.)

(See next page)

5. Design an experiment to test for linkage disequilibrium generated by female choice on a male trait.



Graphical presentation of Kirkpatrick's model. If the frequency of female preference is above the threshold (Tr-), then sexual selection for long tails is stronger that natural selection against long tails. Net selection causes an increase in the freq. of T. Female choice also increases, because allele P covaries with allele T. The overall trajectory is toward the blue line, which is a line of equilibria, where natural selection against the trait exactly balances sexual selection for the trait. Drift in preference above the blue line of equilibria is followed by selection for greater tail length (and, indirectly, greater preference). Drift in female preference below the lines leads to selection reducing mean tail length (and preference). Note that here the slope of the red lines is less than that of the blue line. On the blue diagonal line, a polymorphism is expected in both the preference and the male trait. (graph from Kirkpatrick's model.ppt)