Speciation

- Species concepts
- Mechanisms of Isolation
- Mechanisms of Divergence
- Secondary contact

Divergence

- Genetic drift
  - Following founder effect, drift can promote divergence
  - Probably not a major mechanism of divergence on its own
- Natural selection
- Sexual selection

Divergent speciation with natural selection

- If important ecological resources are of only a few distinct types, then ecological specialization results
  - E.g. eat apples or eat hawthorn berries
  - *Rhagoletis pomonella*
  - Apple maggot fly, apple race & hawthorn race
  - Males and females recognize food sources
    - Mating takes place on the fruits

Sympatric speciation in apple maggot flies

- *Rhagoletis* and Hawthorn plants native to N. America
- Apple trees introduced around 300 years ago
- Apples and hawthorns are NOT geographically separated
  - Not allopatric, they are sympatric
- Genetic differences have evolved between hawthorn and apple races in less than 300 years

Host preferences

- Fruit preferences (apple versus hawthorn) results in assortative mating
  - Apple finding males mate with apple finding females
  - Hawthorn finding males mate with hawthorn finding females
  - About 94% of fly matings are with same type
    - But that leaves about 6% of matings apple-hawthorn
    - That's still a lot of gene flow

Natural selection and host race formation

- 6% cross mating is high gene flow
- Must be counteracted by something
- Hawthorns ripen about three weeks after apples
  - Timing of development critical so as not to emerge during winter
  - That is, there is selection to be either one type or the other, not in between

Other examples of ecological divergence via natural selection

Species	Type of divergence that is underway	Citation
Lake whitefish	Populations of dwarf versus normal-sized individuals	Lu, G. and L. Bernatchez. 1999. *Evolution* 53: 1491–1505.
Three-spine sticklebacks (freshwater fish)	Benthic (bottom-dwelling) versus limnetic (open-water dwelling) populations	Hatfield, T. and D. Schluter. 1999. *Evolution* 53: 866–873.
Sockeye salmon	Sea-run versus lake-dwelling populations	Wood, C. C., and C. J. Foote. 1996. *Evolution* 50: 1265–1279.
Pea aphids	Different host plants	Via, S. 1999. *Evolution* 53: 1446-1457.
Army worms	Different host plants	Pashley, D. P. 1988. *Evolution* 42: 93–102.
Soapberry bugs	Different host plants	Carroll, S., H. Dingle, and S. P. Klassen. 1997. *Evolution* 51: 1182–1188.
Goldenrod ball gallmakers	Different host plants	Brown, J. M., W. G. Abrahamson, and P. A. Way. 1996. *Evolution* 50: 777–786.
Blueberry and apple maggot flies	Different host plants	Feder, J. L., C. A. Chilcote, and G.L. Bush. 1989. *Entomological Experiments and Applications* 51: 113–123.
Heliconius butterflies	Different habitats and types of warning coloration	McMillan, W. O., C. D. Jiggins, and J. Mallet. 1997. *Proceedings of the National Academy of Sciences, USA* 94: 8628–8633.

Divergence via sexual selection

- Remember, species concepts are about reproductive isolation and gene flow
- Assortative mating reduces gene flow between groups
  - Promotes divergence

Sexual selection, speciation and Hawaiian Drosophilids

- Complex courtship displays on leks
  - Leks are display grounds
  - Males fight for good display sites
  - Females select among male displays

Head shape

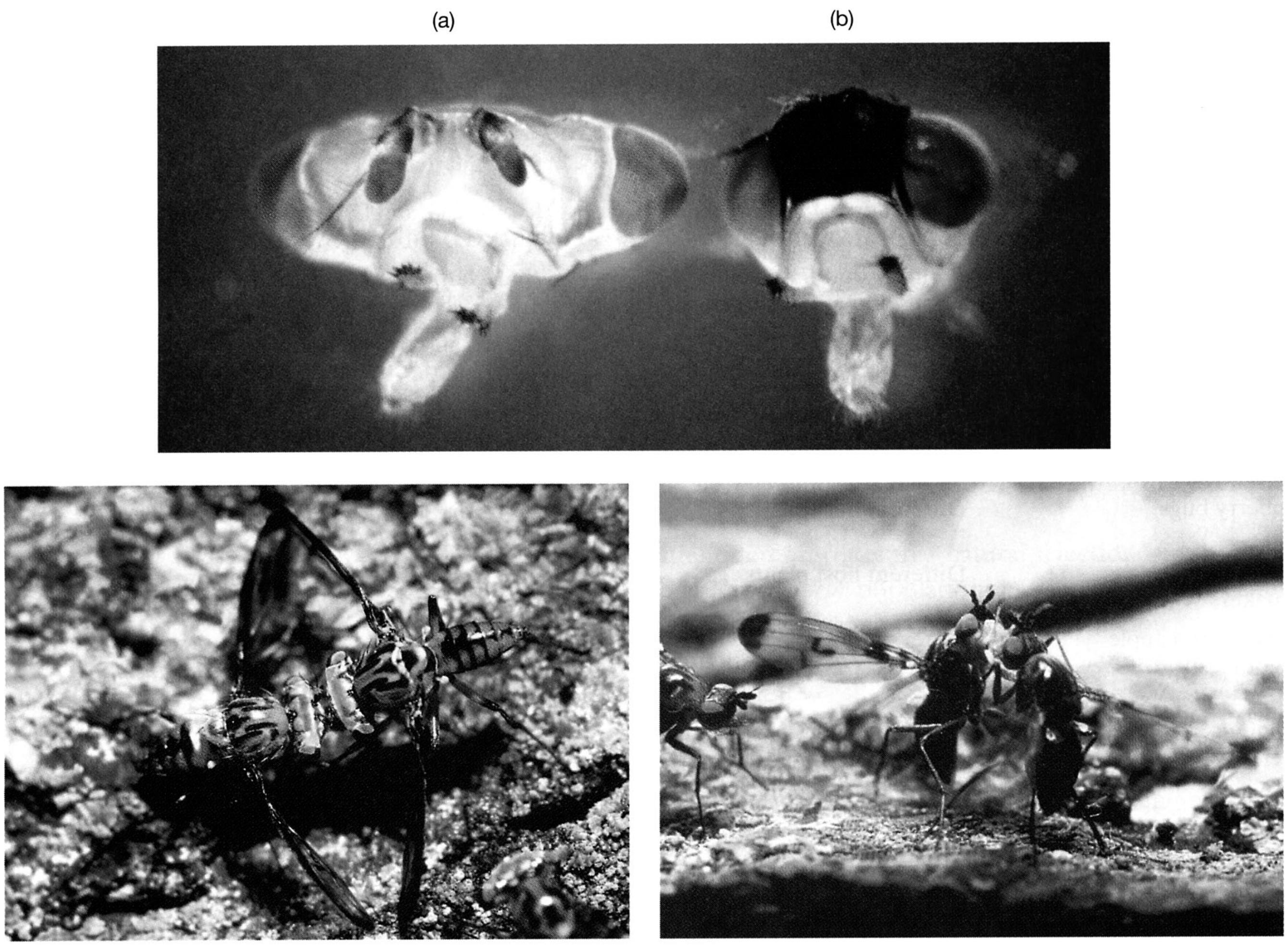


Figure 12.12 **Contrasting head shapes and fighting strategies in Hawaiian *Drosophila*** (a) Male *Drosophila heteroneura* have wide heads. As the photo at the bottom left shows, they butt heads to establish display territories on a lek. (b) Male *Drosophila silvestris* have normally shaped heads. They fight over display territories by rearing up and grappling with one another. (Kenneth Y. Kaneshiro, University of Hawaii)

Selection on head shape

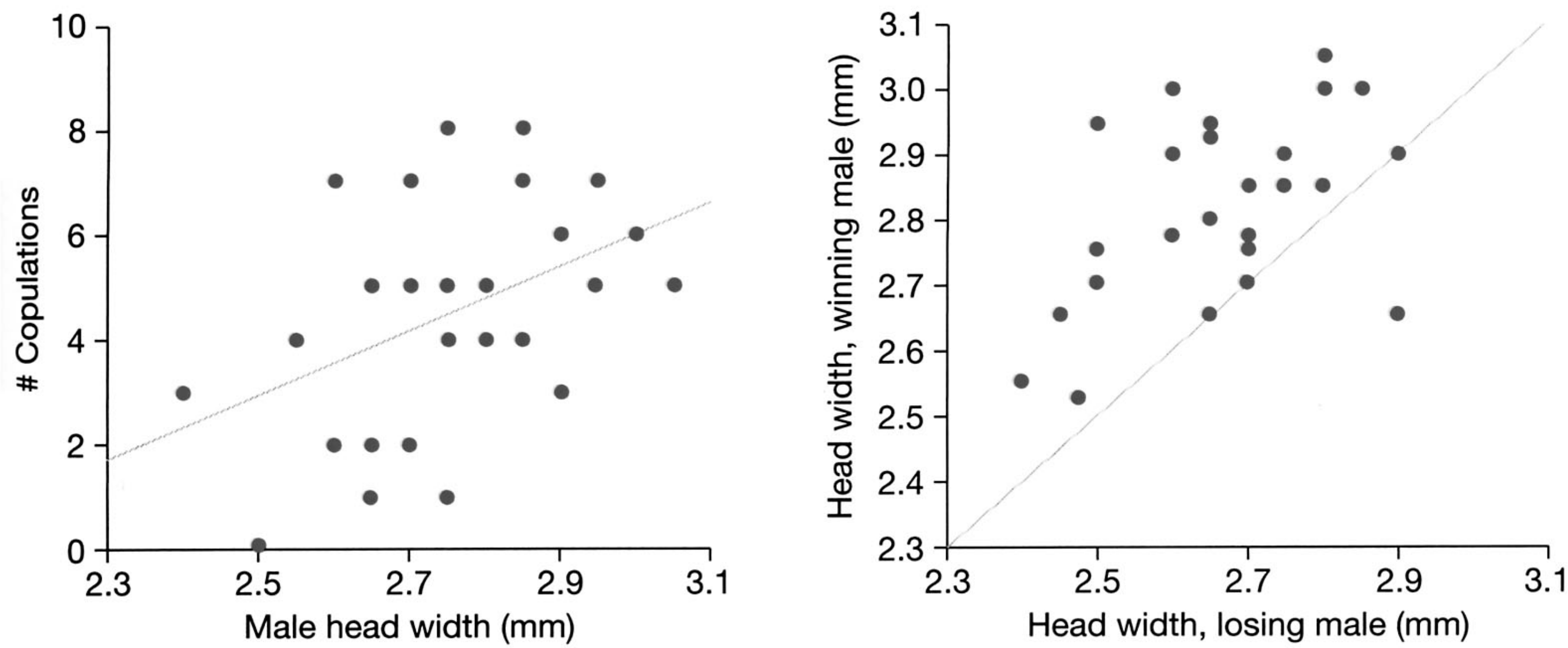


Figure 12.13 **Evidence for sexual selection on head width in *Drosophila heteroneura***

What happens after divergence

- Suppose they are completely distinct
  - Then they continue to diverge (drift, selection) until they are reproductively incompatible
    - Could not produce fertile hybrid offspring
- Suppose they are partially distinct
  - If they diverged in allopatry, and they meet again, called secondary contact

Secondary contact and hybrids

- Could be divergence in allopatry (drift and/or selection) completely isolates them as species
- Could be that divergence in allopatry made them distinct, but still able to hybridize
- What happens to hybrids determines what happens to the possible speciation event

Hybrid possibilities

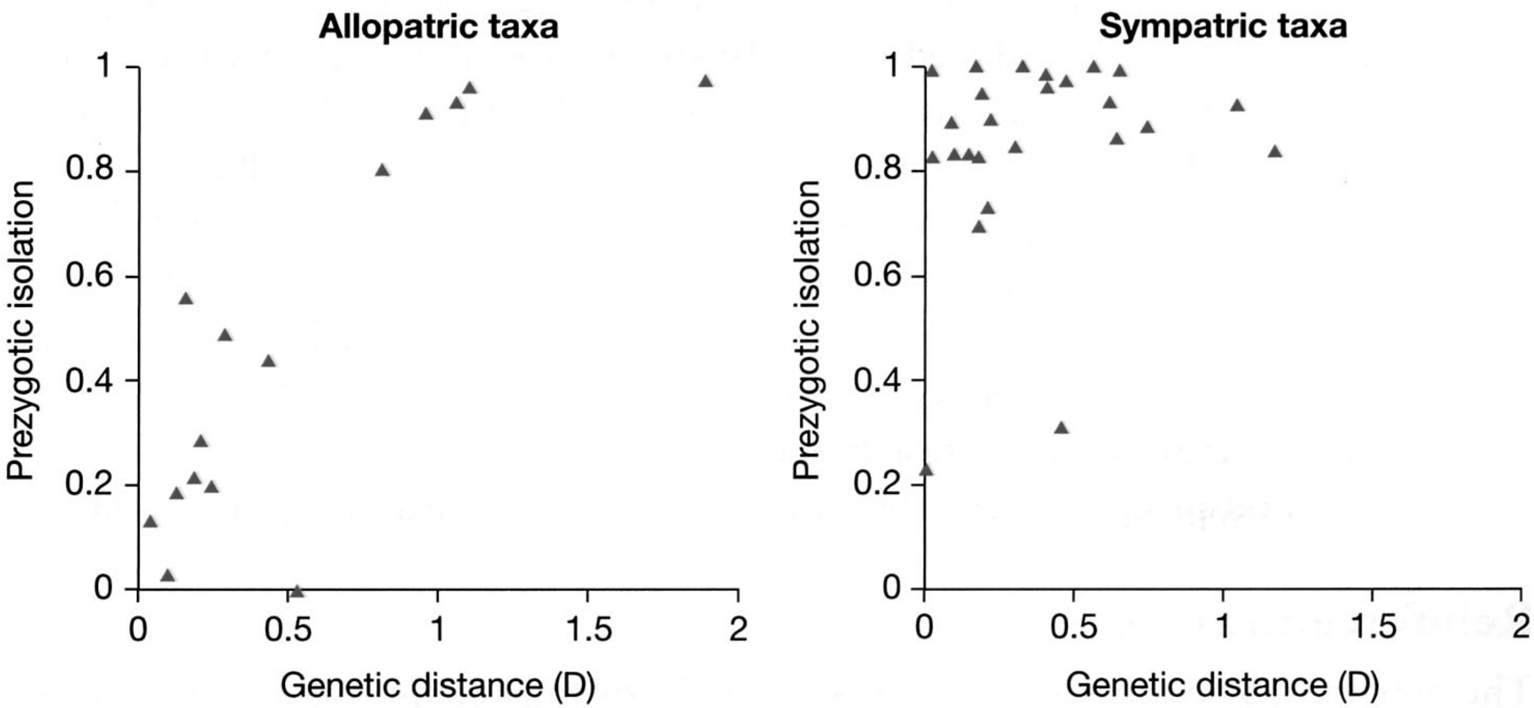
- Hybrids infertile, no gene flow
  - Speciation complete
  - Isolation is post-zygotic
- Hybrids have reduced fitness but are fertile
  - Some gene flow, speciation in progress
- Hybrids have same or higher fitness
  - Gene flow may eliminate differences, no more speciation event
  - Or, gene flow may be limited to zone of contact
    - Stable hybrid zone

Reinforcement

- Suppose hybrids are produced and they are either infertile or have reduced fitness
  - That selects for parents that don’t make the mistake of mating with wrong kind
  - That is the *post-zygotic isolation* that has already occurred selects for *pre-zygotic isolation*
  - That is called *reinforcement*
- Reinforcement promotes speciation

Reinforcement predicts

- Pre-zygotic isolation evolves faster in sympatric species pairs



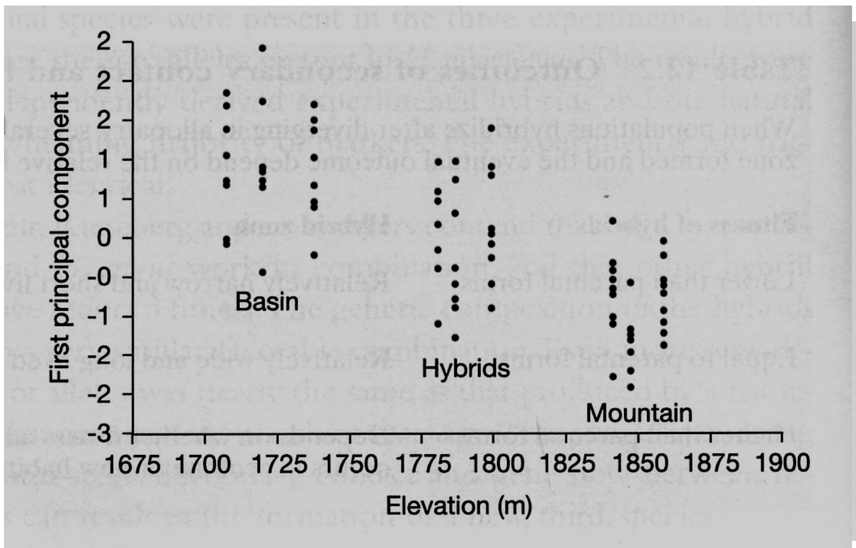
Outcomes of hybridization

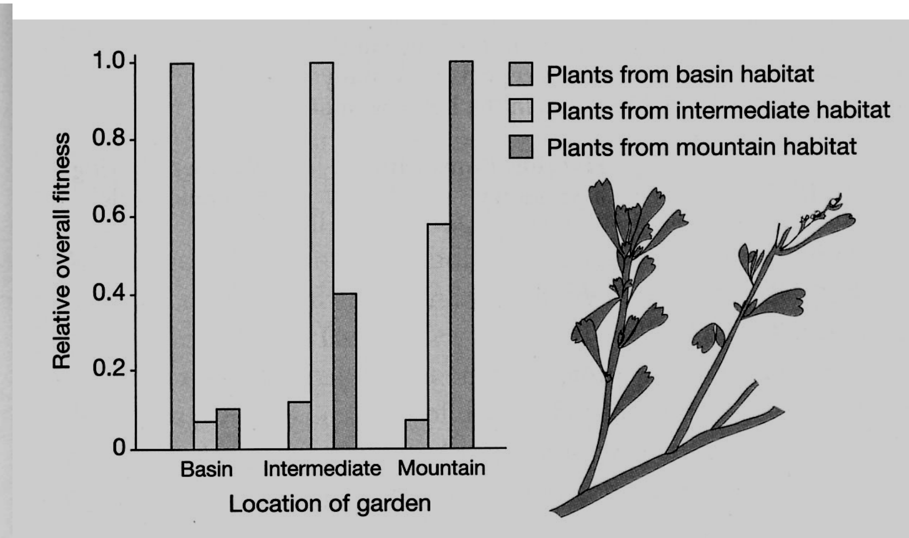
Table 12.2 Outcomes of secondary contact and hybridization

When populations hybridize after diverging in allopatry, several different outcomes are possible. The type of hybrid zone formed and the eventual outcome depend on the relative fitness of hybrid individuals.

Fitness of hybrids	Hybrid zone	Eventual outcome
Lower than parental forms	Relatively narrow and short lived	Reinforcement (differentiation between parental populations increases)
Equal to parental forms	Relatively wide and long lived	Parental populations coalesce (differentiation between parental populations decreases)
Higher than parental forms	Depends on whether fitness advantage occurs in ecotone or new habitat	Stable hybrid zone or formation of new species

Big sagebrush subspecies example





Population	*N*	Number of inflorescences		Number of flowering heads	
Basin	25	19.92	(6.16)	175.1	(124.9)
Near basin	25	17.72	(6.59)	174.4	(92.5)
Hybrid	27	20.11	(6.75)	372.7	(375.9)
Near mountain	25	17.04	(6.50)	153.7	(75.2)
Mountain	25	16.80	(6.34)	102.0	(59.4)

Genetics of speciation

- Traditional view genetic architecture radically different
  - (traditional as in before much data collected)
- Sources of data:
  - Hybrid studies using classical genetics
    - Haldane's rule
  - Quantitative trait loci mapping
    - Pinpointing and characterizing genes responsible for isolation

Classical genetics

- Haldane's rule
  - Heterogametic sex more likely to be inviable or sterile
  - Mammals and most insects
    - Males XY females XX; males heterogametic
  - Birds and butterflies
    - Females ZW males ZZ; females heterogametic

Haldane's rule data

Group	Trait	Hybridizations with asymmetry	Number obeying Haldane's rule
Mammals	Fertility	20	19
Birds	Fertility	43	40
	Viability	18	18
Drosophila	Fertility and viability	145	141

Why? Not yet clear.

Probably due to alleles on sex chromosomes that interact with autosomal loci to cause inviability. Homogametic sex has species typical X-linked and species typical autosomal, but heterogametic sex has species typical autosomal but heterospecific X-linked.

QTL mapping

- Quantitative Trait Loci
  - loci that code for quantitative (continuously varying) traits
  - Using hybrids and backcrosses look for statistical associations between marker loci and traits of interest
- Results to date suggest that often a few genes contribute substantially to reproductive isolation