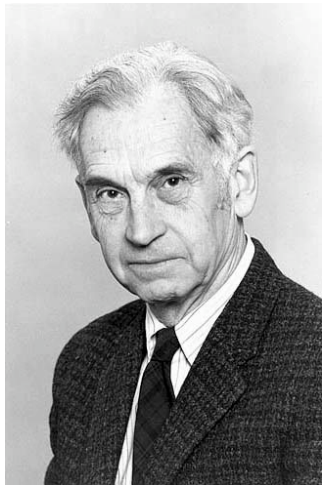
Species and Speciation I

by
Dr. Evil

In 1928, the German ornithologist Ernst Mayr (1904-2005) went off to New Guinea to collect, study, and classify a bird family known as "birds of paradise," along with various other tropical bird families. (That's his Malay assistant Sario on the left.)

At first, Mayr was baffled by the incredible diversity that he found. Birds like *Dicrurus paradiseus* varied greatly over their geographic range, but there didn't seem to be any obvious way of neatly splitting them up into species, subspecies, etc.

Mayr (much older, and a professor at Harvard, when this picture was taken) realized that species couldn't be defined purely on shape, color, etc. He devised the *biological species concept*: a species is defined as a set of potentially interbreeding populations. Two species are separate if their members cannot interbreed successfully.



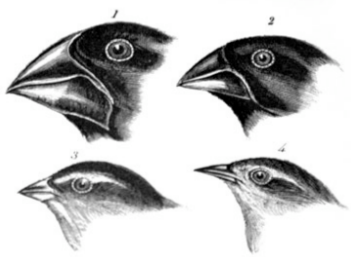
Mayr also proposed a model for how new species form: *allopatric speciation*.

- *Allopatric* means "different homeland"
- Starts with a population of one species becoming divided into two (or more) by a geographic or physical barrier that individuals cannot easily cross.
  - If this happens by organisms migrating or being carried to a new habitat, it's *dispersal*. . .
  - If the organisms don't move themselves, but the barrier comes up within the range of the population, it's *vicariance*. . .

Allopatric model of speciation

- Separated populations will tend to become different
  - The populations may be subject to different selective pressures, if they end up in different environments.
  - Alleles in one population cannot now be exchanged with the other (we say that *gene flow* is blocked).
  - One population may also have an unusually high or low frequency of certain alleles, purely by "luck of the draw"—this is the *founder effect*.
- Given enough time, the separated populations diverge into separate species, which cannot interbreed even if the barrier disappears.

The Galápagos finches and other Galápagos life forms would probably be an example of *dispersal*—a population of South American finches must have dispersed over 600 miles of open water to the islands. This is not a barrier that finches can normally cross (maybe they were blown there by a storm, but we may never know the precise details). Then finches must have dispersed again, repeatedly, from one island to the next.



On the other hand, the four different species of *desert pupfish* in springs and streams of the Mojave desert would have speciated by *vicariance*. We have evidence that there was once a fairly large system of lakes and rivers in the Mojave, 10,000 years ago, when the climate was cooler and wetter. As the climate became hot and dry, populations of pupfish were isolated in spring-fed remnants of the old lake system, and each has evolved into a separate species.

Can we actually observe allopatric speciation?

- A few clamworms (*Nereis acuminata*) were collected from the ocean in 1964 at Long Beach, California, and raised in a lab
- In 1986, four pairs of these worms were brought to Woods Hole, Massachusetts, and raised at WHOI
- In 1992, attempts to cross the Woods Hole population with worms from the original site *failed*.
  - *Source*: Weinberg, J. R., V. R. Starczak and P. Jora. 1992. Evidence for rapid speciation following a founder event in the laboratory. *Evolution* 46:1214-1220.

Males refused to take care of hybrid eggs—and even when eggs were artificially reared, they failed to develop. By the biological species concept, there are now two *cryptic* worm species.

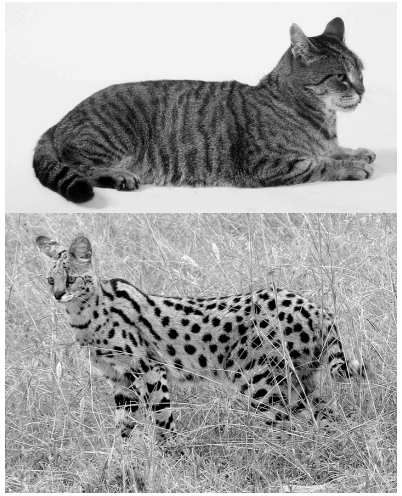
The BSC and Reproductive Isolation

- The biological species concept is based on *reproductive isolation*
  - *Prezygotic isolation* is due to factors that operate before sperm meets egg
    - Behavioral isolation—individuals don't interbreed because of different mate recognition behaviors
    - Temporal isolation—individuals don't interbreed because they mature at different times
    - Ecological isolation—individuals don't interbreed because they occupy different niches
    - Gametic isolation—individuals don't interbreed because of some sort of biochemical incompatibility between gametes, or between gametes and parental tissues

One of the more notorious forms of prezygotic isolation is *mechanical isolation*. In many species of insects, crustaceans, and other arthropods, the male and female sex organs have complex shapes, and fit like a key and lock. Different species may simply not fit each other; in some cases, attempted hybridization has been observed to result in the male's appendage snapping off.

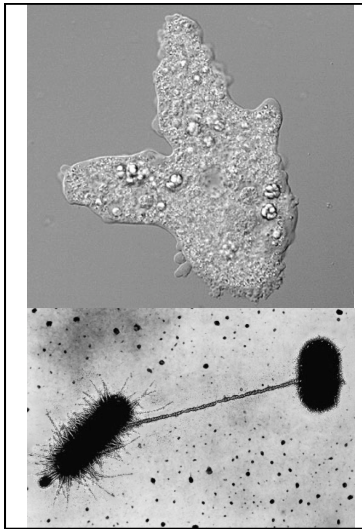
The BSC and Reproductive Isolation

- Biological species concept, continued:
  - *Postzygotic isolation* is due to factors that operate after sperm meets egg
    - Zygote mortality—the egg is fertilized but cannot develop any farther
    - Embryo inviability—the embryo stops developing and dies after a certain point
    - Hybrid sterility—hybrids may survive but are unable to breed
    - Reduced hybrid fitness—hybrids may survive but be poorly adapted, weak, prone to die, etc.



Several of these barriers may operate at once. When domestic cats (*Felis domesticus*) were bred with *servals* (a small wild cat native to Africa, *Leptailurus serval*), mating was difficult because: servals often refused to mate with domestic cats; the gestation periods were different (65 days for domestic cat, 75 for serval); and hybrid litters were often absorbed, aborted, or born prematurely.

A problem with the biological species concept, however, is that reproductive isolation isn't necessarily absolute. Domestic cats and servals are reproductively isolated in several ways—and yet it has proved possible to breed hybrids, and then back-cross them to domestic cats, creating a breed known as the *Savannah*. So do we have one species or two?. . .



Another problem is that the BSC isn't easily applicable to asexual organisms—such as most amoebas, which have never been observed reproducing sexuall—or to bacteria, which can incorporate DNA from almost any source. Microbiologist Sorin Sonea once observed that, according to the BSC, there is only one species of bacterium. . .

The BSC sometimes gives answers that seem incongruous. These two birds *look* different, and they live in different areas. . . but, in a small part of Colorado, they overlap, interbreed, and produce fertile hybrids. One species or two?

Cyanocitta cristata (east USA)

Cyanocitta stelleri (west USA)

On the "flip side", the western meadowlark (left) and eastern meadowlark (right) are physically almost identical, but they don't interbreed (and they also have very different songs). These are *cryptic species*.

Sturnella neglecta

Sturnella magna

Kirk's dik-dik (*Madoqua kirkii*), a small African antelope, includes three karyotypes that differ because of chromosome fusions, inversions, translocations, etc. . . .

. . . and crossing individuals with different karyotypes produces sterile hybrid offspring—even though the two look identical.

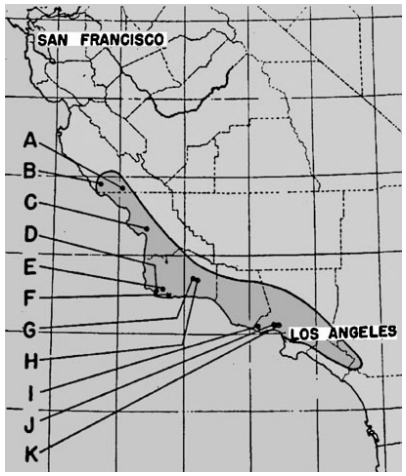
On the other hand, polar bears and brown bears are considered to be different species. . . .

. . . and yet, at least in zoos, the two have hybridized and produced fertile offspring. Brown bears from certain SE Alaskan islands have DNA sequences that are closer to polar bears than to other brown bears.

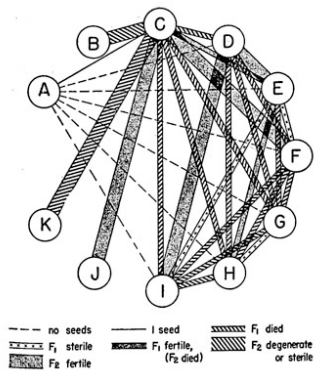
A classic study of this California wildflower shows how much worse the situation can get. . .

Case Study I: *Clarkia deflexa*

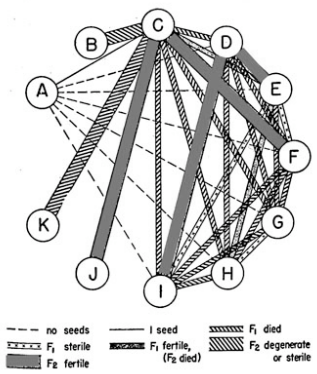
- *Clarkia deflexa* (now known as *C. bottae*) is a wildflower common in southern California, along with other species in the genus
- *Clarkia* is annual and lives in colonies; normally it outcrosses, but self-fertilization has been observed
- In the 1950s, Harlan Lewis experimentally crossed individual *C. deflexa* from eleven different populations in southern California
  - *Source:* Lewis, H. 1953. The mechanism of evolution in the genus *Clarkia*. *Evolution* 7: 1-20.



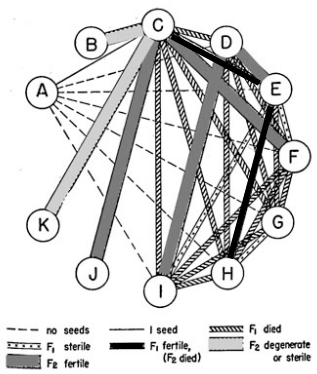
Map of the range of *Clarkia deflexa* along the California coast, with the locations of the eleven populations indicated. . .



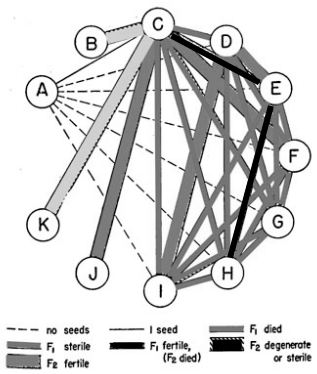
Lewis's original data plotted as a web—different line patterns expressing just how interfertile each pair of populations was. This is a bit hard to read, so. . .



Green indicates complete interfertility through the F2 generation. . . .



Yellow indicates that F1 was fertile but F2 either died or was sterile. . .



Red indicates that F1 died or was sterile, and thin black lines are cases where no F1 generation was even produced.

In part to try to handle some of the difficulties of the BSC, some alternative concepts have been proposed, but they aren't flawless either.

- Biological species concept—defines a species by inability to interbreed with others
- Morphological species concept—defines a species by its unique features
- Ecological species concept—defines a species by the niche it inhabits
- Behavioral species concept—defines a species by its *SMRS—specific mate recognition strategy*

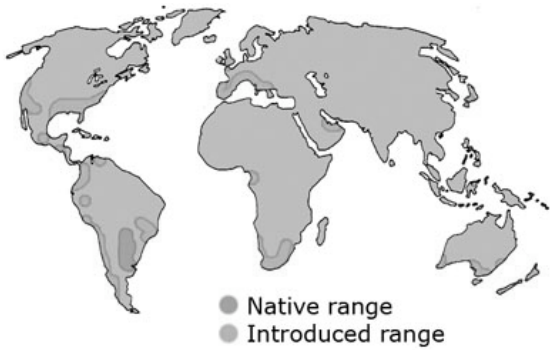
An example of the founder effect: *Porphyria* is a human disease that can cause skin lesions, digestive problems, and mental disturbances. One form of porphyria happens to be unusually common among South Africans of Dutch descent—because, among the small Dutch population that settled there, one member (Ariaantje Adriaansse, an orphan who came over in 1688) happened to be carrying the allele.

Another example: Congenital deafness in 19th-century America affected about 1 in 5700 people. But on the island of Martha's Vineyard, off the Massachusetts coast, the incidence was as high as 1 in 155 (in one town, it was 1 in 25). Reason: A few of the colonial settlers were either deaf or carriers of the allele—and until recently, Martha's Vineyard was culturally isolated from the mainland.

In its native South America, the Argentine ant (*Linepithema humile*) lives in colonies—and ants from genetically different colonies attack each other, because they sense different hydrocarbons on each other's exoskeletons.

L. humile has been introduced to California, Europe, and Japan—and there, in part because of the founder effect, all ants are so genetically similar (at least in the genes involved in recognition) that they don't attack each other.

Instead, they form supercolonies—sets of interconnected, multi-queen colonies that can freely exchange workers. The largest extends 6000 km (3600 miles) along the Mediterranean coast.



An example of a bottleneck: *Achromatopsia* is the complete or near-complete inability to see any colors. It's extremely rare worldwide (1 in 33000 people in the US). But on the tiny island of Pingelap in the Pacific Ocean, almost 10% of the people are affected.

This is partly due to inbreeding, but also due to a typhoon and crop failure in 1775 that reduced the population to 20—one of whom (the chief) just happened to be a carrier of achromatopsia!

Bottlenecks don't always result in unhealthy populations. The population of Samaritans, a breakaway Jewish sect now restricted to small areas of Israel and Palestine, has been as low as 150 in recent years (today there are about 650). They show genetic traces of it (such as linkage disequilibrium at many loci) but no debilitating genetic disorders. . .

But what is a *species*?

- Bottlenecks and the founder effect don't have to cause speciation (in the human examples you saw last week, they have not).
- But if two populations are separated permanently, bottlenecks and the founder effect can contribute to genetic divergence and thus the formation of new species.
- But. . . *what's a species?*

Adaptive Radiation

- Founder species encounters new, unoccupied ecological niches. . .
  - . . . and rapidly speciates into a large number of closely related species occupying different niches: a *species flock*.
  - Some classic examples:
    - Galápagos finches (14 species)
    - Hawaiian honeycreepers (28)
    - French Polynesian land snails (120)
    - Hawaiian fruit flies (700+)
    - African Rift Valley cichlids (1000)

Hawaiian Honeycreepers

- Hawaii is 2000 miles from nearest mainland
- One group of birds, the honeycreepers (Family Drepananidae) have undergone an adaptive radiation (23 species, some now extinct)
  - Different beak types
  - Different food supplies (usually nectar of native flowers, sometimes insects, seeds, fruits)
  - Parallel to the Galápagos finches in many ways

Vestiaria coccinea (‘I’iwi)

Himantione sanguinea (‘Apapane)

Hemignathus munroi (‘Akiapola’au)

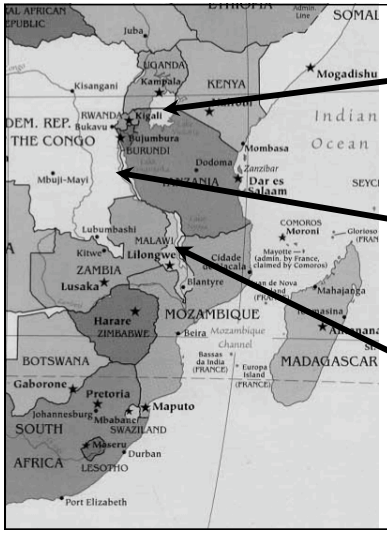
Palmeria dolei (‘Akohekohe)

African Rift Cichlids

- Classic examples of “species flock”
  - Large lakes in East African Rift valley
  - Lake Victoria contains 300 species of *cichlid*, a type of fish.
    - Actually. . . it *did*, before humans introduced a predatory fish, the Nile perch, which ate most of them. About 200 species of cichlid are probably extinct now.

African Rift Cichlids

- Other lakes, especially Tanganyika and Malawi, contain similar flocks of cichlid species
  - Total: 1000 species in all the East African lakes, some of which are popular in the aquarium trade
  - Differences in color, size, shape, food, breeding behavior and parental care. . . .



Lake Victoria

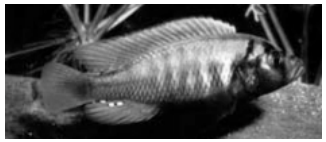
Lake Tanganyika

Lake Malawi

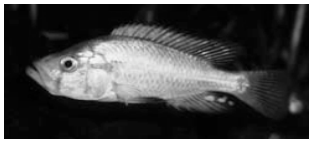
The next slide shows six of the 300+ cichlids species native to Lake Victoria alone. Note the variety. . .

Prognathochromis perrieri

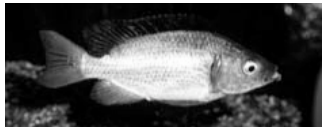
Xystichromis phytophagus



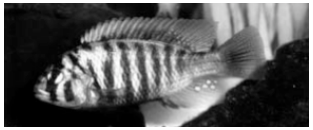
Astatotilapia nyrerei



Pyxichromis orthostoma



Oreochromis esculenta



Neochromis migricans

How fast?

- Lake Victoria completely dried up 12,400 years ago. (How do we know? There's a "fossil soil" layer under the silt of the lake.)
  - The 300 species of cichlids in Lake Victoria must have descended from a common ancestor in less than 12,000 years. (Yow!)
  - A small lake, Lake Nabugabo, has been separate from Lake Victoria for only 4,000 years—yet it has five cichlid species found nowhere else
  - Plausible case of *peripatric* speciation: when lake is low, isolated ponds may form around perimeter.

Lake Tanganyika has held water for 3.5+ million years—and as you might expect, its cichlids are even more diverse in shape than those of younger Lake Victoria.