Lecture 7 – The Nature of Mammalian Species

We've been noting the number of species present in various groups and structuring lab by referring to individual species. We should take a look at what a species is; obviously, it's critical for conservation and management.

I. Naming Species

The practice began in 1758 with Carolus Linnaeus and the 10th edition of *Systema Naturae.*

There is a formal set of rules for naming and diagnosing species.

For animals this is contained in the International Code for Zoological Nomenclature.

Latin Binomial --> Genus species (e.g., *Sorex palustris*)

Sometimes subspecies names are included but these are not required, and subspecies are perhaps best viewed as "incipient species" (although that's not a universal view): *Tamias ruficaudus simulans*.

II. Species Concepts and "The Species Problem".

I think one of the biggest ironies in science is the difficulty with the **definition of species**.

We all have an intuitive feel for what a species is, but an explicit, universal definition has proven very elusive. This is called **the species problem**; it's incredibly hard to define what a species is.

We have no trouble going out into a particular locality and sorting the diversity we see into discrete packages. With a little training, we can identify virtually any organism to its species (if it belongs to a species that has been described).

However, as we expand the scope of our attention geographically, the discrete boundaries start to become obscure, and exactly what a species is becomes quite ambiguous.

The scope of this issue is often underappreciated, but since 2000, 7340 papers have been published on it. In 2023, ~221 papers have been published to date related to "the species problem." (Google Scholar).

A thorough discussion of species concepts is really beyond the scope of a mammalogy course, but we should have at least a little awareness of the topic.

A. Biological Species Concepts. Developed by Ernst Mayr, a bird systematist.

This is the concept that we learn as introductory biology students, and it's the concept that has classically been used in mammalogy.

Sets of populations that are reproductively isolated from other such groups of populations.

That is, a species is the most inclusive set of populations that can potentially interbreed.

Reproductive Isolation (RI) is the criterion, and the study of isolating mechanisms has long been an active field.

Reproductive isolation results in separation of gene pools (no gene flow between).

Almost all research on the process of speciation adopts the BSC and focuses on the accumulation of RI.

There are **prezygotic** isolating mechanisms, that act before fertilization.

This is often as simple as a geographic barrier that prevents interbreeding between groups of populations

It's more interesting when these involve changes in reproductive behavior and or timing that decrease the probability of mating.

There are also **postzygotic** isolating mechanisms, that act after fertilization.

Familiar examples include hybrid sterility; mules are sterile offspring between a horse (*Equus caballus*) and a donkey (*Equus asinus*).

Hybrid breakdown occurs when hybrids are fertile but have reduced fitness/fecundity.

Speciation biologists often disagree with respect to the relative importance of pre- versus post-zygotic isolation in speciation. Both are clearly important, but evidence is accumulating that prezygotic isolation often in the initial catalyst.

The BSC is tied to the classical model of speciation, **Allopatric Speciation**.

An ancestral species is split into two by formation of a barrier (this hypothetical river).

Divergence occurs over a long period of time while emerging species are isolated.

This could be due to any of several forces, including drift and or differential adaptation.

If the daughter lineages come into secondary contact, they may be reproductively isolated.

So, secondary contact is required to test the criterion of reproductive isolation.

So BSC has been the primary concept that mammalogists have used, but there are several problems with it.

1) Allopatric populations (if no secondary contact occurs in nature).

The Idaho ground squirrel, *Urocitellus brunneus*, had two subspecies that had been proposed to represent different species.

The two subspecies are allopartic, so the criterion of reproductive isolation is not testable (Hoissington et al. 2012. J. Mamm. 93: 589).

Taxonomic decision under BSC here becomes a judgment call.

Is the degree of differentiation large enough that there would be reproductive isolation were the two to come together naturally?

2) Emphasis is placed on sexual reproduction. Templeton has pointed out that this is problem under two conditions. (Templeton, A. 1989. The meaning of species and speciation: a genetic perspective. In: *Speciation and its consequences* (eds. Otte D, Endler J). Sinauer Associates, Sunderland,MA)

Too much sexual reproduction: It's long been recognized that hybridization is rampant.

This is especially true for plants, where we see all kind of hybrids.

Even within mammals, we see lots of evidence of hybridization.

Cricetids - *Peromyscus leucopus/gossypinus* (white-footed and cotton mice) hybrids (e.g., Barko & Feldhamer, 2002. Amer. Midlands. Natur.).

Sciurids – There is lots of hybridization among *Tamias* species (e.g., Good et al. 2003. Evolution; 2008. Mol. Ecol.; Sullivan et al. 2014. Heredity).

Cervids – *Odocoileus hemionus*/*virginianus* hybrids occur at a low frequency across a broad area of sympatry.

Primates – There's hybridization and introgression between *Papio hamadryas* and *P. anubis* (e.g., Charpentier et al. 2012. Mol. Ecol.).

Too little sexual reproduction: Although all mammals reproduce sexually, this is not true for lots of other groups.

Many vertebrates (~ 70) have no sexual reproduction (parthenogenetic lizards & fish) where every lineage is isolated from every other.

Reproductive Isolation is not an applicable criterion.

Even when there is sexual reproduction, mating systems may not be amenable to this criterion: for example, obligate sibling mating.

Parasitoid wasps oviposit in tarantulas. The eggs hatch and the larvae remain inside the spider, feeding on it. They then actually pupate inside the spider. When the adults emerge from pupation, the males come out first, and mate with their sisters as they are emerging. Because of this mating system, each clan is reproductively isolated from every other and should be recognized as distinct.

Because of these problems, many systematists have abandoned the BSC.

A **huge array of species concepts** has been developed & there's no consensus on which species concept should prevail over all others. We should address a few though.

B. Pylogenetic Species Concepts – A group of related concepts.

Evolutionary Species Concept of G. G. Simpson in the 1940's.

A group of populations with its own evolutionary tendencies and a unique evolutionary fate.

This concept is very difficult to apply because the criterion is "unique evolutionary fate'" but it focuses on evolution rather than reproduction

The ESC has been modified somewhat.

Phylogenetic Species (strict sense) - groups of populations that are diagnosable from other such groups of populations by fixed differences. Diagnosability is the criterion, hence this is sometimes called the dPSC.

In its strictest manifestation, a single character is enough as long as all individuals in all populations of one group have one state that is unique to that group.

Advantages:

In cases of allopatry we're not forced to make a judgment call. If there's a fixed difference, we can recognize different species.

Removes the emphasis on reproduction so hybridization and parthenogenesis are not really problems.

One problem: The dPSC over-recognizes diversity. Recent controversies in the taxonomy of African bovids has centered around this (See e.g., Zachos, 2018. PDF on course website).

Bigger problem: If we look at different characters, we may get different species boundaries.

Tamias ruficaudus example; two subspecies, *T. r. rufucaudus* & *T. r. simulans*.
Bacular morphology splits the populations one way. PSC could recognize as distinct.
Genetic data split the population another way.
Problem with the PSC as some envision it is that a single fixed difference is all that's required - which would you use?

This problem of incongruence has led to a further modification.

Genealogical Concordance Species Concept - A group of populations that are diagnosable by > 1 character.

This concept also relies on diagnosability, but more than one character must exhibit a similar pattern; there must be **concordance**.

If we go back to the *Tamias ruficaudus* example, if we had uncovered the same partitioning of the populations into the same groups with the genetic data, then we would have had evidence to recognize two distinct species under this concept.

Advantages of the GCSC:

Has the same advantages as the PSC; it's useful in allopatry and does not emphasize sexual reproduction

Also, it is predictive and testable.
A taxonomic decision is a hypothesis. Under the GCSC, if we recognize two species as distinct, we actually are predicting that additional characters will be concordant. Taxonomic hypotheses therefore become more testable.

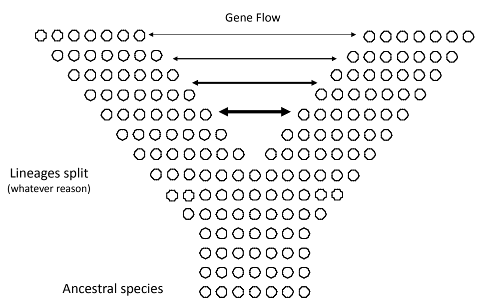
Problems of the GCSC

It really is the most rigorous of the species concepts.
Ignores some processes (hybridization) and will tend to **underestimate diversity**.
This actually has very important conservation implications.

So, there are no universally applicable species concepts that are problem-free.

The problem really is that we are trying to place a boundary on a continuum.

As I said earlier, as we discover that there's lots of cryptic hybridization, a new model of speciation that accounts for it has been formulated. This is **Divergence with Gene Flow** (Pinho & Hey, 2010. Ann. Rev. Ecol. Evol. Syst.).



The process of speciation is often very gradual. We can depict it as such:

The time horizon we're working at is really critical.

This is in direct contrast to the classical model of speciation, in which divergence accumulates only in the absence of gene flow between daughter lineages.

This view of the problem is leading many evolutionary biologists (and philosophers of science) to view species as artificial constructs that have no basis in reality.

There still is no good solution to "The Species Problem."

Currently, systematists are forced to choose a species concept, defend its choice as most appropriate for a particular group, and then make taxonomic decisions on that basis.