

For the rest of the semester, we're changing focus on evolutionary processes acting at the level of populations (microevolution) to processes acting at the species level and beyond (macroevolution). We'll start by looking at what species are and how new species arise, then discuss how evolutionary biologists reconstruct evolutionary history. We'll finish by looking at the history of life on earth, including human evolution.

Notes on this chapter: I'll discuss most of the topics in about the same order as are in the book, but my terminology and organization differ somewhat; I've also added some material that isn't in the book. Skip "The Phylogenetic Species Concept", pp. 404-406 and section 12.4, "The Genetics of Differentiation and Isolation" at the end of the chapter.

Topic outline

I. Species concepts

- A. Are species real units in nature?*
- B. Two species concepts*
- C. Applying species concepts: the case of the red wolf*
- D. Defining species vs. recognizing species*

II. Speciation

- A. Anagenesis vs. cladogenesis*
- B. Speciation is a three-step process*
- C. Mechanisms of isolation*
- D. Mechanisms of differentiation*
- E. Reproductive isolation*

III. Hybridization

- A. Outcomes of incomplete reproductive isolation are complex*
- B. Hybrids may be equally or more fit than parents*
- C. Hybrids may be less fit than parents*

I. Species concepts

- A. Are species real units in nature? Or are they, like higher taxonomic categories (genera, families, etc.), essentially arbitrary categories we use to organize biological diversity for our own convenience?**
 - 1. People seem to have recognized as real entities groups of "organisms that reproduce after their own kind" for very long time**
 - 2. Very good agreement between modern biologists' species and those of various "native" cultures – indicating that species designations aren't arbitrary**

3. Reproductive barriers between species are very real -- so it seems that some kind of “real”, biological phenomenon is separating groups
 4. So, the conclusion for the majority of biologists is that, yes, species are “real” entities – but what, exactly, are they?
- B. Two species concepts illustrate difficulty of defining species
1. At least eight different species concepts have been proposed (and taken at least somewhat seriously) over the last ~ 50 years
 - a. diversity of concepts reflects
 - i. complexity in natural systems
 - ii. difficulty with developing concepts that are broadly applicable = empirically testable in a wide range of organisms
 - b. most concepts recognize that what makes species “real entities” in nature is that each constitutes a separate gene pool – and that the “separateness” of the gene pools gives rise to differences in
 - i. morphology
 - ii. “evolutionary fate”
 2. The **morphological species concept** – old (“typological”) and new (“phenetic”) versions
 - a. In its original form, this is the idea that Mayr refers to as the “**typological species concept**”
 - i. This was the “standard” concept (along with reproducing after own kind) pre-Darwin; stemmed from premise that species were specially and individually created
 - ii. Idea = every species has an ideal form or type (sound familiar?): individuals belong to that species if they don’t vary too much from the type
 - iii. Remnants of this way of doing things still persists in our formal designation of type specimens (or series) when new species named

- iv. Because we know now that species aren't created according to "types", this form of the morphological species concept isn't used any more
- b. In its modern form, is often called the **phenetic species concept** = "morphospecies" in text
 - i. "phenetic" comes from same root as phenotype – refers to the characteristics of an organism without regard to phylogeny
 - ii. phenetic species concept defines species based on overall degrees of morphological similarity and difference, without regard to relationship, reproductive isolation, etc.
- c. Advantages and disadvantages of phenetic species
 - i. advantage: is very useful when working with fossils and other organisms for which we lack ecological, behavioral data
 - a) on your own, read on pp. 406-407 how Jackson and Cheetham demonstrated that morphological species of bryozoans are also reproductively isolated
 - ii. disadvantage:
 - a) doesn't work well in all cases, e.g.:
 - i) **cryptic species**
 - species that are extremely similar morphologically in spite of being reproductively isolated
 - using phenetic species definition, cryptic species get "lumped" as same
 - ii) **polytypic species**
 - = species characterized by strong polymorphism (e.g., pepper moths; yellow-shafted and orange-shafted morphs of Common Flickers; etc.) – but still with gene flow, no reproductive isolation

- using phenetic species definition, polytypic species may get “split” into different species
 - b) level of similarity necessary to qualify a group as a species is arbitrary, so can't really be tested empirically (i.e., level of similarity that one investigator thinks is sufficient to define species may be insufficient for another)
3. **Biological species concept (BSC)**
- a. Defined by Mayr in 1942: *a species is a group of actually or potentially interbreeding natural populations reproductively isolated from other such groups.*
 - i. Principles began to arise late 1800's; formalized by Mayr as part of modern synthesis.
 - ii. Stresses notion of species as “a protected gene pool” -- as a group of individuals that share genes with each other but not with members of other groups
 - iii. this is currently the most widely used concept
 - b. Advantages and disadvantages
 - i. advantages
 - a) definition incorporates reproductive isolation explicitly – and this is what most biologists think is the key to species as protected gene pools
 - b) it makes uniform, clear, testable predictions that can be used to determine whether or not two groups are separate species
 - c) predictions are practical to test in a wide variety of organisms
 - ii. disadvantage = predictions either can't be made or aren't testable in a variety of kinds of organisms – e.g.
 - a) fossils (data on potential for interbreeding usually very difficult to find!)

- b) asexual species – definition simply doesn't apply
 - c) allopatric species (how do we measure “potential” to interbreed? – not impossible, but sometimes not very easy)
 - d) species with incomplete isolation (e.g., ring species; species with stable hybrid zones)
 - c. Problems with BSC have important practical implications – BSC is definition used in the Endangered Species Act – so difficulties applying it can make a real difference in the extent to which groups of organisms can be protected by law e.g. . . .
- C. Applying species concepts: the case of the red wolf (*Canis rufus*)
1. Background:
 - a. Red wolf was first named as separate species by Audubon and Bachman in 1851
 - b. Red wolves were found historically in the SE and SC USA, from Florida to C Texas and north to S Indiana and Missouri.
 - c. morphologically, are ~ intermediate in size and general appearance between coyotes (*Canis latrans*) and grey wolves (*Canis lupus*)
 - d. were common historically, but by early 1900's had been ~ eliminated throughout much of range; by 1980, were extinct in the wild
 - e. before going extinct in the wild, remnant populations showed extensive interbreeding with coyotes
 - f. species was listed as endangered and captive populations were used to establish and introduce new populations in part of SE U.S
 2. Problem: taxonomic status is unclear – red wolves may be hybrids between coyotes and grey wolves, in which case they lose their status under the ESA
 - a. two hypotheses for origin of red wolves:
 - i. “ancient origins” hypothesis: red wolves are modern descendants of the lineage that gave rise to wolves and coyotes

- a) current hybridization is due to breakdown of red wolf social structure and increased interaction with coyotes as a result of habitat loss and disturbance
 - b) under this hypothesis, red wolves qualify as species under the BSC, and therefore qualify for protection under ESA
 - ii. "modern hybrid" hypothesis: red wolves are a lineage of recent hybrids between grey wolves and coyotes with no unique genetic characteristics of their own
 - a) note that the cause of current hybridization with coyotes is the same as above
 - b) but under this definition, red wolves don't qualify as species under BSC (they're not reproductively isolated), so theoretically can't be protected
 - b. evidence:
 - i. morphological data show that
 - a) before ~ 1930, red wolves were clearly identifiable morphological species intermediate in appearance between grey wolves and coyotes – suggesting no hybridization with either at that time
 - b) after 1930, red wolves become morphologically more similar to coyotes, suggesting recent hybridization with coyotes
 - ii. genetic data mixed
 - a) no diagnostic differences between red wolves, coyotes
 - b) 1999 comparison of DNA evidence from modern red wolves, coyotes, grey wolves suggests recent origin through hybridization
 - c) 1996 comparison of mt and nuclear DNA evidence suggests ancient origin through hybridization
3. Are red wolves a separate species under the BSC? hard to say
- a. origin by grey wolf-coyote hybridization as recently as ~ 2000 years ago

consistent with both morphological and genetic data

- i. note that origin by hybridization in and of itself doesn't prevent red wolves from being good species under BSC
- b. BSC requires reproductive isolation – are red wolves reproductively isolated from coyotes?
 - i. modern red wolves hybridize readily with coyotes – that suggests not
 - ii. morphological data suggests that hybridization with coyotes is a recent phenomenon – so may still qualify as good species
 - iii. unfortunately, genetic data don't help much:
 - a) if we had fixed differences between red wolf, coyote populations, then we'd have good evidence for reproductive isolation
 - b) but lack of fixed differences doesn't necessarily prove that hybridization has been ongoing – could be that
 - i) isolation hasn't been long enough to fix differences
 - ii) differences exist but haven't been found (not all genes have been examined!)
 - iii) likelihood of either of these hard to assess
4. For now, red wolves still granted specific status and still protected – but what will happen in future is unclear.

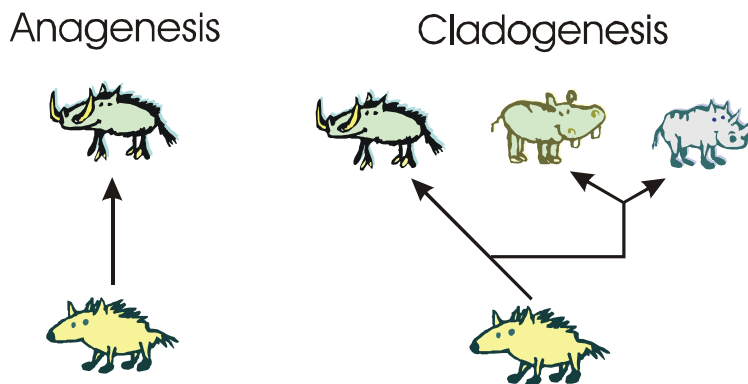
D. Defining species vs. recognizing species

1. As a matter of practice, although we define species according to whichever criteria we favor, we still recognize species (for the most part) based on appearance
2. Whichever criteria/definitions we use, we will still have some “gray” areas that are hard to resolve, e.g.
 - a. fossil species that show change within a lineage over time
 - b. ring species
 - c. incipient species

3. Reasons for difficulty coming up with simple, widely applicable species concepts vary, but include the fact that species are the result of evolutionary processes acting over long periods of time (next subject!) -- and we're seeing "snapshots" at various stages in that process.
4. So, interestingly enough, the fact that it's hard, sometimes, to identify "boundaries" between species is actually great evidence that evolutionary change has happened and is still happening!

II. Speciation

A. Anagenesis vs. cladogenesis



1. When we follow the history of lineages over time, two broad patterns may appear – it's important that we be able to distinguish them:
 - a. **Anagenesis** = change within a single lineage over time
 - i. sometimes referred to as **phyletic change**
 - ii. doesn't really increase biological diversity because doesn't add new lineage
 - iii. as matter of practice, species undergoing phyletic change may be given multiple names, each recognizing a different "phyletic species" (this is especially the case with fossil groups)
 - iv. "phyletic species" may "qualify" as new species under the phyletic species concept, but not under the BSC or most other species

concepts – why not?

- b. **Cladogenesis** (what I refer to when I say “speciation”)
 - i. a. process by which one lineage “splits” into two or more “daughter” lineages
 - ii. this is the process that actually increases biological diversity – it adds new isolated gene pools/evolutionary lineages
 - iii. note that new lineages qualify as new species under BSC and many other species concepts
 - iv. in modern usage, most biologists (including me!) mean this when they talk about “speciation”
- B. Speciation is a three-step process – these steps are always necessary, even though the mechanisms for each step may vary
 - 1. The establishment of a barrier to gene flow leads to genetic isolation among populations
 - a. remember that any species consists of a group of populations
 - b. migration (gene flow) constantly “mixes” alleles, homogenizing the gene pool
 - c. for a new gene pool to be established, gene flow must be interrupted somehow
 - 2. Disruption of gene flow leads to the genetic (and consequently morphological, behavioral, ecological, etc.) divergence between species.
 - 3. If divergence continues long enough, populations will become reproductively isolated – i.e., won’t be able to interbreed even if members come into contact.
 - 4. Once reproductive isolation is achieved, speciation has occurred.
- C. Mechanisms of isolation = mechanisms establishing barriers to gene flow are usually classified based on the geographic distribution of parent, daughter species
 - 1. in **allopatric speciation** , geographic distributions of diverging populations

do not overlap

- a. in all allopatric speciation models, the barrier to gene flow is geographic/climatic (e.g., mountain range, river, desert, etc.) = physical isolation
- b. barriers may arise via one of two processes – **dispersal** or **vicariance**:
 - i. **dispersal** = movement of individuals to previously unoccupied habitat
 - a) classic e.g. = *Drosophila* radiations in Hawaiian islands
 - i) over 500 named species + ~ 350 still waiting to be formally described; huge ecological variation among species
 - ii) leading explanation for extreme diversity is that islands (and habitats within islands) were successively colonized by small founding populations, each of which was then physically isolated from its source population
 - b) how can dispersal hypotheses be tested?
 - i) two basic predictions follow from founder hypothesis:
 - closely related species should usually be found on adjacent islands (why?)
 - sequence of speciation (“branching”) events should be similar to sequence of island formation
 - ii) test by working out phylogenetic relationships among species and comparing branching pattern to position, age of islands; in this case, both predictions met (fig. 12.7)
 - ii. **vicariance** = geologic and/or climatic events that create physical barriers to gene flow (e.g., mountain uplift; climate change; rise in sea level; etc.)
 - a) e.g. = establishment of the isthmus of Panama was vicariant event that separated marine organisms into Caribbean and Pacific populations

- i) separation took place ~ 3 million years ago
 - ii) for some organisms, this is long enough to lead to speciation
 - iii) e.g., Knowlton et al. identified populations of snapping shrimp that seem to comprise seven pairs – one Pacific and one Caribbean – of closely related morphospecies
 - b) how can vicariance hypotheses be tested? Knowlton et al.'s studies of snapping shrimp are good example
 - i) vicariance hypothesis is that rise of Isthmus of Panama split 7 species into 7 pairs of populations separated by land
 - ii) this hypothesis leads to two specific predictions:
 - for each Pacific species, closest relative should be a Caribbean species (i.e., the closest relative of the Pacific species should be the one from which it was most recently separated)
 - degree of divergence among members of each species pair should be correlated with timing of separation (in this case, timing would be based on species ranges)
 - iii) test by working out phylogenetic relationships and comparing to predictions; both predictions met (fig. 12.8)
2. In **sympatric speciation**, the distribution of diverging populations overlap (there is no physical barrier to gene flow)
 - a. this is thought to be a rare event because few mechanisms can create a strong barrier to gene flow among populations that are not physically separated
 - b. two general mechanisms either known or thought to work:
 - i. **polyploidy**: isolation due to change in chromosome number
 - a) as we discussed earlier, polyploidy is common in plants
 - i) may arise as in conjunction with hybridization =

allopolyploidy

- ii) may arise without hybridization = **autopolyploidy**
- b) when chromosome number is multiplied, polyploid gametes will be reproductively isolated from parent plants
- c) this seems to be a very common mode of speciation in most plant groups (bryophytes, ferns, flowering plants)
- d) doesn't seem to be a major mechanism in animals
- ii. isolation due to ecological differentiation – in theory, this possible under a limited set of conditions:
 - a) Populations exhibit some kind of stable polymorphism (e.g., **multiple niche polymorphism**, as in black-bellied seed crackers) – this provides initial impetus for divergence
 - b) Selection must favor **positive assortative mating**: individuals mating with “other” form must have reduced fitness – this acts as the barrier to gene flow
 - c) Thought to be rare in animals; but known or suspected in some
 - d) e.g. #1 = Green lacewings
 - i) two species have completely overlapping range
 - ii) one lives on conifers; one in meadows/deciduous trees
 - iii) differ in color (camouflage) and timing of reproduction
 - iv) proposed scenario:
 - start with multiple niche polymorphism = using different trees
 - selection favored different camouflage colors
 - selection acted against “hybrids” via their reduced camouflage on either kind of tree
 - different timing of breeding was the mechanism that helped promote assortative mating; now part of isolating mechanisms

- e) e.g. #2 = host-switching in phytophagous (plant-eating) insects
 - i) this may apply to many species, but will illustrate with famous example of *Rhagoletis pomonella* (apple maggot fly – more later)
 - ii) general scenario
 - some individuals colonize new host
 - differences in host immunology/physiology/morphology etc. select for different characteristics in insects; this gives rise to polymorphism
 - host fidelity = mechanism of assortative mating; also becomes isolating mechanism

D. Mechanisms of differentiation: how do differences accumulate once gene flow is disrupted?

1. Genetic drift

- a. as we know, the effects of drift can be very strong when populations are small
- b. Ernst Mayr believed that drift would be very important in allopatric speciation explained why in his model of **peripheral isolation**:
 - i. thought it was more likely for vicariant and/or dispersal events to separate populations on the periphery of a species range from populations at core
 - ii. thought that populations on periphery were likely
 - a) to be small
 - b) to be somewhat different from populations at the core because they likely faced more extreme environmental conditions
 - iii. so, when peripheral populations were isolated, drift would tend to cause relatively rapid divergence
- c. current evidence in favor of the model is mixed – seems that

- i. overall genetic diversity in founding populations is not necessarily small (although it can be)
 - ii. dramatic changes due to drift require extremely small populations
 - iii. very little evidence supporting marked genetic differences between peripheral and central populations
 - iv. very little evidence that small founding populations (established by humans introducing exotics) that have persisted for last ~ 150 years show dramatic changes in genotype
 - d. conclusion: drift undoubtedly plays some role, and may be a powerful force for divergence in some cases, but not as much or as strongly as Mayr proposed
2. Natural selection is expected to lead to genetic (and morphological, behavioral, ecological, etc.) divergence if isolation leads to environmental differences among groups of populations
- a. not a very big “if”: both vicariance and dispersal are expected to result in environmental differences
 - b. illustrate role of selection with *Rhagoletis pomonella* = apple maggot fly
 - i. background:
 - a) fly found throughout NE and North Central US
 - b) flies feed (and lay eggs, and breed) on fruit – historically, on hawthorns
 - c) basic life history:
 - i) adults mate on or near fruit
 - ii) females lay eggs in fruit on tree
 - iii) eggs hatch within ~ 2 days; larvae develop through 3 stages in the fruit where they hatch – takes about a month
 - iv) when fruit falls, larvae leave and burrow into soil where they pupate and spend the winter in diapause

- v) emerge in summer, start cycle over again
- d) when apples introduced < 300 years ago, flies started feeding on apples
- ii. question: have flies feeding on apples diverged from those feeding on hawthorns – and, if so, has selection favored different characteristics for flies on different hosts?
 - a) note: if flies are part of same population, then won't find genetic, morphological, behavioral differences between them
 - b) Feder et al. found significant differences in frequencies of alleles for 6 different enzymes – suggesting that some genetic divergence is taking place
 - c) but, because there are no fixed differences, results also suggest that gene flow is still taking place
- iii. For differences to persist in spite of gene flow, selection must be acting to maintain them – what morphological/behavioral/physiological differences between populations does selection favor?
 - a) Feder et al. noted that apples ripen ~ 3 weeks earlier than hawthorns do
 - i) means that flies using apples will enter diapause sooner and experience “longer summer” as pupae = longer time between when they enter diapause and when weather warms up again
 - ii) so selection should favor slower development time: if “apple” flies follow same timing as “hawthorn” flies, will emerge from diapause before winter is over
 - b) performed elegant test of hypothesis that selection acts on genes associated with timing of development:
 - i) took pupae from hawthorn fruits and divided into groups
 - ii) exposed each group to temperatures mimicking summer, winter,

spring

- iii) groups differed in the number of warm days before “winter”
 - remember, “hawthorn” flies experience shorter summers – less time between hatching and when they must enter diapause
 - similarly, “apple” flies experience longer summers – they need to stay in diapause longer to emerge in the spring
- iv) as flies emerged in “spring”, assayed the frequencies of the alleles that are known to vary between populations
- v) prediction: flies surviving long springs (equivalent to flies surviving after developing on early fruit) will have same enzyme frequencies as “apple population” flies
- c) hypothesis was confirmed: selection favors differences in timing of development and that is responsible for enzyme differences (fig 12.11)
 - i) note that this experiment mimics, in a single generation, what’s been happening in nature over the course of ~ 300 years!

- E. Reproductive isolation: for speciation to be complete, divergence must eventually lead to mechanisms that prevent gene flow even when groups come back into contact
1. Dobzhansky was one of the first evolutionary biologists to think about how this might work; he proposed the hypothesis of **reinforcement**:
 - a. given enough genetic divergence between populations while they were in allopatry, hybrids should have lower fitness than individuals in either parent population – this could be because
 - i. incompatibility of developmental programs in parental species
 - ii. ecological differences between parent species result in different adaptations – which are disrupted by hybridization

- b. if hybrids have lower fitness than parents, selection should favor individuals that choose mates only from their own population
 - c. more specifically, selection will favor traits (anatomical, behavioral, ecological, etc.) that prevent interbreeding – these traits are called **reproductive isolating mechanisms**
 - d. result is reproductive isolation – the final step in speciation
 - e. Current evidence in favor of this hypothesis is mixed:
 - i. in some cases, reinforcement does seem to be important in establishing reproductive isolation
 - ii. in others, it seems that genetic divergence while populations are in allopatry gives rise to reproductive isolating mechanisms directly
2. Regardless of whether or not reinforcement is involved, we can recognize a number of different kinds of reproductive isolating mechanisms – following a modified version of Dobzhansky’s classification, they are:
- a. **pre-zygotic isolating mechanisms** = hybrid zygotes never form
 - i. **ecological/habitat**: diff. populations exploit different parts of the environment
 - a) e.g., in *Rhagoletis*, flies prefer to mate on the same kind of fruit in which they developed = **host fidelity**
 - ii. **seasonal/temporal**: breeding occurs at different times, seasons
 - a) e.g., many species of salamanders and frogs breed in the same ponds, but at different times
 - iii. **ethological**: behavioral differences prevent individual of one species from “recognizing” or being attracted to individual of another sp.
 - iv. **mechanical**: anatomy of genitalia prevents intromission
 - v. **gametic**: gametes not attracted to each other
 - a) e.g., recognition proteins on sperm, egg, incompatible
 - b) sperm are inviable in female reproductive tract (animals) / pollen is

incompatible with style tissue (plants)

- b. **Post-zygotic isolating mechanisms:** Hybrid zygote forms, but because genomes are incompatible, has reduced fitness at various stages – these form a continuum of isolating mechanisms
 - i. **hybrid inviability:** zygote dies before adulthood (sometimes before birth)
 - ii. **hybrid sterility:** hybrid reaches adult, but is infertile
 - iii. **hybrid breakdown:** hybrids fertile, but their offspring aren't
- III. Hybridization: what happens when reproductive isolation isn't complete?
- A. Outcomes of incomplete reproductive isolation are complex,
 - 1. generally depend on
 - a. fitness of hybrids relative to fitness of non-hybrids
 - b. structure (size, ecological characteristics) of hybrid zone
 - 2. Because outcomes are complex, we'll review only a few, and only in very general terms
 - B. Hybrids may be equally or more fit than either parent species
 - 1. This can have several possible outcomes
 - a. If higher fitness is associated with a novel habitat type, result may be the formation of a new (third) species – this seems to have happened in at least some plant and animal species
 - b. If higher fitness is associated with an ecotone = habitat that is transitional between two different habitat types, result may simply be the formation of a stable hybrid zone
 - c. if hybrids have equal fitness across both parental habitat types, then eventual outcome will be coalescing:
 - i. differentiation between parental population stops (hybridization reintroduces gene flow)
 - ii. populations merge back into single species

2. Hybrids with relatively high fitness are common in plants, which leads to major concern over use of genetically modified crop plants: what happens if engineered genes “escape” from crop species to weed species via hybridization?
 - a. scenario is not far-fetched: many commercial crop species are grown in areas that also support native “weedy” relatives
 - b. Arriola and Ellstrand demonstrated this possibility using sorghum (important crop) and johnsongrass (a close relative and major weedy “pest”)
 - i. sowed an experimental field with sorghum that had a distinctive allozyme marker (= unique allele for an enzyme)
 - ii. planted seedlings of johnsongrass at various distances from crop field
 - iii. harvested johnsongrass seeds and raised progeny
 - iv. tested offspring for presence of allozyme (presence indicates hybridization)
 - v. demonstrated significant crop-to-weed gene flow via hybridization
 - c. Question: what would happen if, instead of a neutral allozyme marker, crop-to-weed gene flow involved engineered genes for resistance to pests or pathogens? Could get “superweeds” – a major concern
- C. Hybrids may have lower fitness than parents
1. If selection against hybrids is strong, then get reinforcement; hybrid zones will be relatively narrow and transient
 2. If selection against hybrids is relatively weak, outcome may be relatively wide, relatively long-lived hybrid zone – in this case, hybrid zone is maintained by selection-migration balance: if selection against hybrids is weak enough, it can be balanced by formation of new hybrids by parental forms migrating into hybrid zone and interbreeding.