Chapter 18. Macroevolutionary Patterns and Phylogeny

Barry Sinervo©1997-2007

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Identifying Patterns of Evolutionary Change

Throughout the chapters I have focused on a microevolutionary perspective regarding the evolution of behaviors. In the consideration of the mechanisms of natural and sexual selection, I focused on the behavioral traits being shaped by the success of individual organisms, or in levels of selection groups of organism. Mechanisms of natural and sexual selection are referred to as **microevolutionary processes**. The power of natural, sexual or social selection can lead to rapid evolution in a trait that is favored by the environment. Adaptation is subject to constraints that limit the direction that evolution can take a species. Constraints on evolutionary change can arise at a number of levels. We have already focused on constraints on adaptation that arise from the design of sensory structures, as well as the physical environment around the organism -- these are the constraints of proximate mechanisms.

A number of authors have advocated the idea that a species is constrained by its own phylogenetic history, the precise evolutionary trajectory that it has undergone over the millennia of slow change, novel adaptations, and evolutionary branching events that we call speciation. During the evolution of a group, certain features that evolved in an adaptive context may actually limit the possible evolution of other features. For example, once birds developed wings and powered flight, this adaptation makes it necessary to limit the number of eggs that a female is carrying to only a few eggs at any point in time. Thus, most birds labor under the constraint that they cannot produce the eggs all at once like a lizard and birds lay eggs in a sequence, one at a time. This constraint then makes it necessary to alter many other reproductive

behaviors to make allowances for the fact that hatchlings might be of different age (e.g., yolk steroids to increase aggression of later hatching progeny, Chapter 15). Such **phylogenetic constraints** surely exist but they are difficult to identify. If birds evolved flight only once, then this gives evolutionary biologists only a single example to analyze, which is not a very large sample size. In addition, proof of the existence of such constraints relies on the comparative method. In most cases it is very difficult to experimentally manipulate the trait of interest. Such higher order processes, which might limit or alternatively channel evolutionary change in certain directions, are referred to as **macroevolutionary processes** and the constraints that build over time, as a lineage evolves, are referred to as **phylogenetic constraints**.

What is the comparative method?

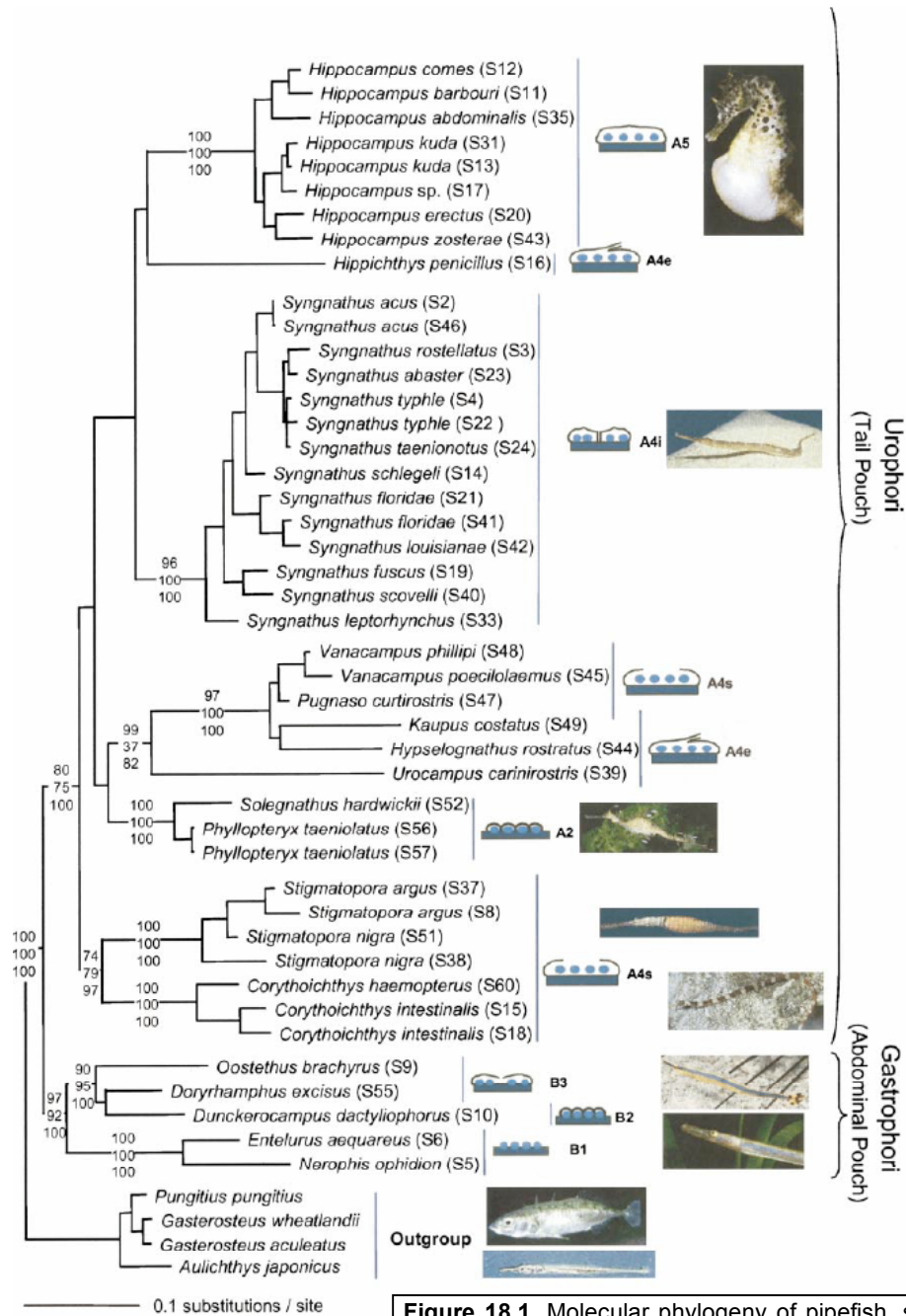Throughout this book I have introduced key phylogenetic concepts:

1) In Chapter 1, evolution of avian *vs*. mammalian care was used to illustrate constraints on mating systems due to female only care.
2) In Chapter 5, evolution of Müllerian mimicry (butterflies) and evolution of Aposematic mimicry (*Ensatina* salamanders) require application of phylogenetic methods to establish that a trait has arisen from a given ancestral condition. In the case of butterflies, phylogenetic evidence was used to determine that *H. cydno* and *H. melpomene* have diverged to mimic *H. sapho* and *H. erato*, rather than vice versa, establishing which is model and mimic.
3) In Chapter 11, evolution of paternal care in sticklebacks was clarified on a phylogeny (e.g., sequence of refined adaptations).
4) In Chapter 14, the phylogeny was used to determine that a Müllerian mimic of the *Pitohui* bird evolved independently from the model *Pitohui*, but that other *Pitohui* species exhibit Müllerian mimicry as a shared ancestral trait. In dart-poison frogs multiple instances of evolved mimicry was shown for a trimorphic species.
5) Evolution of hippocampus volume and general brain volume was linked to the evolution of food hoarding (Chapter 17). The cognitive load that food hoarding imposes favors evolution of larger brains as a correlated evolutionary change.

For example, we have already put the comparative method into practice when we ask questions concerning differences in male parental care among: sticklebacks, pipefish, and seahorses (point 3). We identified the changes in environment that may have been influential in promoting the evolution of male biased care. In the case of mating systems, any operational sex ratio can lead to sexual selection on males versus females, and might even change the primary care-giving sex from female to male. What we lacked for a complete consideration of the comparative method was an idea of the history of evolutionary change in these groups. To understand the history of change, we have to develop a notion of phylogeny and **cladistic** relationships. Here I develop the formalism of evolutionary biology for analyzing ancestor-descendant relationships and the inferences one can make from a phylogeny.
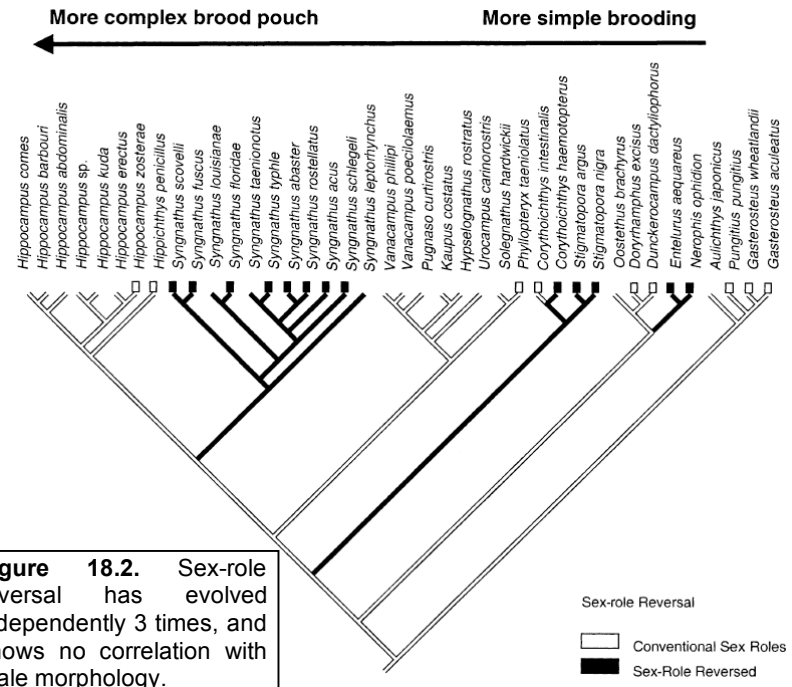
The Evolution of Male Care in Sticklebacks, Pipefish, and Seahorses

Sticklebacks, pipefish, and seahorses belong to the same family of fish and this group is noteworthy in the animal kingdom for the evolution of highly advanced male care. We have already considered the role of ecology in shaping the mating system. This system is also illuminating with regards to the role of ecology in governing the evolution of mating systems (Wilson et al. 2002).
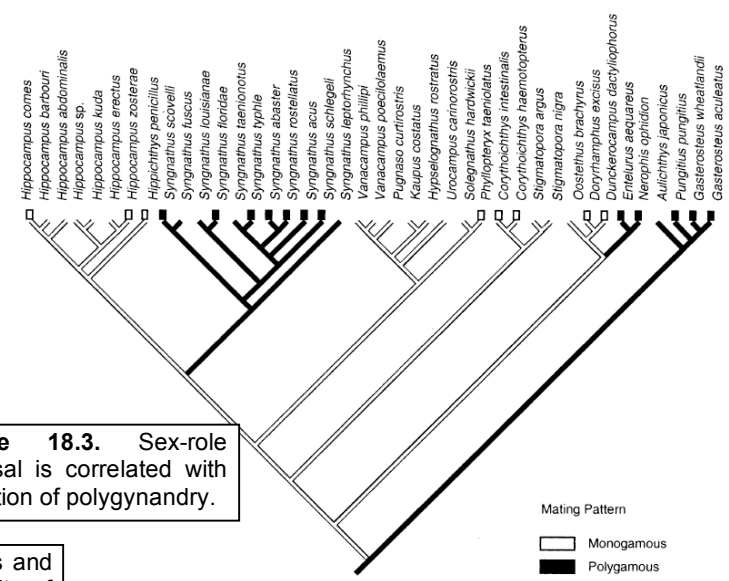
The evolutionary relationships among these three groups is roughy as follows: Sticklebacks → Pipefish → Seahorses. The morphological complexity of the male's brood pouch varies among the species comprising the clade (Fig. 18.1). These differences have to do with the complexity, and quantity of nutrients transfer to embryos, along with the degree to which the marsupium is folded and enclosed. For example, in the ancestral form the stickleback, there is a certain amount of paternal care, but all they really do is fan the eggs until they hatch -- there is no transfer of energy. In pipefish males, the brood pouch is quite elaborate, but no real placental connections take place between the father and young. Finally, the seahorses have the most complex brood pouch with a system for transferring nutrients. Evolution of more advanced brood pouch maps quite well onto the phylogeny for the group, but the correlation of the complexity of the pouch with sex–role reversal where females are ornamented and dimorphic in size (Fig. 18.2) is not perfect.

Figure 18.2. Sex-role reversal has evolved independently 3 times, and shows no correlation with male morphology.

Sex-role Reversal

☐ Conventional Sex Roles
■ Sex-Role Reversed

Figure 18.3. Sex-role reversal is correlated with evolution of polygynandry.

Mating Pattern

☐ Monogamous
■ Polygamous

Figure 18.1. Molecular phylogeny of pipefish, seahorses and sticklebacks (outgroup). Diagrams illustrate the complexity of folds of the male brooding structure (from Wilson et al. 2002).

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Although the phylogeny indicates that male brooding structures have been highly conserved over the evolutionary history of the group (Fig. 18.1), sex roles appear to have reversed multiple times, independent of pouch type variation within the family (Fig. 18.2). The lack of correlation between sex roles and brooding structures (Wilson et al. 2002) may be partly explained by results from several recent studies, which demonstrate that sex roles and intensity of competition for mates can be predicted by differences in potential reproductive rates between the sexes, which are influenced by environmental factors such as ocean temperature. During a warm breeding season, males have shorter pregnancies and are available more frequently for mating than under colder ambient water temperatures (Vincent et al. 1994). Even though females always compete for access to mates in *Syngnathus typhle*, they will compete even more intensely when temperatures are reduced, due to a more female-biased operational sex ratio caused by the extended period of male pregnancy (Vincent et al. 1994; Ahnesjö 1995). This implies that levels of sexual dimorphism in females can in fact rapidly evolve and be elaborate or alternatively be rapidly lost.

Despite a lack of association of brood pouch structure and sex-role, sex-role reversal is positively associated with polygamous mating patterns (compared Fig. 18.1 and 18.2), whereas most non-reversed species mate monogamously, suggesting that selection for polygamy or monogamy in pipefishes and seahorses may strongly influence sex roles in the wild. The take home message is that phylogenetic analysis reveals traits that tend to be coupled by selection or those that are uncoupled by selection.

Phylogenetic Analysis

The fundamental topology underlying all phylogenetic analysis is the phylogenetic tree. The idea of a tree representing the evolutionary history of a group was so compelling to Darwin that he included a figure of this process in his book the Origin of Species. Darwin was not one to include many pictures, as this is the only figure in the entire book. A phylogenetic tree traces genalogical relationships among species much like a family tree traces genalogical relationships among individuals in a field pedigree. The formation of new lineages or species takes place by the Speciation Mechanisms. In a given tree, these events are evolutionary branching events, which were described in Chapter 5.

The pattern of *correlated changes* in a genealogical relationship within a species arises from *correlational selection* or *assortative mating*. The constraints on trait covariation in a genealogical relationship are due to either pleiotropy (e.g., one gene affects two or more traits) or the gene epistasis due to a social game (see Chapter 11). The correlated changes that arise in a phylogenetic tree can arise from correlated evolution of traits, either within a single species, or between two distinct co-evolving lineages. The absence of certain correlated character states in a phylogeny may reflect potential constraints on an evolving lineage, or alternatively an adaptive necessity (this trait only works with in this combination). Therefore, the phylogenetic tree can be used to add evidence to inferences made within a population regarding pleiotropy and correlational selection as the source of trait correlation. If traits are pleiotropic within populations, then this may constraint evolutionary branching events and lead to correlated trait change on the phylogeny. Alternatively, if a stable social game always arises with certain combinations of colors, then the same signal meaning for colors will be reliably self-assemble independently on different branches of the tree.

We first need to consider tree topology and names for features on the tree to develop the working vocabulary of phylogenetic analysis. A branch point where it thought that two separate **lineages** arose is termed a **node** or the **common ancestor** of the members of the lineage. The group of species that are all **descendants** of the common ancestor are called a **clade**. Thus, the phylogenetic tree is also referred to as a cladogram in that it describes all ancestor-descendant relationships in a graphical form. The vertical axes for a cladogram reflect time.

Evolutionary biologists have many ways of assigning time to the vertical axis. The most intuitive component of time that we might imagine is real time as drawn from the fossil record. For example, the common ancestor of all homonid lineages is thought to be *Australopithecus ramidus* , an ape that appeared in the fossil record 4.6 million years ago. *Australopithecus ramidus* gave rise to the lineages of Australopithecines of which its most famous member, a skeleton called "Lucy", is thought to be a member of the species, *Australopithecus afaraensis*, that gave rise to all lineages of *Homo* as well as other branches of *Australopithecus*. In addition to fixing the vertical axis based on time, molecular biologists can calibrate the number of amino acid

substitutions in a protein or the number of nucleotide base pairs in a gene with what is known as the molecular clock. If change in these molecules is constant over time and for all bracnches on the tree for a clade, one could calibrate the molecular clock or rate of change in amino acid residues or base pairs using a single fossil that marked the divergence of two clades. Where fossil calibration is not available, information on simple genetic distance is used as a measure of "time".

The steps involved in any phylogenetic analysis are as follows:

1. Identify an **outgroup** with ancestral characters.
2. Construct a tree using characters that are neutral from the perspective of evolution. In this regard trees based on molecular data such as DNA sequences are usually preferred to trees based on morphology, which is subject to natural selection (some morphology may be relatively neutral and just the product of evolutionary history). Many methods are used for constructing trees, but we will focus on the principle of **parsimony**.
3. Identify the origin of **adaptations** on the tree and make *associations* (e.g., correlations) between the origin of adaptations and some other traits in a lineage that either **constrain** or **pre-dispose** the evolution of the adaptation in the group of interest.

Outgroups: Polarizing Ancestral and Derived States

The concept of an **outgroup** is crucial for interpreting the changes that might have occurred in a lineage. For example, an appropriate outgroup for hominid lineages would be the great apes. If you were to look at the behavior of the great apes (e.g., the genus *Pan* or chimpanzees) and found aspects of their behavior that is similar to modern representatives of the hominid lineages (i.e., *Homo sapiens*), one might infer that such behaviors were also found in all extinct forms of the hominid lineages. The outgroup of chimpanzees presumably arose from the common ancestor in the remote past, and both humans and chimps share this common ancestor. Under Charles Darwin's paradigm of "descent with modification", one might assume that there was no modification in the transmission of behaviors. For example, consider the tool using abilities

of humans. Jane Goodall has reported that chimpanzees use small twigs to get termites out of tree holes -- a clear indication of tool use. Is there evidence of tool use in fossils. Yes, good tools have been found associated with the fossils of *Homo habilis* and all later hominids. However, evidence for tool use in the Australopithecines is sketchy at best. But also notice that chimps use twigs, wooden tools, that are unlikely to fossilize, and even more unlikely for us to recognize them as tools even if we were to find them.

The hominid example serves to illustrate the limitations of any phylogenetic analysis. You cannot necessarily increase your sample size -- there is only one extant species of *Homo* from which to draw information. However, other outgroups could be used to refine our inferences. For example, humans are most closely related to chimps. Gorillas are the species of great apes with which we share moderate relationships. Orangutans are the most unrelated. One could in principle date divergence of gorillas, which do not use tools, from chimps and Homo to perhaps date the origin of tool use in the family pongidae.

The phylogenetic argument implies that all Australopithecines used some kind of tools because tool use is shared by living members of clade (us) and our nearest outgroup -- the non-hominid chimpanzees. This is an argument based on **inference**, not direct observation of the ancestors of hominids. In many cases the condition of traits in the common ancestor are reconstructed from information provided by the outgroup. It is often assumed that the outgroup has more primitive traits than the clade of interest. Indeed, this feature of outgroup choice is often crucial to phylogenetic inference. This is because we are interested in two kinds of changes in a lineage. We are interested in clades that have:

1. shared ancestral characters, and
2. shared derived characters.

A **shared ancestral character** is found in the outgroup, and in those members of the clade that have not experienced any modification of the trait from the state found in the common ancestor. This is because we infer that if the outgroup species shares the trait and it is found in some clades, the species in these clades must have received the trait in an

unmodified form from the common ancestor. An opposable thumb is found in all members of the pongidae, and it is generally thought that an opposable thumb is an important requirement for a tool using hominid Other animals have evolved tool use. One of the most famous examples involves a Galapagos finch that manipulates twigs with their beaks to obtain insects in much the same way as chimpanzees. Birds have found alternative evolutionary pathways for tool use to evolve, the beak.

A **shared derived character** is ideally found in some subset of the clade and in nearly all members of that sub-clade. By inference we might hypothesize that those members of the clade with the shared derived character possess that character because the character arose once, in the common ancestor that is found at the node of the clade of interest. Chimps and Homo share the trait tool use but it is not found in outgroups more removed from this sub-clade (gorillas or orangutans).

The Principle of Parsimony and Construction of Phylogenetic Trees

How do you make cladograms?

In the absence of fossil information (which is true for most species on the planet), how on earth do you make trees? You use the information from shared derived *versus* shared ancestral traits. The same principle applies to all kinds of information (e.g., molecules to morphology).

Willi Hennig (1951) is credited with coming up with a simple rule for reconstructing the evolutionary changes that have occurred in a clade, which has revolutionized the way comparative biology is carried. First let me contrast phylogenetic analysis before and after Hennig. In the dark ages, a professor would study a group, and after a lifetime of work, they would draw a tree. The construction of the phylogenetic tree did not take place with any formal rules in mind. To learn how to draw such trees, students would enter into a lengthy apprenticeship of sorts and pick some smaller group of the large clade. In many cases the systematists would consider the concept of shared derived characters in the construction of their tree but no formal rule was used.

Hennig formalized use of shared derived characters by enunciating the

principle of parsimony. The tree in which the fewest evolutionary steps are required to connect the different branches of a tree is considered the most parsimonious tree. In making such an assumption to connect branches of the tree, we assume that evolution is conservative and that evolutionary change does not occur all over the tree. Remember that any tree is our best guess about the pattern of evolution for phylogenetic relationships among species. *A phylogenetic tree is a hypothesis of the pattern of evolution*. Inferences are used in the construction of trees.

Let us examine a hypothetical example of how we would draw a the most parsimonious tree from the following traits and let us assume that ancestral is scored as 0 and advanced is scored as 1:

Table 18.1	trait 1	trait 2	trait 3	trait 4
species A	0	0	1	0
species B	1	1	1	1
species C	0	1	1	1
outgroup	0	0	0	0

The simplest way to construct the most parsimonious tree by "hand" is to identify pairs of species with the most derived set of characters as they have changed quite a bit, and to identify the species that have the most primitive set of characters. For example, species A only differs from the outgroup in a single trait, trait 3. In addition, the other two species also differ from the outgroup in trait 3, but they also differ in a number of other traits. Thus trait 3 distinguishes our clade of species A, B, and C from the outgroup and it also tells us that the branch from A to the outgroup should be closer to the ancestral node compared to the branches for species B or C. Draw branch A on a piece of paper.

Now let us look at species B and C. Species C has three derived traits, and species B has four derived traits. Again species C is closer to the node than species B, but it is farther from the node than species A. We have a tree based on the 4 traits and this tree has minimized the changes.

How many changes are required in drawing the tree?

We can map the changes onto the tree with a "notch" and label the traits, and count that four changes are required. You can draw any other topology and you will require more changes than the four we see. Draw some other ancestor descendant relationship and test this out.

In practice, real data and real trees have conflicting information among character states. One character suggests a different phylogeny and ancestor, than if we consider a different character. What if the distribution of traits among species was as in Table 18.2.

Table 18.2	trait 1	trait 2	trait 3	trait 4
species A	0	0	1	0
species B	1	1	**0**	1
species C	0	1	1	1
outgroup	0	0	0	0

I have highlighted the single between Table 18.1 and 18.2 in bold. Trait 3 and trait 1 provide a different set of trees. Species B and C each have 3 derived traits, but we cannot figure out which branches first. There are 2 "most parsimonious trees", each of which requires 5 evolutionary steps (B first or C first). These 2 trees are shorter than all other possible trees.

Such problems typically arise from either: **convergence** in which the same character arises many times on the tree or from **evolutionary reversals** where a derived state reverts back to the ancestral state.

There are different kinds of parsimony, which allow for reversals in evolution. Thus, reversals are not a problem arising from the analysis, but really a problem in the initial assumptions. However, multiple origins of characters on various branches of the tree is difficult for the principle of parsimony. Consequently, characters that researchers tend to choose in tree building are ones that minimize evolutionary reversals or multiple origin of characters, which is called **homoplasy**. This is true if

Figure 18.4. Families of salamanders with open boxes indicating obligate paedomorphs, and solid indicating evolution of direct development. Groups like Ambystomatidae, Dicamptodontidae, and Salamandridae exhibit paedomorphs and metamorphs in the same species. A classic case of convergence. You cannot make a very parsimonious tree assuming a fully metamorphic ancestor and **homoplasy** is rampant. There has even been an evolutionary reversal from direct development (loss of metamorphosis) back to metamorphosis (M*).
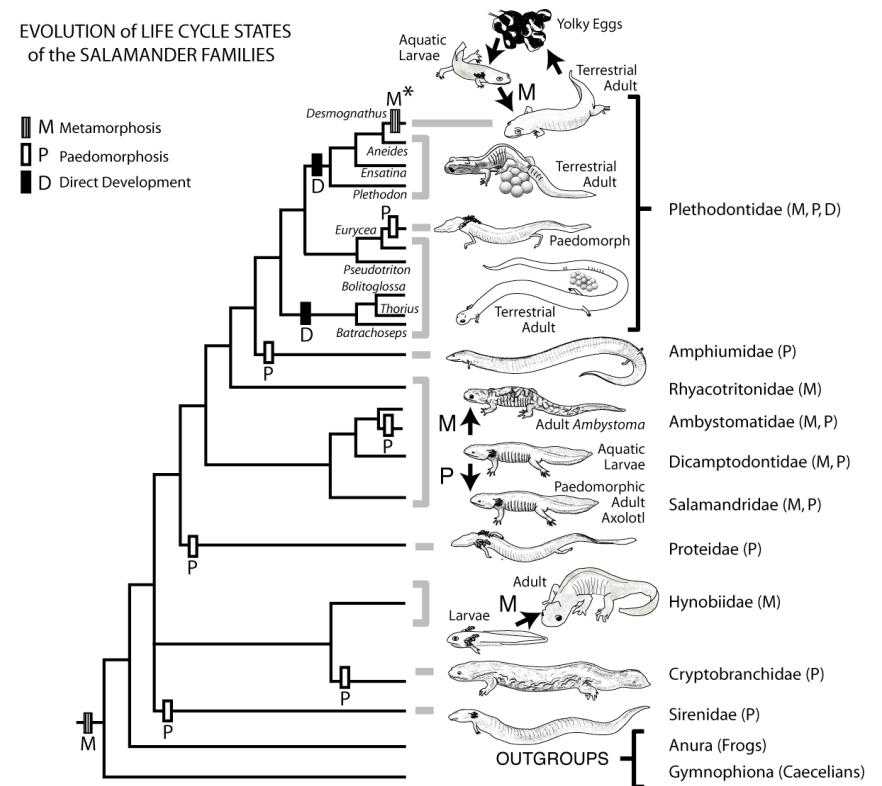
one is interested in using characters to construct trees. The homoplasy of paedomorphosis is common on a phylogenetic tree for salamanders (Fig. 18.4). This is because it is adaptive in stable environments (caves or predator free ponds, see Chapter 12 on Dispersal) and evolves readily.

Phylogenetic Inferences of Adaptation

While multiple origins of a character or homoplasy generates problems from the point of view of constructing trees, it is a good thing from the point of view of the analysis of adaptations. If a trait evolves a number

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of times on a tree we have a much larger sample size to use in our tests of the conditions that might drive the evolution of a trait. The more independent events that we observe the more data we have on the conditions that might favor the evolution of a behavioral trait.

The single most important principle of the comparative method based on phylogenetic analysis:

The characters that are used to construct a tree should be different from characters used to infer the evolution of an adaptation.

This rule is simple to put into practice for a student of behavior. Do not use behavioral traits to make the tree. Use behavioral traits to study of adaptations. Let's put the ideas into operation with a not-so-hypothetical example taken from paleontology.

Were Dinosaurs Dead-Beat Dads?

Exploring alternative reproductive tactics in reptiles presents a challenge given the diverse nature of these taxa. Modern reptilian lineages have ancient histories and are **paraphyletic** (no strict single common ancestor). Some extinct reptilian groups such as dinosaurs undoubtedly exhibited alternative reproductive tactics. Dinosaurs exhibited elaborate sexually dimorphic ornaments (e.g. hadrosaurs, Horner 2000) indicating the potential for strong sexual selection. In addition, dinosaurs exhibited many social behavior patterns such as herding (Lockley *et al*. 2002) and communal nesting (Horner & Makela 1979). Effects of social selection, sexually selected ornaments, and life history tactics comprise the basic selective attributes that are conducive to evolution of alternative tactics. In particular there is

Figure 18.5. Adult and juvenile *Psittacosaurus*. Erosion has truncated several skeletons, including the adult. Skeletons in the centre sit topographically lower than those at the perimeter, suggesting an original basin-like feature (nest). One skeleton at lower right is draped over an edge of this structure. The absence of internal sedimentary structures makes it impossible to discern whether the basin topography is the result of sedimentary, biological or post-depositional processes. Juveniles not adjacent to the adult generally lie subparallel to one another, showing no preferred orientation of the cranial end (Meng et al. 2004)

a dichotomy between **precocial** (Geist & Jones 1996, Varricchio *et al*. 1997) and **altricial** young (Horner 2000) in various dinosaur lineages. This dichotomy in mode of development is strongly associated with the mating system in the surviving descendants of dinosaurs, the birds.

Many of you are familiar with a famous fossil find from Montana. Jack Horner has made dinosaur parental care nearly a household concept with his discovery of a dinosaur rookery that for all intents and purposes resembles the kind of rookery one might find in a seabird colony. *Maiasaurus*, which translates as *good mother*, was colonial nester. They placed their nest-like mounds of earth very close to one another, based on the dense pack observed in fossilized colonies or rookeries.

### Dinosaur and bird evodevo: altricial *vs* precocial

Scientists have examined fossil embryos using CAT scans and slicing bones (Side Box 18.1) and can study embryo development. From bone structure of these nestlings, Horner argued that the nestlings were incapable of roaming the landscape. They have an **altricial** pattern of bone development. Altricial birds, like most songbirds participate in a phase of extended parental care. In altricial birds, the chicks are born relatively helpless, and parents feed nestlings over an extended period. This strategy contrasts with that of most ducks in which the chicks hatch in a **precocial** developmental state, and immediately leave the nest and forage on their own. The mother stays with chicks and guards her little flock of young, but the birds take care of their own feeding and locomotion. The bone development of altricial and precocial birds is quite different (Side Box 18.1). So from an argument based on functional morphology of fossil embryo and chick development, it is a pretty safe to infer that *Maiasaur* nestlings were altricial and remained in the nest for a long period of time. At the very least, the mother tended to their needs.

Box 1: bone morphology of extinct and extant archosaurs
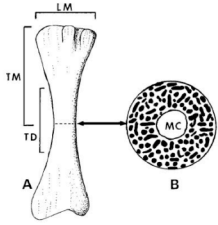
Embryos of extinct archosaurs like egg-laying *Orodromeus* and *Troodon* (A, B) show voids in the center while the embryonic *Maiasaur* shows a greatly reduced void reminiscent of a modern passereine (see panel to the right). D (and enlarged view C) shows an embryonic hypachosaur with very dense fibrolamellar structure (c.f., the *Maiasaur*), while F shows a *Lambeosaur*.
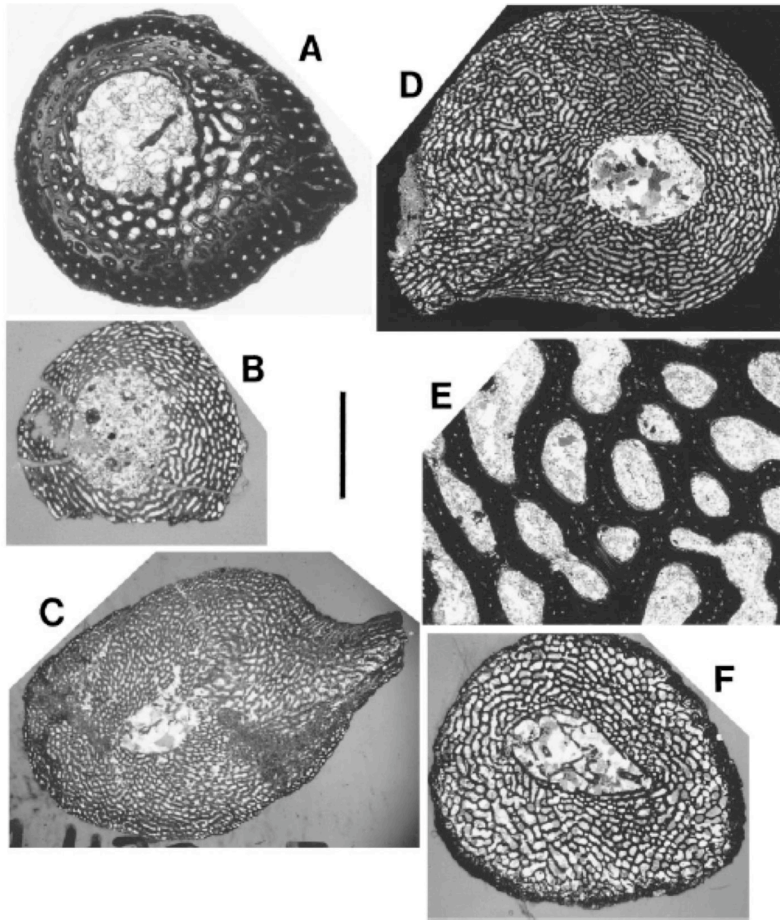
Only modern archosaurs like a passerine embryos have a femur or tibia with elaborate fribromellar organization. Most femurs of adults and embryos have voids in the center (A- Snapping turtle, B, C (enlarged view of B) adult alligator, D - neonate alligator, E- adult ostrich, F, G is an enlarged view of F)- adult emu, H - embryonic meadowlark.
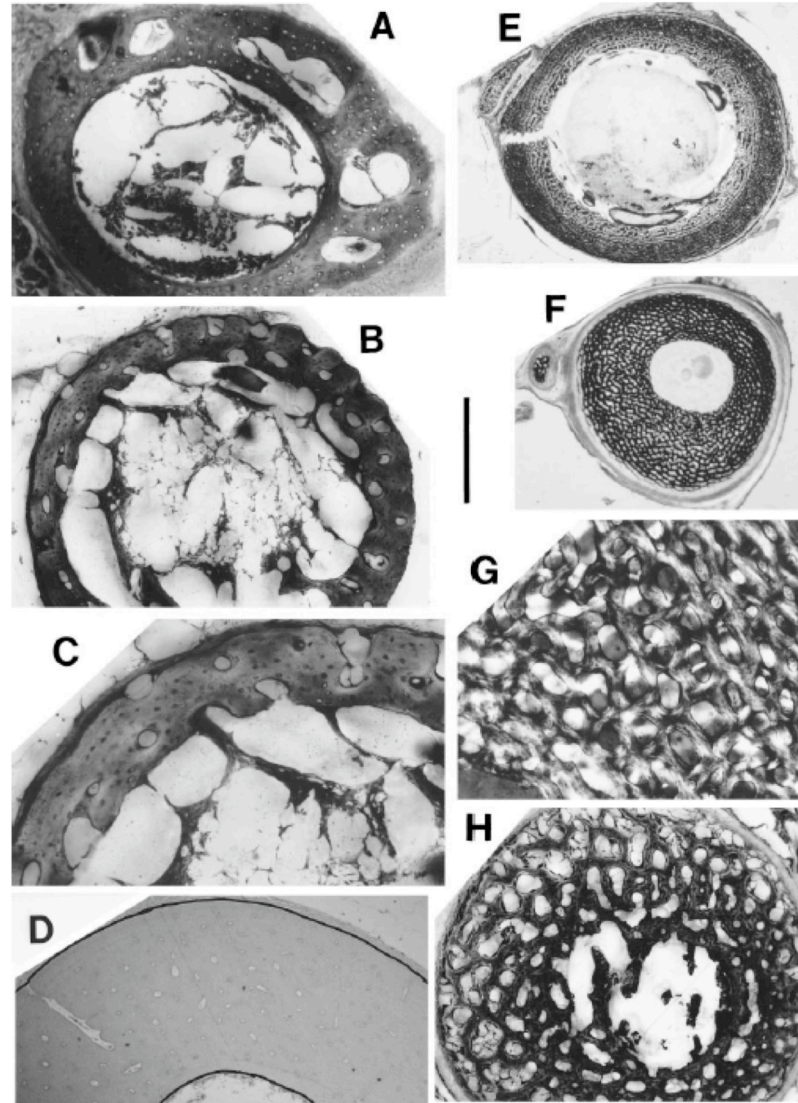
So where were the dino-dads? Did dino moms have length paternity battles to get paternal payments, or were dads just as caring as the moms? Consider an argument based on comparative biology.

In the vast majority of altricial birds, both parents participate in the care of young. This is not true for precocial birds. Based on a straightforward argument of comparative biology, if altricial birds have biparental care, then it is likely that *Maiasaurus* also had biparental care.

Now lets consider a phylogenetic argument. Dinosaurs do not have any extant living relatives -- or wait do they? It is generally agreed that birds arose from the middle of the dinosaur clade and are living relatives of dinosaurs. The most ancestral dinosaur like form happened to be like a crocodilian, and it is generally agreed that crocodiles are more closely related to birds than other living reptiles. As an aside, this example illustrates an important point. While the systematics of vertebrates allies crocs with other reptiles, a phylogenetic analysis would place them more closely related to birds (thus the term **paraphyly** which is applied to reptiles). The classification of crocs with other reptiles implies that the class reptilia is **polyphyletic** or a group that is comprised or members from different clades. Reptiles are not a natural phylogenetic grouping of animals. Such *classification schemes* are from the bygone days of dark-age of clade-free systematics.

Back to care. If we consider birds to be extant dinosaurs or the nearest living relatives of dinosaurs, then this suggests the possibility that some dinosaurs could have had female/male-based biparental care and in particular, female/male-based is more likely in altricial birds. Next, is there evidence for parental care in crocs. Yes, females guard the nest, and when little crocs hatch they begin vocalizing. The parent uncovers the hatchlings and transports the young to the water. In some crocs even the males participate in this behavior and it appears that male and female crocs can protect their young for some time after they hatch. Because crocs are an outcrop in nearly every dino/bird phylogeny, this suggests that dinos undoubtedly had the capacity for male parental care. Male/female care in the outgroup and in an extant group strongly points to *Maiasaurus* as having both male and female care and I suggest that we revise the name to *Patersaurus* reflect this behavioral possibility.

Among the modern vertebrate classes, female mating behavior patterns can be as diverse as those seen in males. The same tactical distinction between single and multiple mates can be made for female reptiles. Indeed, polyandry may be the most common mating system for reptiles. However, having one versus multiple partners in both sexes poses a different problem in reptiles compared with studies of other taxa such as mammals (Ciszek 2000) and birds (e.g. dunnocks, Davies & Lundberg 1984, Davies 1985). The classical explanation for polyandry is a socially mediated switch that is often related to the amount of parental care given by males. For example, male dunnocks provide extensive care of young at the nest, freeing females to visit nest sites of other males. However, few extant reptiles exhibit paternal care or elaborate levels of maternal care after oviposition with a few exceptions. The exceptions include crocodilians, in which there is often female (Platt & Thorbjarnarson 2000) and occasionally male (Lang *et al*. 1986). Protection until after hatching is seen in skinks, where some nest guarding has been observed (Duffield & Bull 2002); and live-bearing crotalids snakes, where Greene (1988) has reported guarding of progeny. Therefore, reptilian dinosaurs, being allied with birds and crocs, are likely to have had caring males.
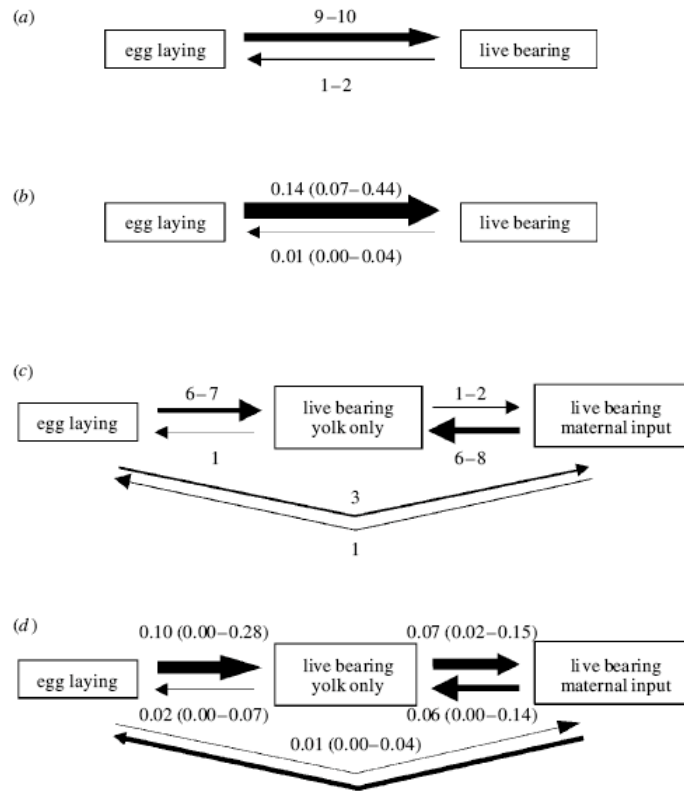
The evolution of care in vertebrate mating systems

Phylogenetic inference can be used to answer basic questions regarding the evolution of mating systems, from ancestral conditions to more highly derived states. However, the null hypotheses used need not assume that any state is ancestral. In this case phylogenetic analysis can reveal whether some transitions are more prevalent than others. In this case, perhaps the state that is changed is the ancestral state, while the modified condition is derived.

Figure 18.8. All potential transitions among parental care states, allowing for either sex to remain with or abandon the young. Are these transitions equally likely in the phylogeny of vertebrates?
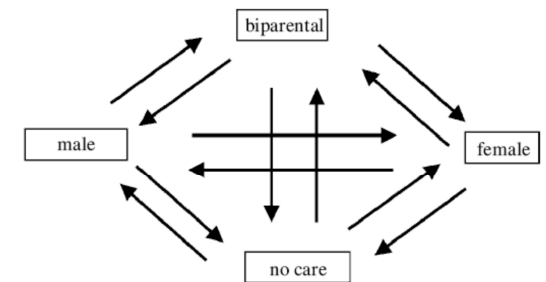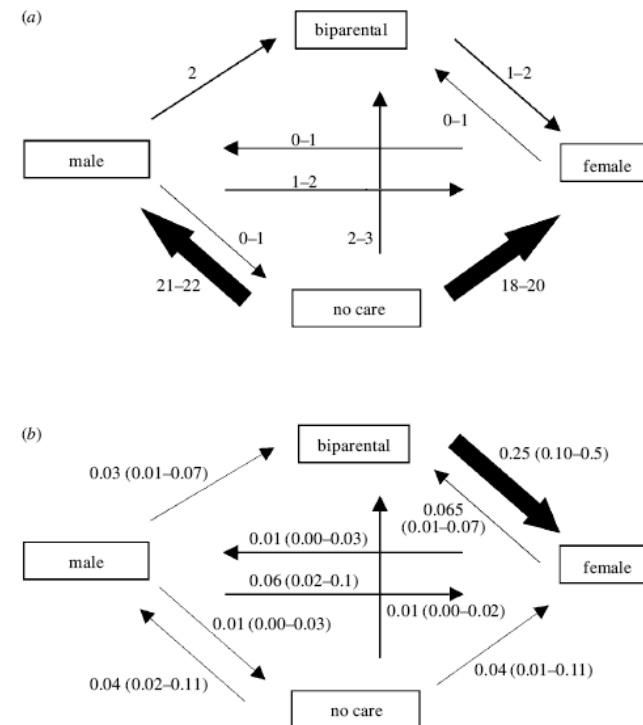
Often such analyses are intuitively appealing such as an analysis elasmobranch fishes (Reynolds et al. 20002), which suggests that egg-laying is ancestral while live-bearing is derived (fig. 18.9ab). However, a more fine scaled analysis in which the intermediate evolutionary step of simple egg retention vs. maternal input (i.e., from placentas, etc) is included, indicate that there are also a number of reversals from maternal input back to yolk only births (fig. 18.9cd).

Analyses of other vertebrate groups such as frogs similarly suggest that egg laying is ancestral. If one simply looks at the number of events, more advanced care arises quite often (fig. 2a). However, the vast majority of species have no care, thus, relatively few changes are actually recorded if one considers the small probability of change from no care to advanced care (figure 18.10b). On figure 18.10b the probability of change is actually quite high from biparental care to female care, relative to any of the other evolutionary transitions.


Figure 18.9. Evolutionary transitions between egg laying and live bearing in elasmobranch fishes: (a) overall number of transitions with various forms of live bearing combined, (b) as in (a) but in this case per-node probabilities of change between states, (c) live bearing divided into yolk only (no nutrient after fertilization) and subsequent maternal input (**matrotrophy**), (d) as in (c) but calculated as per-node probabilities of change between state (Duly and Reynolds 1997).

Figure 18.10. Transitions among four parental care states in frogs and toads (anurans). New analyses from Beck (1998) and Clough and Summers (2000) on the evolution of parental care in dendrobatid frogs indicate that dart-poison frogs (see Chapter 14) rapidly evolve either male care or female care. The presence of warning color and toxins (BTX) has undoubtedly freed this group to evolve much more elaborate care than other species of amphibians (from Reynolds et al. 2002).

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Considering the most likely evolutionary changes in parental care in all vertebrates provides some interesting generalizations that can be made regarding the probability of reversals to the ancestral condition (Fig. 18.11). At the beginning of this chapter, I noted that evolutionary reversals may be quite rare. Dollo conjectured that this might be true and we refer to this hypothesis as Dollo parsimony. The transitions of care-giving among vertebrates suggest that loss of care *is* actually quite rare (e.g., viviparity → oviparity). The reason for Dollo's law is that many systems cannot revert back to an ancestral state once gene function has been modified or deleted. This is an example of **constraint**. A final point is the unique position of primates in the dominant movement from female care to biparental care. This change in the mating system of primates has profound genetic effects that are discussed below in the section on genomic imprinting, and in the section on human evolution.
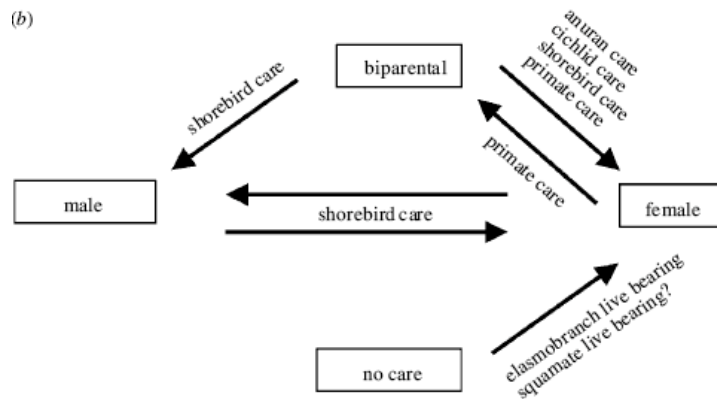
Figure 18.11. Dominant directions of change in male and female parental contributions to offspring, including care and live bearing. The strength of evidence for each pattern is discussed in the text, but note that evidence for transitions involving birds and teleost fishes is preliminary and awaits formal analyses (Reynolds et al. 2002).

The Evolution of Leks

Recall the definition of a Lek (Chapter 2) in which you find clusters of males, and females that visit a lek primarily to mate with one male and then she leaves to care for her young. How do leks evolve?

A lek by definition has (Bradbury 1987):

1. no parental care,
2. few or no resources (i.e., 1 and 2 imply no direct benefit),
3. where males congregate to display and females choose.

Hot spot hypothesis:

1. Females have high overlap areas by random or perhaps habitat limitations,
2. These become areas or hotspots where males are likely to find females,
3. Males often carry out ritualized displays at these locations.

The hotspot idea makes some specific predictions regarding the likelihood of finding a lek evolving in birds. If females have large territories, a lek-based mating system is possible. In contrast, if females have small territories males have to have large territories and no lek can be formed. Birds provide a wonderful group to study the evolution of lekking. One can measure the territory size of females and males. The prediction would be that leks occur in those species with large female home ranges, and small male home ranges.

Jacob Hogland plotted such relationships and found very good fit of the occurrence of leks for species in which males have evolved a small home range and females have evolved large home ranges.

Why causes these species to develop large female home ranges?

The next step would be to map some feature of the environment of each species onto the phylogeny and show correlated selective environment. For example, in the original hotspot idea it was speculated that there might have been a resource that attracted females. Overtime the resource became unimportant relative to the resource provided by the ability of females to choose a male with good genes from among many males. Some of the most spectacular examples of lekking behavior are found in the manakins with elaborate colors and dancings, which are at times even coordinated between pairs of males (see Chapter 13).

Figure 18.12. Coordinated display behavior of 4 manakin species. (**Upper left**). *Pipra serena*. A pair of males chases one another among vertical perches in either buzzy or direct to-and-fro flight. Uncoordinated forms of these displays are primitively present in the genus. (**Upper right**) *Masius chrysopterus*. One male waits on the display log, while a second male flies to the log and performs the log-approach display (white arrows). As the approaching male rebounds down the log, the waiting male rebounds in the opposite direction (dark dotted arrows). The display is then repeated with roles reversed. The log-approach display is primitively present in the *Masius-Corapipo* clade, but the rebound-hop from a stationary position on the log is derived in *Masius*. (**Lower left**) *Pipra fasciicauda*. One male waits on the display perch (right), as the second flies to the perch and performs the S-curved flight display (left). As the flying male arrives, the waiting male drops from the perch and gives a vocalization. The S-curved flight display is primitive to the genus *Pipra*, whereas the coordinated drop from the perch with distinctive vocalization is derived in the *Pipria aureola* clade. (**Lower right**) *Chiroxiphia caudata*. Two to four males on the same perch each flutter in succession from one end of the perch to the other, as the remaining male(s) slide along the perch. This cartwheel display is derived in *Chiroxiphia* (from Prum 1994).

Figure 18.13. Phylogenetic analysis of coordinated and cooperative display behavior in the manakins (Pipridae). Three classes of coordinated behavior are recognized: simple, complex, and complex-cooperative. Coordinated behavior exhibits 5 independent origins and has never been lost (Prum 1994).

Coordinated display behavior has evolved 5 times independently in the manakins, and in one cases has led to a marginal form of cooperation and in the other case virtually obligate form of premating cooperation by males. There are no cases of loss of lekking behavior (Prum 1994).

The coordinated display behavior in birds is only known among lekking species. Coordinated display behavior has been reported in the wild turkey (*Meleagris gallopavo*, Watts and Stokes 1971), the ruff (*Philomachus pugnax*, Rhijn 1973), Goldie's bird of paradise

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(*Paradisea decora*, LeCroy et al. 1980) and the black and gold continga (*Tijuca atra*, Snow 1982). All of these are lekking or arena-display systems. Interestingly, coordinated behavior has evolved five times independently in the small manakin clade but is known in only four other species among the more than 9000 birds. Why is it common in manakins? No one yet knows.

The Evolution of Aposematic Coloration and Gregariousness

In Chapter 14, we considered an experimental test of the predators propensity to learn whether prey were aposematically colored, and found that being gregarious (aggregated) gave the evolution of Aposematic coloration a selective boost. Recall Fisher's (1930) original arguments on kin aggregations boosting the likelihood of aposematism.

Ronald Fisher observed that many aposematic forms tend to also be quite gregarious and congregate in the same locale. Fisher speculated that kin selection may favor such aggregations. An individual may die during the lesson required to teach a naïve predator that the color also results in a bad experience. However, because the predator leaves the remaining kin untouched (e.g., single trial learning), the inclusive fitness of the dead aposematling is positive because the cost of individual death is balanced by surviving kin that live. Gregariousness can easily result from kin groups (e.g., a localized clutch), and such kin groups greatly enhance the probability that aposematic coloration will spread even though brightly colored individuals attract attentions of naive predators.

Sillen-Tullberg studied the evolution of aposematic coloration by mapping both the morphological trait (bright color as a proxy for unpalatability) and the behavioral trait (gregariousness) onto trees. She was more interested in whether the origin of gregariousness was contingent upon unpalatability and aposematic coloration evolving first. The evolutionary scenario for her arguments is as follows:

1. unpalatability evolves in the larvae,
2. However, once unpalatability evolves, this predisposes the group to evolve gregariousness,
3. Thus, one should find individual instances of gregariouneess

nested in amongst those clades that have evolved unpalatability.

Sillen-Tullberg tested these ideas out on several clades of caterpillars. Unfortunately unpalatability is very difficult to score (you have to make a lot of birds barf) -- so she used aposematic coloration as a conservative index of unpalatability. She found that unpalatability did preceed gregariousness most of the time. Gregariousness is a behavior of the female butterfly -- she decides to lay one or many eggs on a plant.
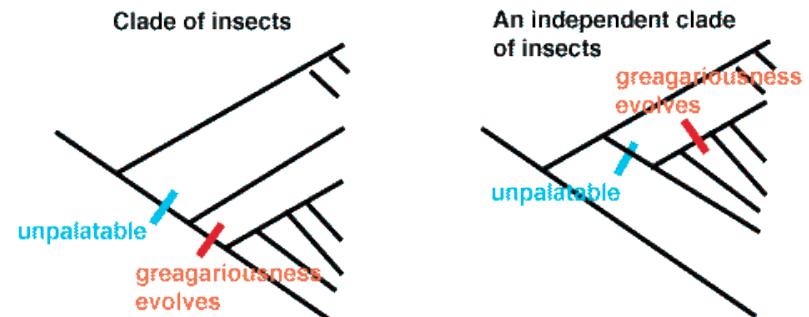
Coevolution of brood parasites and their hosts

In members of the blackbird family, brood parasitism has radiated in a single group the cowbirds. The change occurred once in the blackbirds, thus, we refer to this unique event as an **apomorphy** within the blackbirds. Despite the single origin, a phylogenetic analysis within the parasitic cowbirds reveals a very clear pattern. The most derived members are generalists, while the ancestral members are specialists. Thus, there is a clear progression from a specialist brood parasite to one that infects a greater variety of hosts (Fig. 18.15).
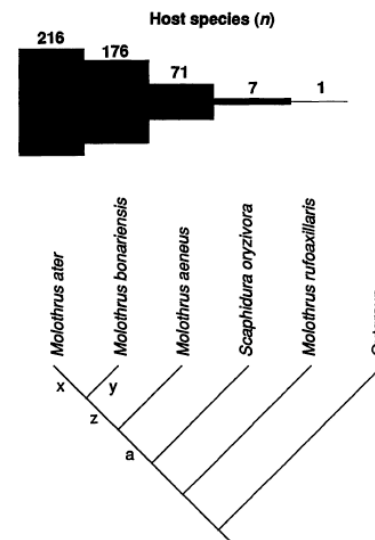
Figure 18.15. Phylogeny of brood parasitic cowbirds. A Single most parsimonious tree was obtained. Numbers of host species reported for each of these brood parasites are presented above the phylogeny.
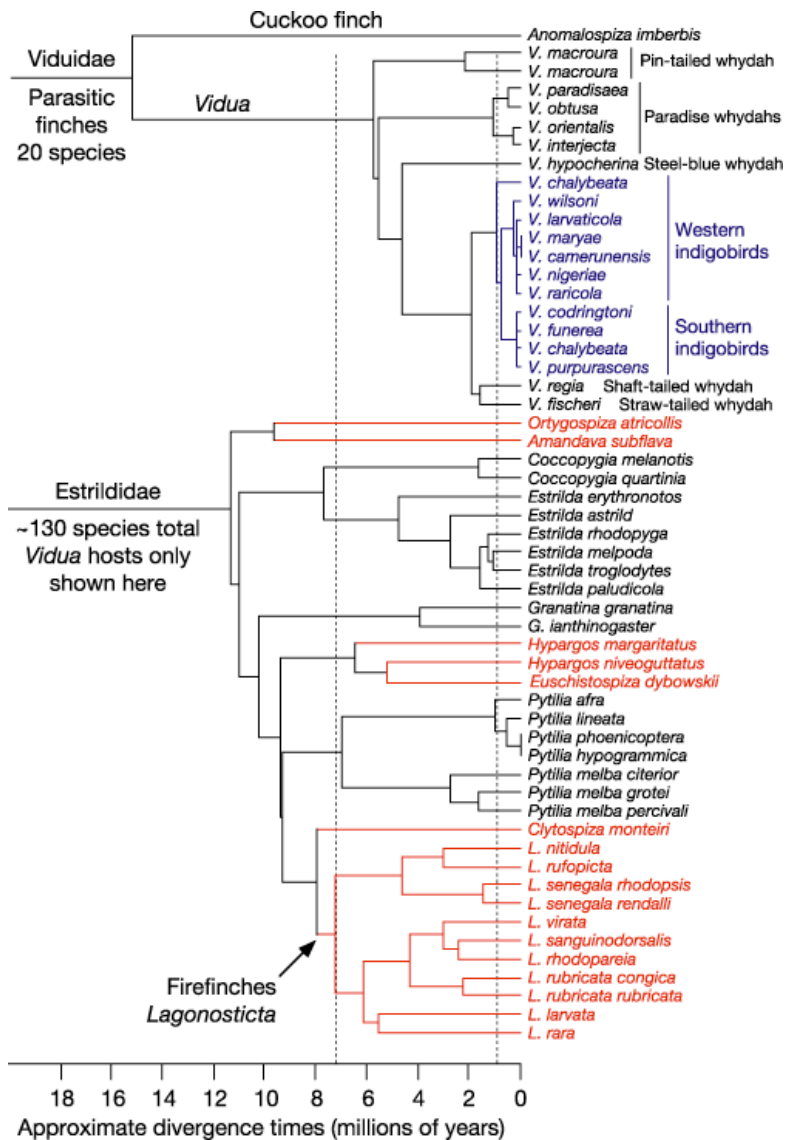
Figure 18.16. The mtDNA phylogeny of brood parasitic finches and their estrildid finch host species. The cuckoo finch is a parasite of several more distantly related warblers. Indigobirds are shown in blue; firefinches and other indigobird hosts are shown in red. Other estrildids shown are hosts of the various whydahs. Dotted lines indicate most recent mtDNA ancestor for indigobirds and firefinches, respectively.

In addition to cowbirds, which have had a modest amount of speciation in the context of their hosts, other groups of birds found in the old world such as cuckoos and the viduine finches have a pattern of speciation that is coevolved with their hosts. Whereas cuckoos and cowbirds have a more genetically programmed form of song learning, the viduine finches are exemplary in that both males and females learn the songs of their hosts and imprint on these songs (Chapter 5). Later during mate choice, females choose males for the quality of song mimicry, and females also choose hosts based on the same preferences. This generates and extremely potent form of runaway in culturally selected traits.

Viduine finches provide a dramatic example of mimetic evolution. Indigo birds, *Vidua*, learn songs of host species, and as adults, males attract females with songs of foster parents (Payne & Payne 1994). Mutual production and preference of mimetic host songs in both sexes reflect sexually and parasitically selected traits. Host-song imprinting of female brood parasites as chicks attracts them to mates and back to the nests of specific hosts in a culturally selected runaway (Payne et al. 2000). In contrast to viduine finches, brood parasites such as cowbirds have innate songs (divergent from their hosts), which results in a more generalized niche in which a single species has parasitized diverse host species (Garamszegi & Aviles 1992, 2005). In contrast, the viduine finches have undergone an extraordinary radiation and it is believed that this radiation has arisen from sympatric speciation, much like host-plant herbivore shifts (outlined below).

Cueing into the hosts sexually selected signals

Testing for the action of **coevolution** entails determining whether there is a reciprocal response of the host to the pressure imposed by the brood parasite. If brood parasites use secondary sexual characters for host recognition, brood parasitism is a potential selection pressure that may create evolutionary constraints against the outcome of sexual selection (e.g. Soler et al. 1999). For example, brood parasites might cue in on the bright plumage of highly dichromatic males, or perhaps aspects of song that are particularly useful in nest location by the parasite. Selection pressures arising from brood parasitism may thus favor hosts to develop less elaborate sexual signals, allowing them to escape this pressure (Garamszegi & Aviles 2005). This adaptive

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response by hosts is expected to be prominent among species that are more sensitive to the costs of parasitism, but weak among host species in which parasitism only exerts a relatively minor fitness impact.

Garamszegi & Aviles 2005) investigated the degree to which a given passerine was parasitized by cowbirds as a function of the sexually selected signals. The used the method of independent contrasts (see Chapter 17) in which the confounding effects of phylogeny were removed from the data prior to conducting a multiple regression of the degree of parasitism as a function of:

1) Song type repertoire size (number of songs used),
2) The number of syllables in the song repertoire (complexity)
3) Inter-song interval (time between song bouts)
4) Degree of dichromatic plumage.

While the plumage characters did not vary in response to degree of brood parasitism, all three of song components did vary significantly with regards to brood parasitism. It is noteworthy that some song components like song type repertoire varied positively with parasitism, but other components like syllable repertoire size and inter-song interval were negatively correlated with degree of parasitism (Fig. 18.17). One could view these patterns of evolved response as a situation in which the brood parasites are attracted to the key sexually selected signal (like song repertoire, see Chapter 8), but at the same time, the host can evolve a counterstrategy and the song can evolve other components that are less likely to be attractive to the cowbirds (e.g., compensation). These components of song should therefore be under fairly strong correlational selection both within a given host species that is heavily parasitized and between the song traits of the host species and recognition systems of the parasite species. However, this conjecture has not yet been tested.
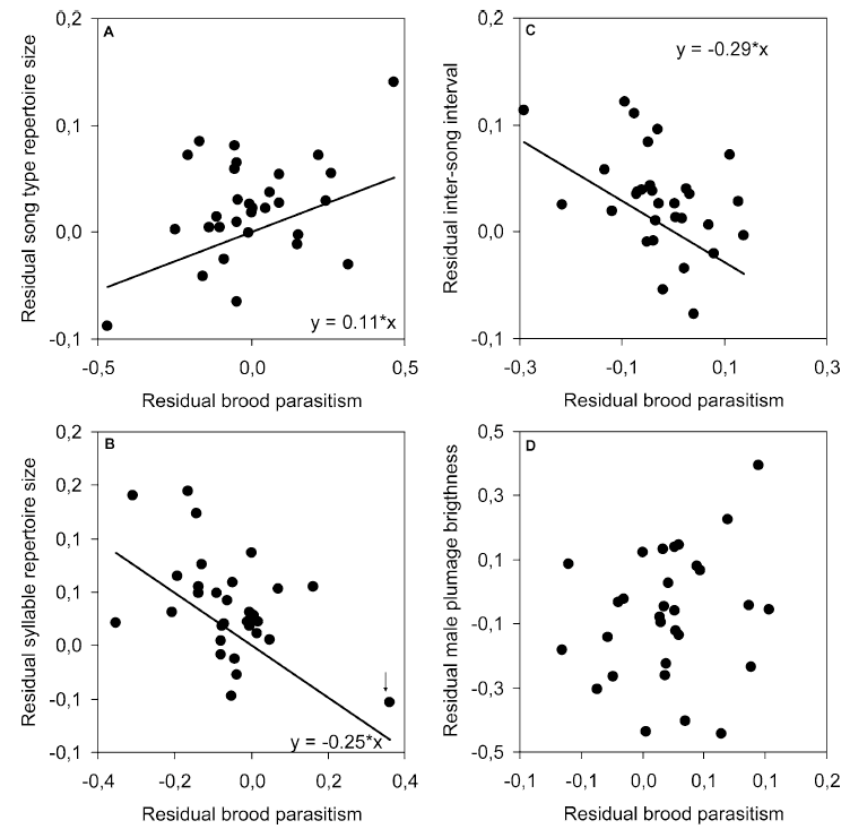
Figure 18.17. Relationship between brood parasitism caused by cowbirds and sexually selected traits of hosts: (a) song type repertoire size, (b) syllable repertoire size, (c) inter-song interval, (d) male plumage brightness). The figures are based on independent contrasts. (Garamszegi & Aviles 2005)

Coevolution of Hostplant toxicity and Herbivore Phylogeny

Recall the conditions for the evolution of hostplant toxicity and the sympatric speciation of their herbivores. This example serves us with a classic case of coevolution. Coevolution in insects and plants relates to the "endless evolutionary arms race" which leads to (Erlich and Raven, 1964 cited in Farrell and Mitter 1994, Berenbaum et al. 1996):

1. the origin of a new chemical defense in some plant groups, which reduces herbivore attack
2. which allows those plants to increase in abundance and eventually diversify and radiate; and
3. subsequent evolution of insects counteradaptations (detoxifying ability and hostplant preference switch),
4. which permits new insect species to radiate into the new adaptive zone represented by the now very diverse plants.

How can we detect the signature of coevolution?

1. First the phylogeny for the host-plant species should parallel the phylogeny for the herbivore.
2. In addition, the complexity of toxins in plants should be found in the youngest clades of herbivores. The host preferences of the herbivores and the ability of the herbivores to detoxify the toxins should mirror the acquisition of plant toxins.
3. Finally, the two groups should show similar ages so that true coevolution is occurring; each branch point coincides with the branch point in the other clade.
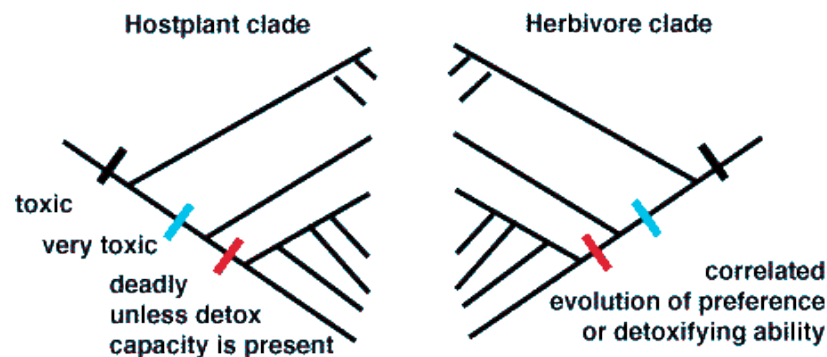
I have cartooned the idealized clades for hostplant and herbivore below. Note that there is a perfect correspondence between clades in the ideal case. Nature presents us with some near perfect examples.
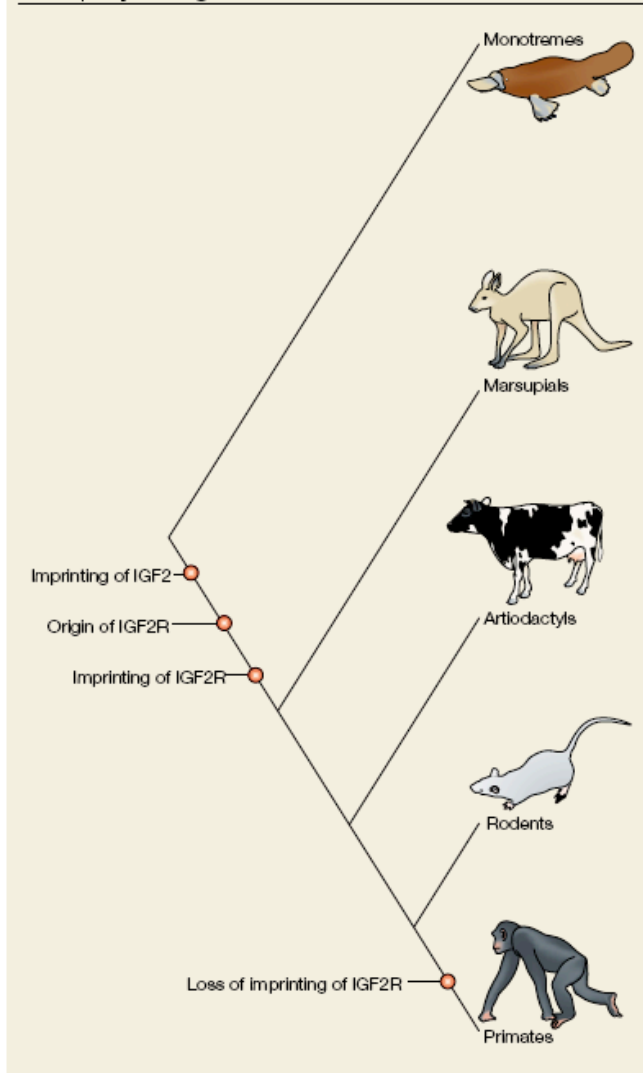
Beetles have a tight association with their hosts, which is required for true coevolution and eggs in that larvae and adults require the hostplant (Farrell and Mitter 1994). The beetle associations with their hosts can be contrasted with monarch butterflies, which feed on nectar as adults, while their larvae feed on milkweed plants. The offspring of butterflies are raised on milkweed, but because adults are not necessarily dependent on the milkweed for food, the coevolution is not seen in the butterfly/milkweed phylogenies (reviewed by Futuyma 1989).

Genomic imprinting: coevolution of imprints between the sexes

Recall the example of genomic imprinting in chapter 11 on **Conflict** that involved the genes IGF-2, which is paternally imprinted and the receptor, IGF-2R, which maternally imprinted in mammals. I suggested earlier, that theories of imprinting predict strong imprinting in animals with great investment in progeny, such as placential or marsupial mammals compared to monotremes. The evolutionary origin of the imprinting in IGF-II is very interesting with respect to monotremes, marsupials, and placentials (Fig. 18.19).

Notice that the origin of imprinting in IGF2 and IGF2R is concordant with the evolution of internal care in the case of marsupials and other more elaborate forms of placentation. This tight coupling between events is expected in our theories of the coevolutionary arms race between males and females in imprinting genes. The most interesting pattern is the loss of imprinting of IGF2R in primate lineages. This loss is thought to arise from the outcome of conflict between maternal and paternally derived alleles in favor of paternal lines (Wilkins and Haig 2003). Thus imprinting of IGF2 has a stronger potential to affect mother-offspring relations than the imprinting of IGF2R. No one really knows *why* the genus *Homo* has lost imprints, but is tempting to speculate that this is because of the evolution of a more monogamous mating system, relative to other primates, and the evolution of much more elaborate male care.

Box 3 | Imprinting of *IGF2* and *IGF2r*

Monotremes

Marsupials

Artiodactyls

Rodents

Primates

Imprinting of IGF2

Origin of IGF2R

Imprinting of IGF2R

Loss of imprinting of IGF2R

Figure 18.19. The phylogenetic sequequence of evolution of genomic imprints among classes and orders of some salient mammals (from Wilkins and Haig 2003)

Proximate and Ultimate Origins of Female Preferences

Stalk-eyed flies and ornament indicator traits used by females

Few studies of organisms allow one to test all the ingredients necessary to discriminate between the competing hypotheses of runaway sexual selection and good genes models (Chapter 10, 11). One of the key pieces of evidence missing in all of the previous studies is the phylogenetic history of sexual selection. How do we know that a male trait under sexual selection in the present-day as an indicator of male quality evolved specifically for the purpose of an advertisement of quality? If a trait evolved for a specific function, then we can refer to the trait as an adaptation that solves a problem of sexual or natural selection. The **origin** of a trait makes individuals in the species better adapted to environmental conditions. When considering the evolutionary origin of a trait, we are delving into ultimate issues that define why a trait evolved. How females choose males and what sensory systems are used, is an issue of proximate mechanism.
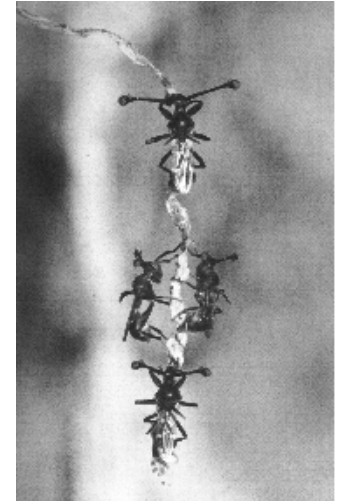
Figure 18.20. Courtship in stalk-eyed flies involves displays by males in a lek. Females tend to choose males with the largest stalks. Leks tend to form on the root hairs of plants. (Wilkinson and Reillo 1994).

We might search for the answer of a trait's origin in the fossil record to get at the evolutionary history of a group, but female choices do not fossilize and many male ornaments are often far to delicate to leave a trace in the rocks. We need flesh, not just bones, to get at the dynamics of sexual selection and mate choice. In recent years, behaviorists have increasingly, turned to this new branch of the comparative method called phylogenetic reconstruction (Brooks and McLennan 1991). A phylogeny is a family tree of relationships that describes the degree to which modern day species are related. The phylogeny is our best guess as to
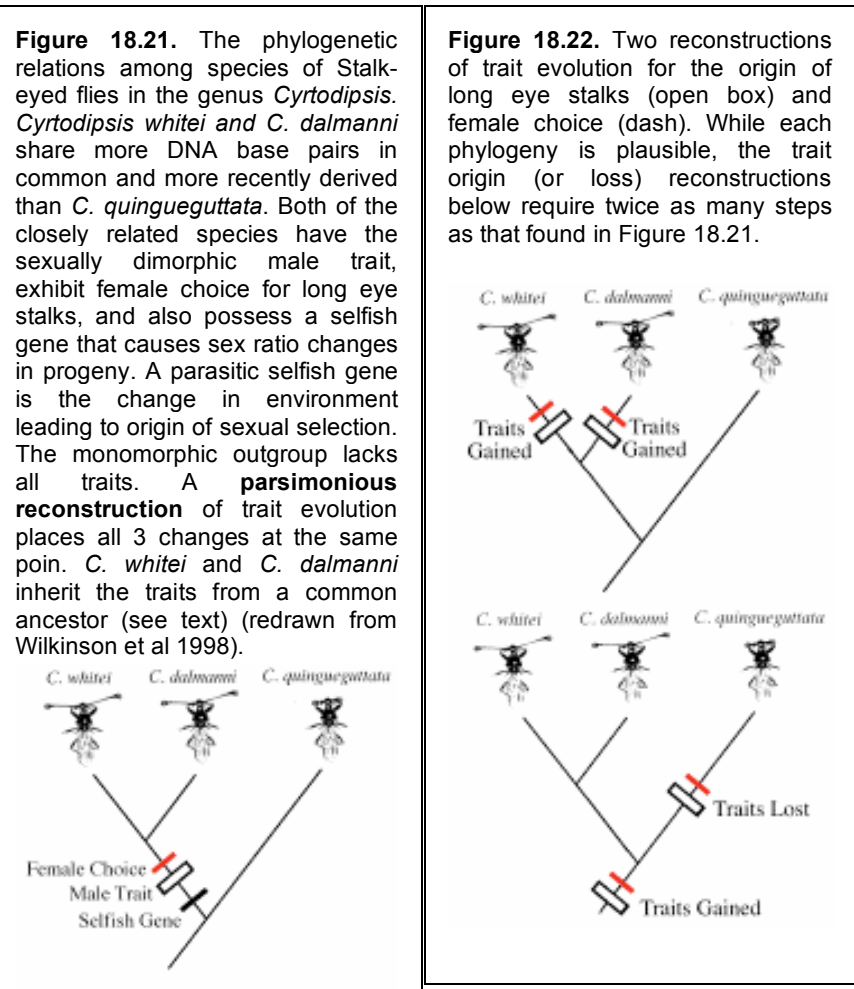
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which modern species are most closely related to one another, and which might be most distantly related. Therefore it is important to remember that a phylogeny is really still just an hypothesis, subject to verfication or refutation, by additional phylogenetic envidence. On a phylogeny, species that are separated by long branches are less closely related compared to species that are separated by short branches.

For example, three species of flies have eyes located on stalks that are quite closely related to each other in a phylogenetic sense (Wilkinson et al. 1998). One of the three, *Cyrtodipsis quinqueguttata* is more distantly related to the other two, *C. whitei* and *C. dalmanni*. In both *C. whitei* and *C. dalmanni*, males possess eyestalks that are far longer than the female's eyestalks. In third species, *C. quinqueguttata*, the eyestalks of males and females are the same length. A difference between the sexes or the degree of **sexual dimorphism** is our first clue that eyestalk length is a sexually selected trait in the males. Wilkinson and colleagues (1998) tested the proposition that males of the two sexually dimorphic species use the eyestalks to attract females. They conducted classic female choice experiments where the female chooses between a short- and a long-stalked male, and manipulative experiments where eyestalk length was varied by the experimenter. Both sexually dimorphic species showed dramatic female choice for long eyestalks, but the monomorphic species showed no female choice for variation in eyestalk length (Wilkinson et al 1998). Eyestalks are sexy, but only in the two species of stalk-eyed flies and not in the third lacking long eyestalks.

The phylogenetic question relates to the origin of the male trait, and the origin of the female choice. Are eyestalks a sexually selected trait that has evolved to solve a new problem faced by *Cyrtodipsis whitei* and *C. dalmanni*. If so, these two species should have arisen quite recently relative to the monomorphic species *C. quinqueguttata*. We can think of eyestalks and female choice as derived traits relative to the more ancestral monomorphic condition seen in *C. quinqueguttata*. The phylogeny for the three species indicates that the branch length for *C. quinqueguttata* reaches deeper into the past compared to the more recent origin of the sexually dimorphic species, *C. whitei* and *C. dalmanni*. We can map the evolutionary changes in eyestalk length and female choice onto the phylogenetic tree. The simplest hypothesis would be that the monomorphic condition is ancestral (quite a logical one, I might add),

and that the sexually dimorphic condition arose once, when the hypothetical ancestor of the two sexually dimorphic species split off from the ancestral monomorphic species. This places the origin of the traits before the two species split off from one another, but after the two split off from the monomorphic species (Fig. 10.26).

We have just reconstructed a plausible evolutionary history for female choice and the male trait using information from the distribution of traits

Figure 18.21. The phylogenetic relations among species of Stalk-eyed flies in the genus *Cyrtodipsis*. *Cyrtodipsis whitei* and *C. dalmanni* share more DNA base pairs in common and more recently derived than *C. quingueguttata*. Both of the closely related species have the sexually dimorphic male trait, exhibit female choice for long eye stalks, and also possess a selfish gene that causes sex ratio changes in progeny. A parasitic selfish gene is the change in environment leading to origin of sexual selection. The monomorphic outgroup lacks all traits. A **parsimonious reconstruction** of trait evolution places all 3 changes at the same poin. *C. whitei* and *C. dalmanni* inherit the traits from a common ancestor (see text) (redrawn from Wilkinson et al 1998).

Figure 18.22. Two reconstructions of trait evolution for the origin of long eye stalks (open box) and female choice (dash). While each phylogeny is plausible, the trait origin (or loss) reconstructions below require twice as many steps as that found in Figure 18.21.

among modern-day species, and the phylogenetic relationships among modern-day species. In our hypothesis of trait origin we assumed that the change between the ancestral monomorphic species and the two more derived dimorphic species only occurred once; this would be the simplest hypothesis. Using this assumption is also referred to as the **principle of parsimony**. Parsimony assumes that evolutionary change is slow enough that more complex hypotheses of trait origin are far less likely than the simplest hypothesis. For example, the two dimorphic species could have acquired the traits in two separate origins. Alternatively, all three species could have acquired the trait through a common ancestor, but the monomorphic species subsequently lost the dimorphic condition. The last two more complex hypotheses would require twice as many total evolutionary steps than the parsimonious hypothesis. In the absence of any other information, the parsimonious hypothesis is taken to be a 'null hypothesis' for the distribution of traits in the phylogeny.

With a working hypothesis in place of when male trait and female choice arose in the phylogeny of stalk-eyed flies, we move on to the next question: why did eyestalk length evolve in the two sexually dimorphic species? To address this question, we need to reconstruct the selective environment that might have led to the stalk-eyed trait being useful in males as an indicator trait for females. Again, there is no fossil record for reconstructing the conditions that led to sexual selection for long eye stalks. Fortunately, there is genetic evidence of a major change that would alter the mating environment of the flies (Fig. 18.21). Its time to synthesize some previously discussed issues of genic selection (Chapter 4) and sex ratio evolution (Chapter 9). The two sexually dimorphic species both possess a selfish gene on the sex-determining X-chromosome that eliminates the Y during meiosis and replaces the missing chromosome with a copy of the X that carries the selfish gene. Like all selfish genes, it is simply over-reproducing itself during meiosis such that males who are infected with the element tend to produce more X-sperm that carry the element than Y-sperm (see Chapter 4, *t*-alleles in mice). This causes a male carrying the selfish gene to produce sperm that carry X-chromosomes. A female that mates with an infected male that carries the selfish element would produce mainly daughters.

The selective consequences of this are straightforward, if we recall that the theory of Fisherian sex ratio favors a 50:50 sex ratio (Chapter 9). Species "infected" with the selfish gene produce female biased sex ratios in both nature and laboratory cultures. Females that produce a biased sex-ratio of female offspring are at a striking disadvantage. Fisherian sex ratio theory indicates that a genotype, which produces a 50:50 sex is evolutionarily stable (see Chapter 8), and the presence of sex ratio bias in stalk-eyed flies means that mothers with female-biased sex ratios are producing lots of female progeny that will have trouble finding mates. A female--biased population is susceptible to invasion by a female that can produce a male-bias. Accordingly, any gene that restores the biased sex ratio in males back to a 50:50 ratio of X to Y sperm would cause 'discriminating' females to produce sons and thereby give their offspring a mating advantage relative to females that mate indiscriminately. Sons would have lots of females to mate with. Such a gene has evolved on the Y-chromosome and this Y_m gene negates the effects of the selfish gene located on the X-chromosome, X_d, which distorts sex ratio. Interestingly, the genes controlling long eye stalks in males is closely linked to the Y_m. Females use the stalk-eyed trait in males as an indicator of their superior genetic background in that males with long eye stalks are more likely to bear the Y_m gene, a gene that restores the sex ratio of their progeny back to a 50:50 sex ratio.

The natural history and genetics of the stalk-eyed flies is the first demonstration of a sexually selected male trait evolving to serve as an indicator of a male's genetic quality. This story has all the elements that are required to support the theory of good genes. The correlation between female choice and the male trait is present in the sexually dimorphic species. When laboratory stocks of the fly are selected for longer or shorter stalks, female choice evolves in a correlated fashion (Wilkinson and Reillo, 1994). Moreover, the stalk-eyed male trait is genetically linked to a gene that rescues individuals from the effects of a selfish genetic element. Finally, eye stalks orginate as an adaptation to indicate male quality.

Wilkinson et al (1998) have suggested that many male Y-linked traits such as guppy spots may be commonly used by females to indicate the presence of selfish genetic elements. Selfish genetic elements may be quite common in nature since distortions in sex ratio are found in guppies, mice (see *t*-allele example, Chapter 4, (Lewontin 1962), and

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Drosophila (Atlan et al. 1997). Female choice for males may be driven by the ever-present force of selfish genes, of which one large class of "sex-ratio-drivers" serves to distort the primary 50:50 sex ratio that is evolutionary stable in the long run. For example, male mice that are heterozygous for the t-allele (+lt, discussed in Chapter 2) likewise produce a distorted ratio of sperm bearing t-allele. Any female mouse with a heterozygous genotype (+lt) will produce sterile sons if they mate with a heterozygous male (tlt causes sterility in 1/4 of her sons). Accordingly, females with a +lt have evolved mate discrimination that allows them to avoid mating with heterozygous males in favor of wild type males (+l+) that are uninfected with the selfish t-allele. The case of infections by selfish genes and female discrimination of males that carry the bad gene (e.g., mice) or carry a good gene (e.g., stalk-eyed flies) is certainly not the only situations in which indicator genes might prove useful. However bizarre, this example serves to highlight the power of sexually selected processes to couple male traits with female choice in the face of a dramatic infection of the genome by a 'parasitic gene'.

**Sensory Bias and Proximate Explanations for Phylogenetic Patterns**

Theories of sensory bias postulate that the evolution of a sexually selected male character arises in a group in which females have a pre-existing phylogenetic bias for certain kinds of signals, and those signals are the ones that males evolve. The basic phylogenetic distribution for the female preference and male trait is as follows:

1. the bias should be present in an ancestral species, but the male trait should not,
2. or, the male trait should be nested in groups in which the pre-existing bias has already evolved.

The principle of parsimony is crucial because the argument above assumes that evolution occurred in the smallest number of changes.

Recently, behaviorists have applied phylogenetic techniques to test the order in which female choice originates in relation to the origin of a male trait. The case of the stalk-eyed flies provides support for the idea that the male trait and female choice evolved nearly simultaneously in response to a change in mating environment; a biased sex ratio. A recent theory (Endler 1992; Ryan and Rand 1993; Ryan 1997) relates to **sensory biases** in the nervous or sensory system of females that predisposes them to pick males for some traits over other males that lack the trait. Females choose males not because they perceive them as sexy per se, but because they are "attracted to them". Such biases are present in the ancestral species and they remain latent in a population until a male evolves a mutation. Because a mutation in ornament "exploits" pre-existing sensory bias found in females, the theory of sensory bias is also referred to as **sensory exploitation**. Certain stimuli (e.g., colors, shapes, movement) may be useful in certain contexts (e.g., feeding and foraging) and the nervous system of females (and males) is honed by natural selection to be efficient at picking out food items from a world that is overly rich in extraneous stimuli. In a sense, these parts of the nervous and sensory system may be co-opted by sexual selection and a mutant male that displays a trait that triggers a heightened response in females may have an advantage. A male's signal may become fine-tuned such that it maximally stimulates the female sensory system.
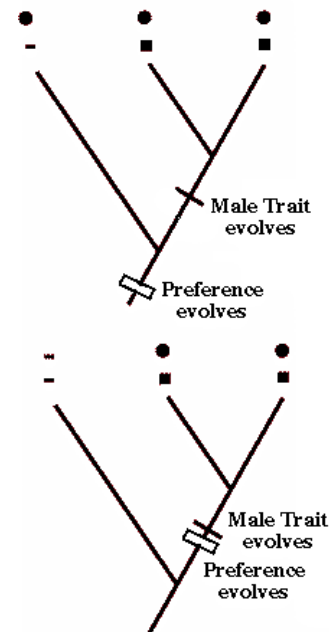

Figure 18.23. Hypothetical relations between a male trait and female preference with regard to their distribution in the phylogeny. The phylogeny describes ancestor descendant relationships between three extant (modern-day) species. Distribution of male trait in extant species is denoted with a square. Female preference is denoted with a circle. Absence of the traits is denoted by a minus. The male trait does not occur in the more deeply branching outgroup in either clade. The outgroup presumably reflects ancestral condition of traits. a) Hypothetical relations that suggest female preference evolved prior to male trait. b) Hypothetical relations that suggest concordant evolution of male and female traits, refuting the hypothesis of sensory bias (from (Sinervo and Basolo 1996).

Theories of sensory bias postulate that sexually selected male traits evolve in a species where females have a pre-existing phylogenetic bias for certain kinds of signals. Evidence favoring the idea of a sensory bias would place the origin of female choice as an ancestral condition (e.g., occurring earlier) relative to origin of male traits. In this chicken and egg argument, evolution of mate choice precedes evolution of male trait.

Alexandra Basolo looked at a large genus of fish, *Xiphoporus*, which have evolved elongated swords on their tail fins (Basolo 1990; Basolo 1995). The sword-tail is used as a sexual ornament. In species where males possess a sword, females prefer males with long swords (no surprise). A phylogeny of *Xiphophorus* indicates that many species have derived swords. One member of the genus, *X. maculatus*, has the "ancestral" condition and lacks a sword. Females in this species are quite content to mate with their swordless males; at least until Basolo tempted them with sworded males. Basolo gave females from this ancestral species a choice between males of their own species which lack a sword, or males of their own species with a surgically attached a sword. To control for the effect of surgery on the swimming ability of the male, which might interfere with his courtship, the first group of control males lacked a visible sword, but they did receive a clear sword tied onto the base of the tail fin. The sworded males received an opaque sword tied on to the base of the tail fin. She placed the two males in a pairwise choice trial and females overwhelming choose males that had a sword tied on!
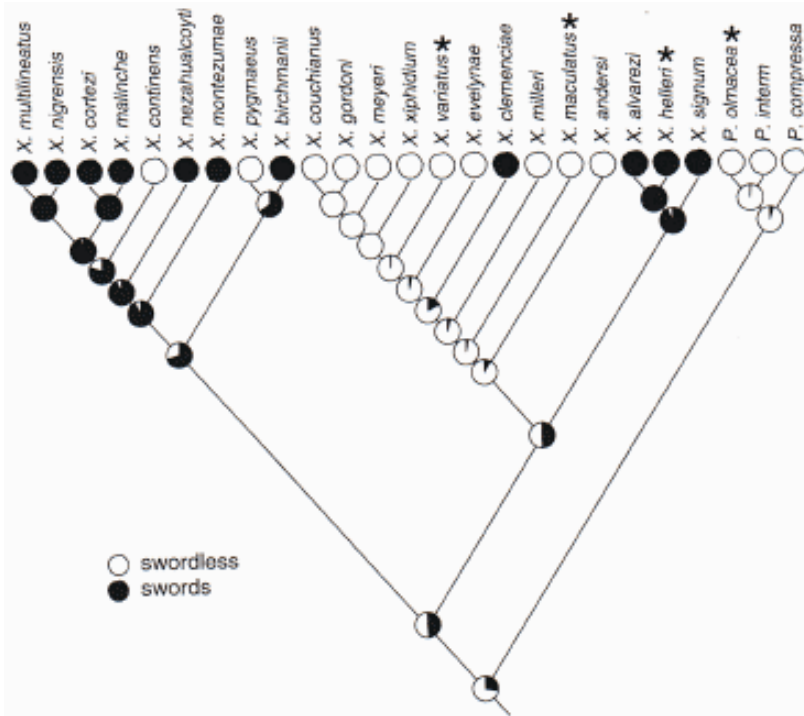
Figure 18.24. Distribution of sworded males in the genus *Xiphophorus* and *Priapella*. Because the females in species whose males normally lack swords (denoted by *) prefer males with swords, Basolo inferred that the preference for swords arose as a pre-existing bias. The "pie-diagrams" below the tips of the tree reflect the best guess condition (probability of sword is proportional to area of black) for the male trait in hypothetical common ancestors that are located at the nodes joining the tips (from (Schluter et al. 1997).

Further work on a more remote ancestral species *Priapella olmacea*. indicate that female preference evolved quite early in the history of this group of fish. Once again, females prefer their own males with swords tied on, even though males do not naturally possess swords. Basolo interpreted the female preference for swords in two swordless species in terms as an "ancestral" or pre-existing bias for sworded males in these fish. The idea also explains the widespread distribution of swords in other species of the genus. Species in the hypothetical ancestor had a pre-existing bias for the sword, and when this trait showed up in some descendant, the sword spread through the population like wildfire. The exact reason for a pre-existing bias in the fish is unclear. Basolo has suggested that the sword may resemble the males gonopodium, which is a penis used to fertilize the eggs in the female's brood pouch. This group of fish has internal fertilization and brood eggs in a female brood pouch. Females will only mate with a male that displays readiness in the form of an extended gonopodium. Basolo hypothesizes that the sword provides a supernormal stimulus that heightens the female's readiness for copulations. Support for the sensory stimulation hypothesis, is provided by strength of female preference in species which possess swords. In these species, the females prefer supernormal stimuli over normal length swords. More work needs to done on the exact sensory mechanisms that predispose female swordtails to choose males with elongate tails.

The tungara frogs provide evidence that males co-opt specific mechanisms for sound reception in the female ear. Ryan and his colleagues have investigated a similar case of phylogenetic sensory bias in the tungara frog of Central and South America (Ryan and Rand 1993). This frog collects at ponds and uses a call to attract females. In a simple experiment, the composition of songs can be digitally altered on the computer and then played through speakers. Females readily respond to the songs being played from a speaker. Positive female choice was scored by movement of the female towards one speaker or the other. Males in two of the species, *Physalaemus petersi* and *P. pustulosus*, possess a more complex call consisting of two parts: an initial whine, followed by a chuck. Males in the other two species, *P. coloradorum* and *P. pustulatus*, do not possess a chuck at the end of the song, but only call with the whine component.

To generate the synthetic chucks in species with chuckless males, Ryan and his colleagues took the species typical whine and digitally mastered a chuck at the end of the song. Choice experiments indicate that females in all species prefer males that have a chuck added at the end of the song, regardless of whether or not the males of their species possess a chuck. Thus, available phylogenetic evidence suggests that the ancestral species consisted of females that had a preference for the chuck. The innovative chuck arose in one branch of the phylogeny, presumably by a mutation, and the ensuing chuck spread through the population because females already had a pre-existing preference for the chuck.

The sensory bias or pre-existing bias found in tungara frogs has a mechanistic basis in the vocal apparatus of the amphibian ear. The mechanics of the auditory apparatus of the amphibian ear also explains the nearly universal

preference that females frogs have for large bodied males. As might be expected, larger males can produce lower-pitched calls than smaller males. These kinds of calls are much more effective at stimulating the female's ear. Specifically, the sound waves enter the female's ear and stimulate a cluster of receptors referred to as the basal papilla, which are sensitive to the range of sounds in lower frequencies. The females also possess an organ called the amphibian papilla which is responsible for fine scale discrimination of sound frequencies. The amphibian papilla is present in the ears of all species of tungara frogs, and the amphibian papilla is maximally stimulated by the frequencies produced by the chuck at the end of the call. Why this derived auditory structure is present in tungara frogs is not known, however, the evolution of the structure would have predisposed this group to the evolution of a male type that could exploit the pre-existing sensitivities of the female ear.
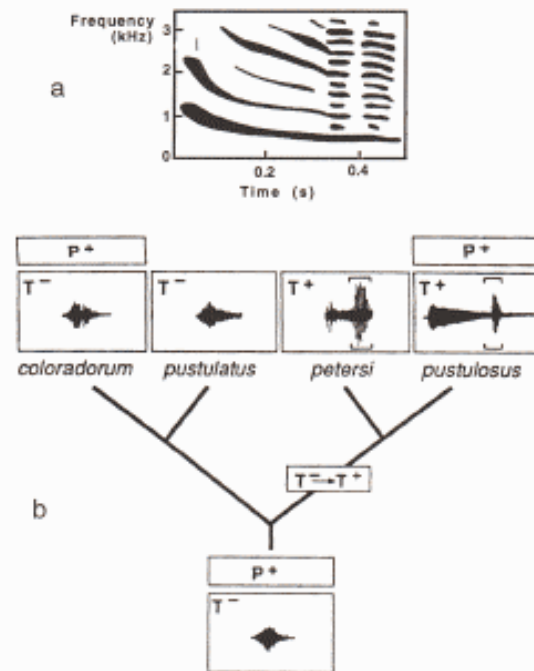
Figure 18.25 a) A sonogram of the mating call of male tungara frogs, *Physalaemus* spp., containing a whine (long horizontal lines) and two chucks (stacked lines at the end). b) The small panel for each species gives the amount of energy in the call over time. The high energy chuck is restricted to the end denoted by brackets. The distribution of female preference and male traits in the phylogeny of tungara frogs: P+ preference present, T+ male chuck present, and T- male chuck absent. Even though the males of the two species considered to be more ancestral, *P. coloradorum* and *P. pustulatus*, do not use a chuck in their calls, females of these species appear to have an ancestral bias or pre-existing predisposition for males with the chuck. Thus, the existence of a chuck in the derived calls of *P. petersi* and *P. pustulosus* are thought to have originated because the hypothetical common ancestor at the root of the tree had females with the pre-existing preference. (from (Kirkpatrick and Ryan 1991).

Study Questions for Macroevolutionary Patterns and Phylogeny

1. What is the principle of parsimony? What is a clade? What is an outgroup? Why is the outgroup crucial in interpreting evolution in a clade? How can we use the concept of an outgroup to reconstruct the pattern of evolution?

2. Why are we interested in shared derived characters and shared ancestral characters?

3. What are altricial and precocial birds? Explain the comparative data on extant (modern-day) birds and embryology that we can use to differentiate precocial or altricial traits with levels of parental care. Explain the phylogentic argument regarding parental care in dinosaurs and birds (hint what is the outgroup for this comparison?).

4. Does unpalatability arise before or after gregariousness in caterpillars? Draw a cladogram to illustrate your answer. How do the results of the phylogenetic analysis relate to Fisher's original hypothesis (Explain).

5. Describe the phylogenetic patterns that support the coevolutionary hypothesis of insect-hostplant evolution. Specifically, what are the three conditions that would support the notion that insects and hosplants are in a coevolutionary arms race? Support your answer with two cladograms (one for insect the other for the plant).

6. Describe the two possible character states for the female preference in the outgroup of a clade in which you are testing for sensory bias. Use diagrams to show how the two possibilities support or do not provide evidence of sensory bias.

7. Does the example of stalk-eyed flies refute the idea of sensory bias? What levels of selection are involved in stalk-eyed fly mate choice (hint what level of selection causes there to be selection on female choice, what level of selection resolves the first level of selection).

8. Describe the evolutionary history of genomic imprinting in mammals and explain the pattern in terms of life history.

9. Compare and contrast acquisition of song in cowbirds and viduine finches. Why group has higher rates of speciation and why? Why group can parasitize the most species and why?

10. Compare and contrast the major lineages of vertebrates with respect to transitions in care giving behavior.