

Evolution and Phylogeny of Communication

T. J. Ord, University of New South Wales, Sydney, NSW, Australia

© 2010 Elsevier Ltd. All rights reserved.

The Legacy of Evolutionary History

In broad terms, the way in which animals communicate with one another is dependent on three key factors: the function of a signal, the ability of receivers in the environment to detect a signal, and the historic interaction of these factors that may or may not be the same as they are today. For instance, many mating calls or displays given by males to entice females to mate with them are under selection to advertise each male's quality as a mate; for example, that he is in good condition or likely to be a good parent. All animal signals must also travel through the environment before reaching receivers, during which time the message of the signal can become degraded because of reverberation, masking caused by noise, or a number of other factors. Certain types of signals are more resistant to environmental degradation than others and some signal types are also better at stimulating the sensory system of receivers than others. Yet, how communication evolves in response to social and environmental selection pressures is dependent on an animal's evolutionary history. Put simply, the evolution of communication generally builds on what was present in evolutionary ancestors. Two species may produce a signal to attract mates and even face the same challenges of transmitting that signal through a noisy environment, but the type of signal each species evolves might be quite different because each species is descendent from different evolutionary ancestors.

Studying how the evolutionary history of a species has contributed to present-day forms of communication presents a difficult challenge for researchers. Behavior is an aspect of an animal's phenotype that rarely leaves a trace in the fossil record. How then is it possible to know what communication was like in evolutionary ancestors, let alone attempt to understand the selective pressures that might have acted on historic signals and shaped the subsequent direction of signal evolution? By comparing the similarities and differences in the form of communication used among closely related species, we can map this variation onto an evolutionary tree, known as a *phylogeny* (Figure 1), and extrapolate back in time to decipher what evolutionary ancestors might have been like and the types of selection pressures they probably faced.

Let us consider an example of mate choice in a group of freshwater fish species from Central America known as swordtails. These fishes got their name because males possess an elongated tail filament that looks like a long sword protruding from the tail fin. Researchers have

shown that females prefer males with longer swords to males with shorter swords. The sword as it is used today advertises to females that a male is in top-notch condition because he can deal with the 'handicap' of having an exaggerated ornament that impedes swimming, yet he can still forage and avoid predators successfully.

Surprisingly, females in other closely related fishes in which males do not possess a sword also exhibit a preference for swords when researchers artificially attach swords to male tails. Obviously, the handicap principle cannot explain the presence of a female preference for tail filaments in species that lack this male ornament. With a clever series of mate choice experiments on different species that did and did not naturally possess swords and mapping findings onto a phylogeny, researchers were able to reconstruct the evolutionary history of both the sword and the female preference for the sword. This is because closely related species often share similar features inherited from a common ancestor. If females of two sister species both show a preference for male swords, it is likely that the common ancestor of these two species also had a similar preference. Using this comparative approach to extrapolate back in time, it was discovered that females evolved a preference for the sword *before* the sword evolved in males. How can females exert a preference for an ornament as specific as a sword when it does not actually exist in males? One explanation is that females did not initially fancy male swords per se, but large male size more generally. Body size in many animals is a good indicator of condition. A cheap way for males to tap into a female's preference for large size is to evolve an elongated tailfin to give the appearance of large size. As swords became increasingly longer over evolutionary time they subsequently became reliable indicators of condition in their own right because of the increased costs associated with impeded swimming performance. By combining information on phylogeny, the communication systems used by species today and the factors that influence signal production and reception, it is possible to use the comparative method to gain considerable insight into how communication has evolved.

In the rest of this section, I will elaborate on the general concepts of how phylogeny and the comparative method can be used to understand the direction and mode that evolution has taken and how phylogenetic approaches can be used to identify the adaptive processes that have shaped the design of animal signals. In the final section, I will provide a brief overview to some of the available methods

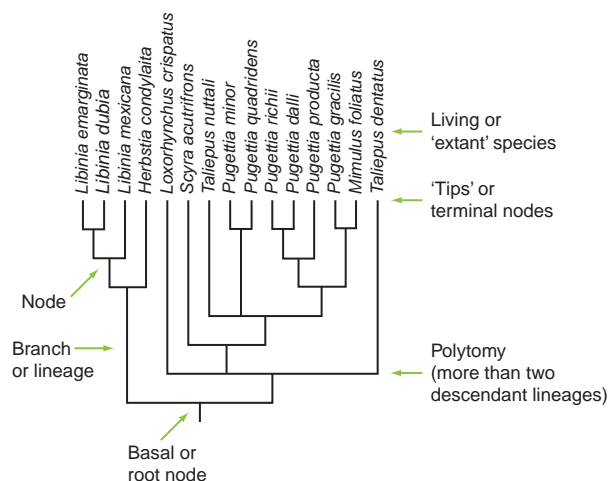


Figure 1 Common phylogenetic terms illustrated by a phylogeny of the decorator crabs. Courtesy of Kristin Hultgren.

that comparative biologists can use to reconstruct ancestor states, estimate the extent to which communication is dependent on evolutionary history, and the ways in which researchers can test hypotheses for the adaptive significance of communication.

Phylogeny and the Trajectory of Signal Evolution

A lot can be learnt from simply documenting when and to whom animals produce signals, and how those signals subsequently affect the behavior of receivers. Experiments might then follow to test the function and/or selection pressures believed to act on signal production through direct manipulation. This might consist of calls being recorded and played back to animals to determine that some call types are preferred by females to others, or the experimenter might induce changes in physiology that affect the production of signals (e.g., manipulations of the general condition of the signaler through dietary supplements) to confirm that signals convey reliable information on the condition of the sender. If a factor has been a general influence on the evolution of communication, then we would also expect other species in the same situation to exhibit similar characteristics and this leads to the obvious comparison of communication systems across species.

In much the same way that you might look more similar to your brother or sister compared with somebody randomly picked out from a crowd, closely related species often share behaviors and have similar ecologies, because they retain those attributes from a common evolutionary ancestor. We therefore need to be a little careful in how we perform comparisons across species. If we do so without regard to the phylogenetic relationships of the species examined, we could erroneously conclude that an association between a signal characteristic and some other factor exists when in fact they occur together because both the

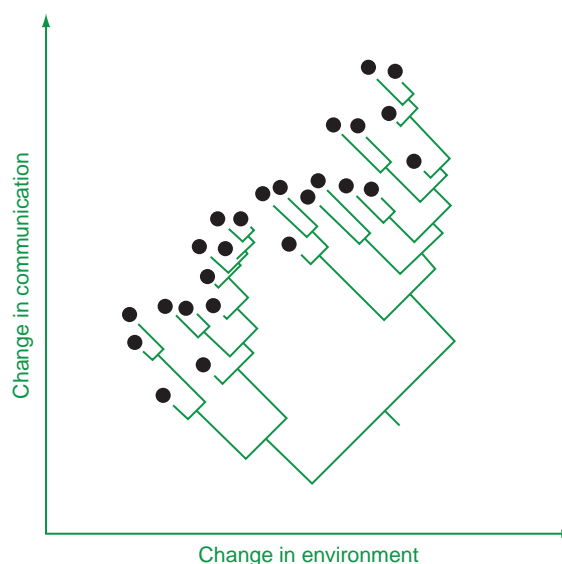


Figure 2 Scatter plot showing the hypothetical relationship between the form of communication used by different species and the environment they live in, combined with the underlying phylogenetic relationships among species. Disregarding phylogeny, a strong positive relationship appears to exist. However, in actual fact much of the variation in communication and the type of habitat species live in is inherited from evolutionary ancestors.

signal and putative 'causal' factor have been inherited together from a common ancestor. Statistically, the complication of treating data from closely related species as independent when in fact they are not is known as 'pseudo-replication' (Figure 2). The extent to which closely related species share similar phenotypes, including the form of communication they use, is measured by estimating *phylogenetic signal*. A high phylogenetic signal indicates that the evolutionary relationships between species predict phenotypic similarities between those species – species that share a recent common ancestor also share a particular trait – whereas low phylogenetic signal reflects that species' phenotypes are unrelated to their phylogenetic relationships – species that share a recent common ancestor do not share the same trait (Figure 3). A related term is *historical contingency*: the tendency for evolutionary elaborations or changes in descendant species to be modifications of historic phenotypes. Historical contingencies therefore relate to changes contingent on what has already evolved in the past.

The degree to which species diverge from evolutionary ancestors is dependent on a number of factors, but at the core of these factors is the rate of genetic mutation. If mutations are rare, the genetic basis of communication will change very little over long periods of evolutionary time, even in the face of strong selection for modification. However, it is difficult to determine the extent to which low mutation rates explain the retention of particular forms of communication over evolutionary time.

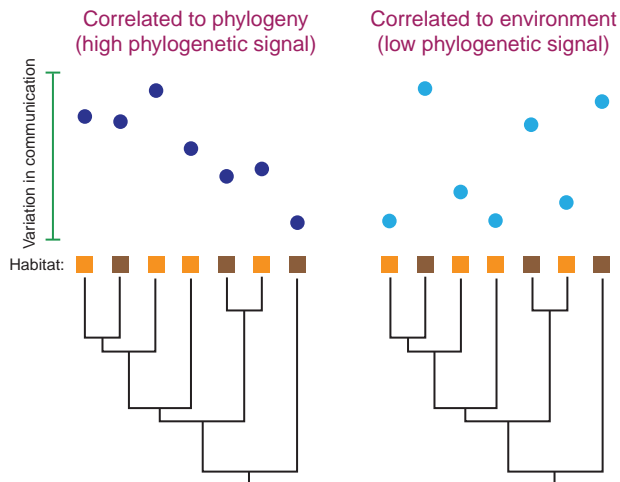


Figure 3 Animals may share communication systems through common ancestry or because they have converged on similar forms of communication when living in similar habitats through natural selection. Each dot represents the mean value of a species for some aspect of their communication, while the squares represent the type of habitat occupied. For example, the graph could illustrate the frequency of a mating call in frogs living in either open grasslands (orange) or closed tropical rainforests (chocolate).

There are statistical methods available for estimating the correlation between communication signals and phylogeny (i.e., the phylogenetic signal), but this can reflect a number of factors, not just low mutation rates. For example, if morphology influences the production of a communication signal (e.g., the shape of the vocal track influences the type of calls that an animal can produce) and if morphology exhibits little evolutionary change because it needs to maintain a functional capacity in another unrelated context (e.g., modifications to the vocal track might influence the ability of an animal to breathe or feed properly), then this will constrain evolutionary change in communication. By the same token, communication signals may change over evolutionary time not because of an adaptive response to selection, but because of random genetic change that culminates in arbitrary changes in signal design.

Ecological determinism is sometimes billed as the antithesis of historical contingency: it refers to conditions where the ecology of an animal primarily drives evolutionary change. Ecological determinism is likely to be an important factor affecting communication, because communication is a phenotypic trait that is often influenced by environmental conditions. Indeed, closely related species living in different habitats are expected to produce divergent forms of communication as species evolve signals suitable for communication in their respective environments. Conversely, distantly related species occupying similar habitats should converge on similar forms of communication (e.g., **Figure 3**). Such *convergent evolution* in which remarkably similar characteristics evolve independently in different species in

response to common selection pressures provides some of the most compelling evidence for adaptive evolution.

Both divergent and convergent evolution are expected to be associated with low phylogenetic signal, because communication in species that exhibit these forms of evolutionary change is dependent on the ecology and not the phylogeny of the species in question. However, this is not to say that high estimates of phylogenetic signal automatically exclude the possibility of adaptation. Ecological determinism can also lead to *stabilizing selection* in which forms of communication are conserved even after species split from evolutionary ancestors. For example, *niche conservatism* occurs when closely related species occupy similar environments, perhaps because they are already adapted to a certain habitat type. While the environment is still an important source of selection acting on communication, because closely related species live in very similar environments, they will also tend to produce similar forms of communication through selection. Communication that conveys honest information on an animal's condition can also exhibit high estimates of phylogenetic signal. There are only so many signal characteristics that can serve as quality indicators and once these evolve, they will tend to be retained with little modification over evolutionary time. Thus, communication may be very similar between species and exhibit high phylogenetic signal, yet still be under the influence of selection.

Mode, Pattern, and Rate of Signal Evolution

A question of special interest to evolutionary biologists concerns the mode by which evolution occurs. The classical perspective of Charles Darwin views evolution as small incremental changes accumulating over long evolutionary time scales. This mode of evolution predicts a series of 'intermediate' links between ancient species and those in existence today, but these are often lacking in the fossil record. Instead, new species seem to appear suddenly in the fossil record and live relatively unchanged for long periods of evolutionary time.

Some paleontologists have suggested that this pattern of sudden changes followed by stasis is a true representation of how evolution occurs. According to this nonincremental view, the formation of new species is accompanied by an intense period of selection that results in a rapid spurt of evolution, followed by long periods of relative stasis where species change very little (perhaps because of stabilizing selection). This process would lead to a more 'punctuated' rather than a 'gradual' mode of evolution (**Figure 4**). Behavioral ecologists might find this debate somewhat esoteric, but it can be quite relevant to the study of communication.

The use of signals during mating is a popular topic in the study of communication, especially how female mate choice might lead to *directional selection* on males for

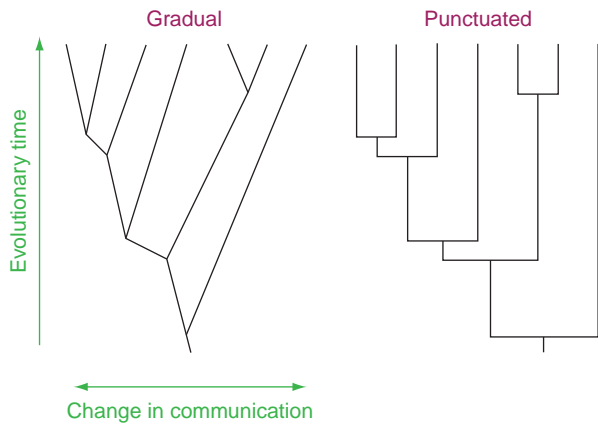


Figure 4 How the evolution of communication would appear under a gradual mode of evolution, where change accumulates over time, or under a punctuated mode of evolution, where change is concentrated at species events (represented by the nodes of the phylogeny, see [Figure 1](#)) followed by periods of stasis. Some forms of sexual selection on communication can be expected to produce a gradual accumulation of change over time, while communication important in species recognition should follow a more punctuated pattern.

increasing elaboration of sexual ornaments and other signals. This process should result in a gradual mode of evolution as modifications culminate over evolutionary time into increasingly more complex mating signals. To produce viable offspring, females must choose a male that is not only in good condition (for example) but also of the same species. Signal characteristics important in species recognition should be under considerable stabilizing selection and only subject to change during speciation when divergence in communication systems between populations is expected to be rapid, a process that should result in a punctuated mode of evolution.

The mode of evolution, whether it is gradual or punctuated, can also help to elucidate the function of different components making up the same communication signal. One of the main hypotheses explaining the evolution of elaborate multicomponent or multimodal signals (signals made up of components that use different sensory modalities, such as an acoustic signal – song – and a visual signal – colorful plumage or courtship dance) is the need to convey multiple messages. One component of a mating signal might communicate “I am of good condition” while another might communicate “I am of the right species,” which will lead to predictable differences in the mode of evolution that each component has taken. We can use phylogenetic comparative methods to determine which component has evolved gradually – consistent with sexual selection – or which component exhibits rapid bursts of evolution followed by relative stasis – consistent with species recognition. Despite being a powerful approach for testing the functional significance underlying the

evolution of different signal components, few studies have documented whether different components used by animals in communication have evolved via different modes of evolution.

We can also infer the presence of potential adaptive functions driving the evolution of communication by studying other phylogenetic patterns. Of particular interest is whether evolutionary changes are skewed toward the tips or base of a phylogeny, and whether new signal components are added to or replace previously existing components ([Figure 5](#)). Communication critical to species recognition should result in evolutionary changes in signal components skewed toward the tips of the phylogeny, because the evolution of species-typical signals will tend to result in new signal characteristics replacing preexisting forms, essentially ‘erasing’ similarities in communication between sister taxa. Communication that advertises the condition of the signaler or some other quality indicator will tend to be conserved with little modification in descendant taxa. This will tend to result in new signal components evolving early or toward the base of the phylogeny. Novel signal components may subsequently evolve, but because characteristics conveying honest information are costly to maintain (otherwise they could be ‘faked’), innovations will tend to replace previously existing signal components. Overall, this will result in low diversity in signal designs across species because signal components will tend to be retained from evolutionary ancestors, but will also result in more instances of evolutionary convergence between distantly related species as similar honest indicators evolve independently in different groups.

We can also expect the rate of evolution to differ depending on the type of selection acting on communication. Unless constrained by low mutation rates, signal characteristics subject to intense forms of selection should evolve extremely rapidly. Yet, even when subject to the same selection pressure, different components making up the same signal can exhibit very different rates of evolution. Multimodal signals are the product of different physiological and morphological attributes in the sender and rely on different sensory systems in receivers for detection. Elaborations of song are generally expected to evolve more freely than ornaments such as body coloration or elaborate plumage, because the latter are tied to morphological rather than behavioral adaptations. Vocalizations are also dynamic signals that can be turned ‘on’ and ‘off,’ but conspicuous ornaments are static and remain permanently ‘on’ unless animals can shed them during periods when they are not required (e.g., winter plumages in birds are sometimes drab compared with the bright, colorful breeding plumages in the summer months). Conspicuous forms of communication attract the attention of not only intended receivers such as mates, but also unintended receivers such as predators. If animals live in an environment with lots of predators, this opposing selective

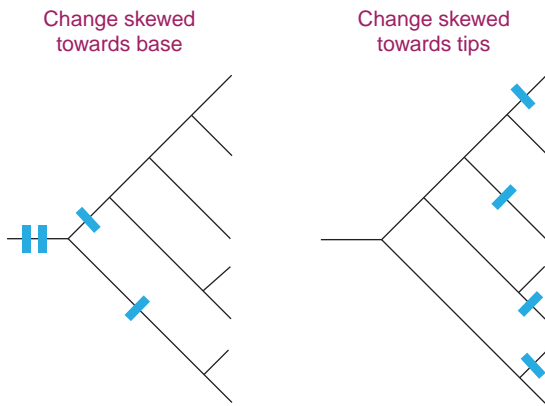


Figure 5 Hypothetical distribution of character evolution where signal components evolved early in the history of a group and are concentrated at the base of the phylogeny, such as components that function as quality indicators, or where the evolution of new signal components appears skewed towards the tips of the phylogeny, such as those that might be important in species recognition.

pressure can limit evolutionary change in conspicuous morphology, while dynamic signals are more free to vary.

Correlated Evolution

I have outlined how communication that is important in species recognition or subject to different types of sexual selection or genetic/physiological/morphological constraints will leave telltale signatures in the mode, pattern, and rate of signal evolution. We can also explicitly test for associations between signal characteristics and the factors predicted to result in these evolutionary signatures. For example, the evolution of mating signals will be tightly linked to the intensity of sexual selection. For those species in which the sex ratio is heavily male-biased, females are a limited resource and males must compete intensely with one another for mating opportunities. One result of this increased competition is the evolution of more elaborate mating signals in males, which predicts a positive correlation across species between how elaborate male mating signals are in species and the degree to which sex ratios are male-biased. Or perhaps we have a hypothesis that certain habitats select for particular forms of communication (e.g., [Figure 3](#)). In both instances, we can incorporate phylogeny into our statistical analyses to partition out the potential confounding affect of shared evolutionary histories and measure how variation in communication across species can be accounted for by social or environmental factors.

Indeed, tests of correlated changes between communication and predicted social or environmental influences are the most common use of phylogenetic comparative methods by behavioral ecologists and there are many studies that provide examples of what can be learnt by

this approach. In my own work on the evolution of color signals in dragon lizards, I have used phylogenetic correlation analyses to show how the diversity of colorful morphologies found across species can be accounted for by the intensity of sexual selection males experience. Furthermore, the type of color signals species have evolved is heavily dependent on whether species live in habitats where lizards are more prone to predation by birds or where communication is more difficult because of visual obstructions and poor habitat light. Other examples are listed in the suggested reading.

Phylogeny, Cultural Inheritance, and Plasticity

Explaining the diversity in animal communication need not be limited to investigating differences and similarities in communication across species. Different populations of the same species can also vary in communication. It could even be argued that if we truly want to understand the processes leading to signal divergence between species, we really should be investigating differences in communication among populations within species, which represent the starting points of evolutionary divergence. A critical step in the evolution of new species is the formation of reproductive barriers between populations. One of the key factors believed to limit members of different populations from interbreeding with one another, and to allow speciation to subsequently occur, is divergence in communication systems, especially those important in mating. The only way to detect divergences in signals that occur prior to speciation is to investigate variation in communication systems at the population-level.

A cautionary note needs to be made here about the assumptions underlying how changes in signal characteristics are acquired when studying signal variation among populations compared with studying signal variation between species. The implicit assumption when studying differences in communication between species is that there is a genetic basis to these differences. This may not always be true between populations, especially when aspects of communication are learned or culturally inherited. A distinction is sometimes made between ‘vertical’ – meaning phylogenetic – versus ‘horizontal’ – meaning cultural – transfer of signal characteristics ([Figure 6](#)). One solution is to measure the phylogenetic signal; if it is high, then signals are more likely to be genetically inherited and if it is low, signals could be culturally inherited. The difficulty with interpreting what phylogenetic signal actually reflects is applicable here. As is true for comparisons across species, error in the measurement of signal characteristics inflates the estimated variation among populations (or species) and can lead to false inferences of low phylogenetic signal. Conversely, culturally inherited signals may exhibit high phylogenetic signal because adjacent populations are more likely to share

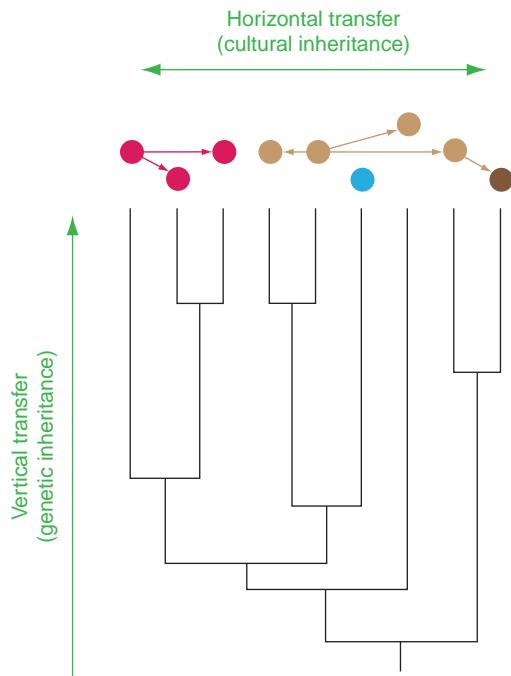


Figure 6 Communication transferred horizontally between populations through cultural inheritance, compared to vertical transfer via ancestry. In this example, the color of each dot might represent a song 'dialect' in different populations of a bird that is transferred through frequent contact or dispersal between populations. The connections between dots represent the social network or direction of dialect transfer.

similar culturally inherited signals because of their geographic proximity compared with more distant populations. Adjacent populations are also more likely to be genetically related and hence a phylogenetic analysis would indicate that communication is correlated with phylogeny.

'Plasticity' is another related issue particularly relevant to the study of the evolution of communication. Plasticity reflects the ability of animals to change their signals depending on the environmental or social conditions experienced at the time of communication. For example, birds in noisy habitats, such as those singing near highways, might produce songs that are much louder than birds singing in quieter areas. This difference could be genetic or plastic; birds in noisy habitats may be genetically predisposed to produce loud songs or alternatively birds in noisy habitats may have learnt to increase the volume of their songs. In the first instance, evolution may have occurred, while in the latter instance, it has not. The consequence of plasticity on the evolution of communication remains an open question and is relevant to investigations of signal variation at both the population and species level.

Neither cultural inheritance nor plasticity should necessarily exclude adopting a phylogenetic comparative

approach, but interpretations of the underlying mechanism used to explain signal variation should be done with caution. Consider an example where we wish to test the hypothesis that species produce communication signals ideally suited for transmission through the environment in which communication is typically conducted. When populations live in different types of habitat, environmentally induced divergence in communication is expected and should in turn promote reproductive isolation between populations. An obvious test is to confirm that differences in communication are correlated to differences in habitat, but we are not sure whether communication is culturally inherited or whether animals can learn to tailor signals to prevailing environmental conditions. Currently, the best approach is to apply a phylogenetic comparative method that explicitly measures the correlation between characteristics and phylogeny and identifies the remaining variance that is associated with the environment. This will control for any pseudo-replication resulting from phylogenetic relationships or factors that might mirror phylogenetic relationships (e.g., closely related, adjacent populations inheriting signal components culturally) and determine whether the environment facilitates divergence in communication. Unfortunately, it is difficult to assess whether communication divergence reflects genetic adaptation or plasticity. Obtaining the answer to this question requires intensive empirical study, such as detailed observations of how animals change the way they communicate according to environmental fluctuations and/or so called 'common garden' experiments in which individuals from one habitat type are transferred to another habitat type and assayed for behavioral change.

New methods are being developed that incorporate geographic proximity into comparative analyses, providing a more direct means to estimate how much of the variance in communication between populations is the result of genetic (phylogenetic/vertical transfer), geographic (cultural/horizontal transfer) or environmental factors. A phylogenetic comparative method that incorporates social network analysis to quantify more accurately the degree to which interactions between individuals from different populations influence the transfer of signal characteristics would be especially useful (e.g., [Figure 6](#)). For now, however, investigators will need to remain cautious with their interpretations of what the underlying mechanisms are that have led to the observed correlations.

A Primer to Phylogenetic Comparative Methods

The number of programs available for applying phylogenetic comparative methods is daunting, so much so that it is difficult to know where to start or even what method is most appropriate for the question of interest.

Box 1

There are a number software packages available that combine a variety of methods together and can be run regardless of a user's platform (PC or Mac). All can be downloaded for free following a quick search online.

- *BayesTraits*: Can be used to test correlations between traits, estimate phylogenetic signal, the mode of evolution, and whether evolutionary change is concentrated towards the tips or base of the phylogeny.
- *COMPARE: Phylogenetic Comparative Methods*: Provides several programs to test correlations between traits using likelihood based methods or independent contrasts, estimates phylogenetic signal, and performs analyses for estimating the rate of evolutionary change in traits. Ancestor reconstructions can also be calculated using likelihood.
- *Mesquite: A Modular System for Evolutionary Analysis*: A particularly useful program for reconstructing ancestor states graphically, using parsimony and likelihood based methods. Options are also available for testing correlations using independent contrasts and other methods.

Most programs are free and available as downloads off the internet or by request from the program's author. I provide a list of some popular methods in [Box 1](#) and a brief outline of some commonly used techniques below. Readers interested in details of various techniques are referred to the suggested reading at the end of the section.

Ancestor State Reconstructions

There are several methods for reconstructing what communication systems may have been like in the past ([Figure 7](#)). The simplest methods are those based on parsimony, an algorithm that maps ancestor 'states' onto a phylogeny by favoring solutions requiring the least amount of evolutionary change. Parsimony approaches are often favored because of their straightforward computation, but they have also been criticized for lacking statistical rigor and for not presenting a realistic view of how evolution occurs. Other methods such as those based on least squares, maximum likelihood, and Bayesian techniques apply a probabilistic approach to finding a mathematical model of evolution that best fits the observed distribution of data across species on the phylogeny. These methods fit various scenarios of how evolution might have occurred – for example, gradual or punctuated, rapid or slow rate of evolutionary change – and calculate the probability that each explains present-day variation in traits. Once the model of best fit is identified, it is then used to assign ancestor states onto the phylogeny.

Phylogenetic Signal, Patterns, and Rates of Evolution

In fitting different models to the data, it is possible to use the parameters of the best fitting models to infer something about the correlation between characteristics and phylogeny or the mode of evolution a characteristic has likely followed. Methods that estimate phylogenetic signal do so by applying mathematical models that in effect transform the phylogeny, essentially stretching or shrinking phylogenetic branches, to simulate the evolution of a characteristic as if it were heavily dependent on phylogeny

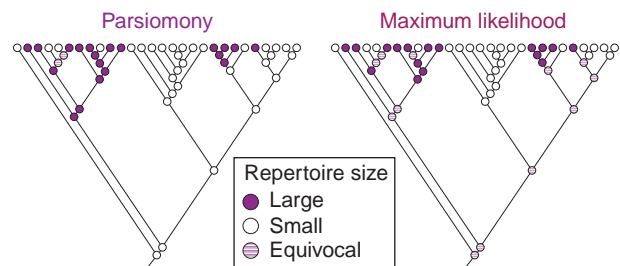


Figure 7 Alternative ancestor reconstructions of the repertoire size or number of distinct components making up communication in species. It is important to note that ancestor reconstructions will depend on both the method and the phylogeny used. In this example, differences are apparent at several nodes throughout the phylogeny. For instance, parsimony reconstructs a small repertoire in the root or most basal ancestor, while maximum likelihood assigns an equivocal state, meaning it is equally likely that this ancestor had a large or small repertoire.

or not at all. Similar transformations to the underlying phylogeny are used to estimate the likelihood that evolution has occurred via bursts during speciation followed by relative stasis, or through a more gradual mode of evolution. Regression slopes of estimated evolutionary change in a characteristic as a function of time since divergence from evolutionary ancestors can be used to estimate the rate of evolution: steeper slopes reflect more rapid rates of change compared with shallower slopes.

Correlation Tests of Adaptation

All taxa are related to each other in one way or another. Not incorporating phylogeny into statistical comparisons across species can subsequently lead to inflated rates of Type I statistical error (i.e., erroneously concluding that a significant effect exists when in fact it does not). Phylogenetic independent contrasts are the most commonly used comparative method for conducting correlation tests. It corrects for phylogenetic nonindependence by transforming species data into a set of differences or 'contrasts' between immediate relatives ([Figure 8](#)). In doing so, it assumes a null hypothesis that

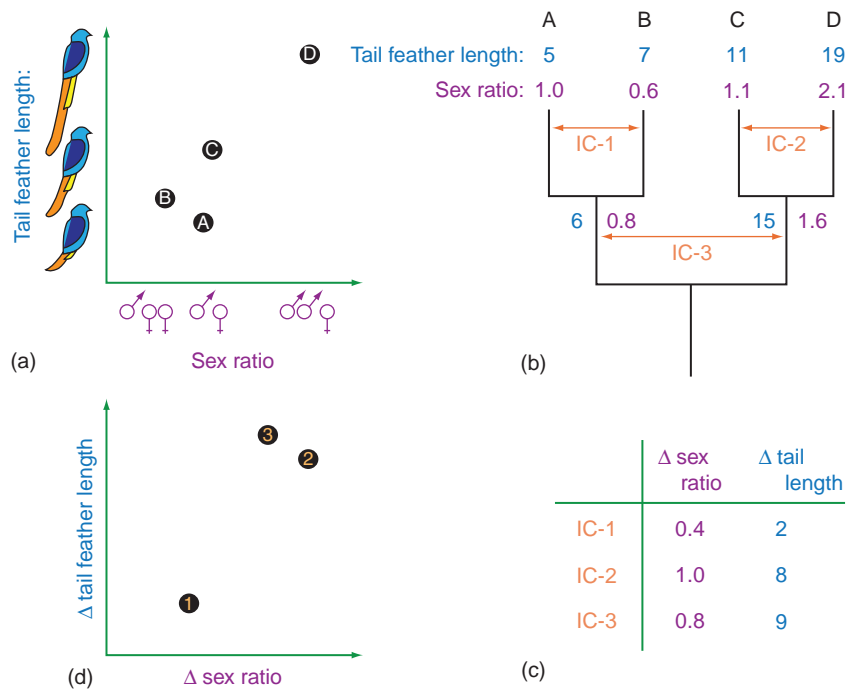


Figure 8 Hypothetical example of how a phylogenetic independent contrast analysis is conducted. Plotting tail length in males by sex ratio suggests increased competition for mates is correlated with more showy tail plumage. (a) To correct for potential bias resulting from shared ancestry, difference scores are calculated between species pairs and ancestor nodes on the phylogeny, (b) to transform the data into phylogenetically independent contrasts, (c). Following this conversion, a positive relationship remains between tail length and sex ratio, (d) suggesting that an evolutionary relationship might exist between the elaboration of tail ornaments and competition for mates.

variation among closely related species is explained by the phylogenetic relationships between those species. Newer methods use likelihood and Bayesian techniques to estimate the relationship between phylogeny and trait expression and control for this level of phylogenetic signal during correlation tests.

Annotated Bibliography

A detailed overview of phylogenetic comparative methods for behavioral ecologists can be found in [Ord and Martins \(2009\)](#). [Nunn and Barton \(2001\)](#) also provide a useful practical guide to several methods. There are a number of books available but most are dated in the methods they present. Nevertheless, they still provide a solid conceptual foundation to comparative biology. These texts are [Harvey and Pagel \(1991\)](#), *The Comparative Method in Evolutionary Biology*, and [Martins \(1996\)](#), *Phylogenies and the Comparative Method in Animal Behavior*. Examples of studies using comparative methods to study the evolution of communication include: acoustic signals in birds ([Seddon, 2005](#)) and frogs ([Ryan and Rand, 1995](#)); color signals in birds ([Doucet et al., 2007](#)), fish ([Garcia and Ramirez, 2005](#)), and chameleons ([Stuart-Fox and Moussalli, 2008](#)); the sword in swordtails ([Basolo, 1990](#));

dynamic visual displays in lizards ([Ord and Martins, 2006](#)); vibration signals in insects ([Henry and Wells, 2004](#)); and electric signals in fish ([Turner et al., 2007](#)).

See also: Electrical Signals; Phylogenetic Inference and the Evolution of Behavior; Swordtails and Platyfishes; Túngara Frog: A Model for Sexual Selection and Communication; Visual Signals.

Further Reading

- Basolo AL (1990) Female preference predates the evolution of the sword in swordtail fish. *Science* 250: 808–810.
- Doucet SM, Mennill DJ, and Hill GE (2007) The evolution of signal design in manakin plumage ornaments. *American Naturalist* 169: S62–S80.
- Garcia CM and Ramirez E (2005) Evidence that sensory traps can evolve into honest signals. *Nature* 434: 501–505.
- Harvey PH and Pagel MD (1991) *The Comparative Method in Evolutionary Biology*. New York: Oxford University Press.
- Henry C and Wells MLM (2004) Adaptation or random change? The evolutionary response of songs to substrate properties in lacewings (Neuroptera: Chrysopidae: *Chrysoperla*). *Animal Behaviour* 68: 879–895.
- Martins EP (ed.) (1996) *Phylogenies and the Comparative Method in Animal Behaviour*. New York: Oxford University Press.
- Nunn CL and Barton RA (2001) Comparative methods for studying primate adaptation and allometry. *Evolutionary Anthropology* 10: 81–98.

- Ord TJ and Martins EP (2006) Tracing the origins of signal diversity in anole lizards: Phylogenetic approaches to inferring the evolution of complex behaviour. *Animal Behaviour* 71: 1411–1429.
- Ord TJ and Martins EP (2010) The evolution behavior: Phylogeny and the origin of present-day diversity. In: Westneat DF and Fox CW (eds.) *Evolutionary Behavioral Ecology*. pp. 108–128. New York, NY: Oxford University Press.
- Ryan MJ and Rand AS (1995) Female responses to ancestral advertisement calls in Tungara frogs. *Science* 269: 390–392.
- Seddon N (2005) Ecological adaptation and species recognition drives vocal evolution in neotropical suboscine birds. *Evolution* 59: 200–215.
- Stuart-Fox D and Moussalli A (2008) Selection for social signalling drives the evolution of chameleon colour change. *Public Library of Science, Biology* 6: e25.
- Turner CR, Derylo M, de Santana CD, Alves-Gomes JA, and Smith GT (2007) Phylogenetic comparative analysis of electric communication signals in ghost knifefishes (Gymnotiformes: Apterontidae). *Journal of Experimental Biology* 210: 4104–4122.