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Evolutionary History of Behavior

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BEHAVIORAL ECOLOGY MEETS PALEONTOLOGY AND PHYLOGENETICS

Uncovering the past history of animal behavior seems impossible; unless we can observe behavior directly, it would appear there is no way to know what the behavior of an extinct animal might have been like. Direct observation seems an obvious prerequisite for the study of animal behavior, but *is it really necessary? Will we never know how the dinosaurs interacted with one another and their environment without a time machine or a way to resurrect them? Can we say nothing about the behavior of the evolutionary ancestors of animals that are alive today?*

Science is about **deduction** and **inference**. Direct observation of the phenomena under study is an advantage, but it is by no means a necessity. Granted, there are some things we will never know about the behavior of extinct animals without direct observation. But much can still be learned about the evolutionary history of animal behavior through some clever detective work and modern scientific methods.

There are two ways the history of behavior can be studied: combining fossil evidence with information from contemporary analogues of similar species alive today, and the reconstruction of past history using phylogenies and the comparative method. The first approach extrapolates the **behavioral ecology** of extinct species by exploiting what we know about the behavior of living species. Behavior is often reflected in the morphology of an animal and other characteristics that can leave traces in the fossil record (e.g., track marks; Mazin et al.,

2009). These preserved characteristics can therefore be used to similarly infer the probable behavior of prehistoric animals. The second approach is similar to the first in the sense that it also uses information on the behavior of living species, but it relies on **_phylogenetics_** rather than fossil evidence to infer the evolutionary history of behavior. By comparing the behavior of species that are phylogenetic close relatives it is possible to reconstruct the likely behavior of the common ancestor of those species. As a basic example, if a set of closely related species hunted in small groups, then it is reasonable to assume that the common evolutionary ancestor of those species also hunted in groups. This **_phylogenetic comparative method_** can be taken even further to investigate the factors that might have influenced the initial evolution of particular behaviors.

Combining fossils with information from living species and the application of the phylogenetic comparative method has led to many important discoveries about the evolutionary history of behavior. These discoveries have in turn helped behavioral scientists understand why animals in existence today behave the way they do and how animals have adapted to their environment. The latter is especially important for knowing how animals respond to environmental change, which has important implications for conservation. In the following sections, examples are presented that illustrate some of the ways scientists have studied the history of animal behavior and what has been learned about how animals respond to natural selection and other evolutionary forces.

LINKING FOSSILS TO THE BEHAVIOR OF LIVING SPECIES

Questions that often arise when contemplating the behavior of extinct species are how social they might have been and whether their behavioral ecology contributed to their ultimate demise. It is understandable why animal **_sociality_** is an especially evocative topic to us because we are a highly social species ourselves. Sociality implies richness in the lives of animals that in itself is fascinating. But the social behavior of animals is also important in shaping the evolution of species, from how they reproduce to how they find their food. Animal sociality is therefore a major focus of research in behavioral ecology. Knowing the constraints on an animal's behavior can also help us understand why some species and not others might have gone extinct. This is important to know so we can predict how animals today will cope with environmental change resulting from human impacts and global shifts in climate.

What evidence do we have for social behavior in extinct species, and how do we know what aspects of behavior might have contributed to species extinction?

Social Sabertooths and Migratory Mastodons

Sabertooth cats (*Smilodon fatalis*) were about the size of the largest tigers in existence today and roamed North America during the late Pleistocene (1.6 million to 10,000 years ago). Fossils reveal powerful forelimbs and massive canines, indicating a formable predator. Classically, sabertooths were believed to have been solitary, like today's cheetahs or American mountain lions. But the large number of fossils clumped together in the Californian tar seeps of Rancho La Brea is at odds with this "lone hunter" lifestyle. When fossils of the same species are found clustered together, it is often taken as evidence of sociality (Ladevéze et al., 2011). For the sabertooth, however, things were ambiguous. The consensus among paleontologists was that sabertooths were attracted to the tar seeps by the sounds of struggling prey caught in the tar and themselves ended up becoming trapped. Debate, however, centers on whether sabertooths were attracted separately or in groups. There were two competing hypotheses. The first hypothesis was that sabertooths were solitary and attracted individually to the tar seeps. The second hypothesis was that sabertooths were social—that is, hunted in packs—and were attracted to the tar seeps as groups.

Testing these hypotheses presented a challenge. The number of sabertooth cats recovered from the tar seeps was the only information *paleontologists* had of what occurred in the Pleistocene. By itself, this information gives only the final outcome, not how that outcome came about. The breakthrough came when paleontologists teamed up with several experts on the behavior of present-day large carnivores (Carbone et al., 2009). These behavioral ecologists had conducted many field surveys of African carnivores by "calling in" predators through playing audio recordings of distressed prey. The researchers argued that these playbacks, which were originally designed to estimate carnivore abundance, were analogous to the sounds of prey caught in the La Brea tar seeps (Van Valkenburgh et al., 2009). That is, the types of African carnivores attracted by the playbacks were, in effect, a real-world simulation of events at the La Brea tar seeps in the Pleistocence.

The behavioral ecologists knew from direct observation and other studies which carnivores attracted to playbacks were solitary hunters (e.g., cheetahs [*Acinonyx jubatus*] and leopards [*Panthera pardus*]) and which hunted in groups (e.g., wild dogs [*Lycaon pictus*] and lions [*Panthera leo*]). Their data showed clear differences in the proportion of solitary and social predators attracted to playbacks (Figure 12.1). With this information in hand, the paleontologists reevaluated the number of sabertooth cats attracted to the tar seeps relative to other types of animals. If sabertooth cats were solitary, as traditionally assumed, their numbers were vastly overrepresented in the La Brea tar
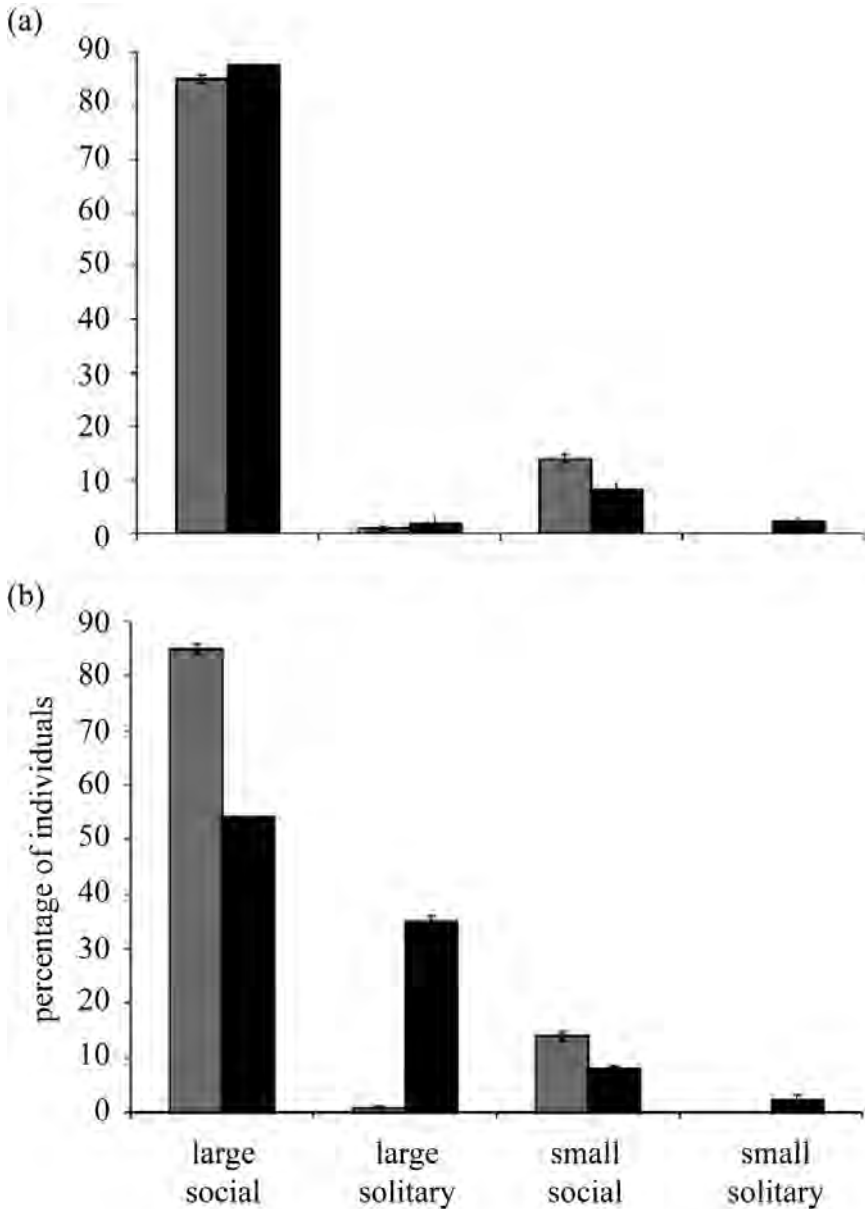
Figure 12.1. Shown in gray are the percentages of African carnivores, grouped by body size and sociality, attracted to audio playbacks of distressed prey animals, which were heavily skewed towards large, pack-hunting predators. In the upper panel (a) shown in black are the percentage of fossilized remains found in the La Brea tar seeps based on the assumption that sabertooth cats hunted in groups, while the lower panel (b) shows the percentage of fossils based on the assumption that sabertooth cats were solitary. Error bars are 95 percent confidence intervals. (This plot is reprinted from Carbone et al., 2009, by permission of Highwire Press.)

seeps according to the number of living solitary predators attracted to audio playbacks (Figure 12.1a). By contrast, if sabertooth cats were social, then their numbers were almost exactly the number predicted by the proportion of group-hunting predators attracted to playbacks (Figure 12.1b). While this data cannot provide conclusive proof, it does offer compelling support for the social hypothesis.

The study of sabertooth cats was possible because there were numerous surviving analogues—for instance, cheetahs, leopards, and lions—that differed in sociality and could be used to deduce the possible behavior of the sabertooth based purely on their abundances in the La Brea tar seeps. But *what if few (or no) contemporary analogues exist for comparison?* This was a problem faced by paleontologists interested in the behavior of mastodons. These massive creatures were related to present-day elephants in the sense that they both belong to the same order of mammals (Proboscidea) and share some similarities in morphology. But the similarities are generally few, and mastodons and elephants were certainly not as genetically related as the sabretooth was to today's big cats (Janczewski et al., 1992; Rohland et al., 2010). Furthermore, the elephants represented the only living analogue of mastodons, so even if they were phylogenetic close relatives, the comparison is limited to one. So when paleontologists wished to investigate the probable migration patterns of mastodons, an alternative approach had to be found.

The question of mastodon migration was a topic of interest to scientists because it might reveal why these large mammals went extinct 11,500 years ago (Hoppe et al., 1999). Mastodons lived in North America alongside another iconic species, the mammoth, which were close relatives to elephants (Rohland et al., 2010). Several hypotheses had been proposed about why mastodons and mammoths suddenly disappeared after having existed for millions of years. One hypothesis related to the impacts of climate change on the environment and whether the behavioral ecology of mastodons and mammoths hindered their ability to cope with the accompanying ecological changes.

We know from many species today that migration allows animals to escape freezing winters or scorching summers and exploit seasonally fluctuating resources at different locations. A spectacular example is the annual migration of thousands of Serengeti wildebeest (*Connochaetes taurinus*) that walk hundreds of kilometers south at the onset of the dry season to follow rainfall and shifting food resources (Boone et al., 2006). To discover the annual movement of mastodons, paleontologists took a novel approach and examined the fossilized remains of their teeth.

In living animals, the isotope ratio in the chemical element strontium found in the enamel of teeth reflects the isotope signature of ingested food.

In the case of plant foods, strontium isotope ratios depend on soil type and vary geographically. Put simply, by measuring the strontium isotopes of mastodon teeth, it was possible to retrace where the animals had been foraging during their lifetime. If mastodons uncovered in southern Florida had migrated to escape the winter from as far north as the Appalachian Mountains in Georgia, then the isotope signatures of their teeth should reflect the differences in isotopes present in the vegetation from the two regions. This is precisely what the researchers found (Hoppe et al., 1999). Isotope signatures revealed frequent mastodon migration over hundreds of kilometers between the Appalachians and southern Florida. In contrast, the isotope signature of mammoth teeth also uncovered in Florida indicated that these animals did not range nearly as far and were not, as previously hypothesized, migratory (Hoppe et al., 1999).

While the migration of mastodon implies that these animals should have been able to buffer themselves against the ecological changes resulting from climate shifts better than mammoths, recent studies on the migration of living species suggested this might not have been the case. Even subtle regional changes in temperature have lead to the mismatch of migration events with seasonal fluctuations, placing the survival of some species in jeopardy (e.g., Saino et al., 2011). It is still unclear the extent to which migration in mastodons and its absence in mammoths contributed to their extinction, but new data on other species—both extinct and living—should help resolve this question. It appears, though, that climate change and whether or not species migrated was not the primary contributing factor for the extinction of the North American megafauna at the end of the Pleistocene (Ripple & Van Valkenburgh, 2010).

Fatherly, Musical Dinosaurs

The repeated discovery of the remains of adult dinosaurs alongside fossilized egg clutches gives a strong indication that parental care was an important component of the behavior of some dinosaurs (Norell et al., 1995). Whether animals provide parental care, and especially who provides parental care, reflects the mating system of species. In birds, males often provide all or part of the parental care (e.g., incubating eggs, feeding hatchings), whereas females are generally the sole caregivers in mammals and in the few reptiles like the crocodile that exhibit parental care. *Were dinosaurs like crocodiles, in which females provided all care, or more like birds, in which males provided care? If dinosaurs were like birds, was vocal communication an integral component of their social behavior as it is in birds? What did those calls sound like?*

In living species, the size of egg clutches reflects the type of parental care exhibited by species. When males provide all care, larger clutches are

maintained than if only females provide care (Varricchio et al., 2008). This is presumably because males do not incur the considerable cost associated with egg production and can invest more in incubating eggs at the expense of feeding. Paleontologists used the relationship of parental care type and clutch size to sex the caregivers in the egg-nesting Cretaceous troodontid and oviraptorid dinosaurs. Based on the size of egg clutches, these dinosaurs were most consistent with a system of exclusive male parental care and not *biparental* or *maternal care* (Varricchio et al., 2008).

Further evidence for male care came from a closer examination of the bones associated with the fossilized egg nests. Female birds and crocodiles leach large amounts of calcium and phosphorus from their tissues during egg production, and this leaves telltale signs in the histology of their bones. Cross sections of fossilized bones confirmed the adult dinosaurs associated with nests were male; there was no evidence of calcium and phosphorus leaching (Varricchio et al., 2008). Taken together, not only were some dinosaurs building nests and incubating eggs (Norell et al., 1995), but paleontologists have been able to determine that parental care was most likely provided by males and not females, pushing back the origin of ***paternal care*** to before the evolution of birds.

Comparisons of behavior among living species have also been able to reconstruct whether dinosaurs communicated vocally and what those calls might have sounded like. The length of the cochlear—or inner ear—correlates closely with the hearing sensitivity of species and can be used to predict the frequency range, the mean frequency, and even the complexity of vocal calls produced by animals (Walsh et al., 2009). The cochlear has been preserved in several fossils, for example the *Archaeopteryx*, a birdlike precursor from the Late Jurassic. Using the equation derived from the statistical relationship between the length of the cochlear and the vocal characteristics of living animals, researchers have argued that *Archaeopteryx* had a vocal repertoire very similar to the present-day emu (*Dromaius novaehollandiae*) (Walsh et al., 2009). This also implies a reasonable complex social life for *Archaeopteryx* because the complexity of communication tends to reflect the level of social complexity in species (Freeberg et al., 2012).

Prehistoric Polygyny

It is common in nature for males to compete aggressively among themselves for access to females. And in aggressive competition, size matters. Large males win more fights, mate with more females, and subsequently produce more offspring. The selective advantage of large males in contests typically leads to the evolution of increasing ***sexual size dimorphism*** in species. That is, males become increasingly larger than females over evolutionary time. If body size

is strongly skewed towards males in fossils, then this is a strong indication that males probably competed aggressive with one another in a ***polygamous*** mating system (***monogamous*** species are typically ***sexually monomorphic*** in size). For example, the sexual size dimorphism of fossils has been used to infer that strong male-male competition and ***polygyny*** existed in the extinct relatives of present-day marsupials from the early Palaeocene (Ladevéze et al., 2011). This implies that the solitary nature of many marsupials today has resulted from a loss of sociality rather than being ancestral as initially assumed.

Which male a female chooses to mate with contributes not only to the evolution of male size—females preferentially mate with large males over small males—but also the evolution of male ornamentation. ***Sexual ornaments*** in males are common in nature and provide valuable cues to females on the quality of a male as a potential mate. This is because only males in top condition can incur the energetic and developmental costs associated with the possession of a large ornament. Classic examples of female-driven male ornamentation are the elaborate plumages of many male birds (e.g., peacock [*Pavo cristatus*] trains). Others include conspicuous rostral appendages, such as fleshy horns, and large throat fans in lizards.

The presence of ornaments in an extinct animal, especially if that animal were confirmed as male, would imply a polygamous mating system. It would also provide strong evidence that females were highly selective about which males they chose to mate with. In present-day animals, ornaments are also often associated with elaborate ***courtship displays***. Determining whether extinct animals had ornaments is helped if the features preserved in fossils are similar in appearance to confirmed ornaments in species today. Unfortunately, common ornaments like feather plumages or fleshy structures are rarely left in the fossil record (*Archaeopteryx* provides an unusually clear example of feather ornamentation). But there are also other, often more bizarre structures preserved in fossils that paleontologists speculate might have also functioned as ornaments. Yet there are also frequently several plausible explanations these structures as well.

In some instances, it has been possible to test alternative hypothesis for the function of elaborate morphological structures (Tomkins et al., 2010). *Pteranodon* were large flying pterosaurs with wingspans of many meters found in North America in the Late Cretaceous, some 85 million years ago. Fossils show these pterosaurs had large, prominent crests on their head (Figure 12.2), which were especially exaggerated in males (i.e., the crests were sexually size dimorphic). Several hypotheses for what these crests might have been used for included a rudder to facilitate flying, a heat-dissipating or -absorbing device to aid thermoregulation, or an ornament used to attract mates. Stranger still
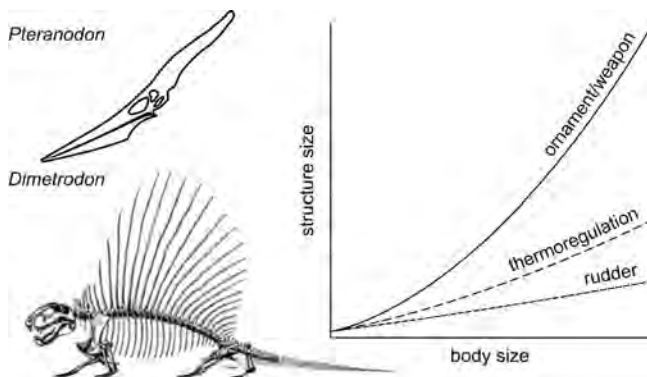
Figure 12.2. Illustrations of the head crests of the flying Pteranodon and dorsal sail of Dimetrodon alongside predicted allometric slopes if crests or sails functioned as ornaments, as devices for thermoregulation, or as rudders (in Pteranodon). The estimated allometry of head crests was ×6.94, while for dorsal sails it was ×1.73; these estimates were consistent with the allometry of ornaments. (Sketches of Pteranodon and Dimetrodon are reprinted from Tomkins et al., 2010, by permission of University of Chicago Press.)

were the massive sails found on the backs of *Dimetrodon* and *Edaphosaurus* dinosaurs (Figure 12.2; these animals provided the inspiration for many a 1950s Hollywood monster movie). These large predators lived during the late Carboniferous and early Permian around 300–260 million years ago in North America and Europe. The classic hypothesis was these large sails were structures used in thermoregulation. But it was also possible that they might have been ornaments.

Behavioral ecologists who have studied male ornamentation in living species have discovered the size of ornaments commonly exhibit ***positive allometry*** (Kodric-Brown et al., 2006). Positive allometry occurs when larger individuals have disproportionately larger structures—like ornaments—compared to smaller individuals. This allometric pattern is believed to happen whenever ornaments are costly to produce. Larger animals are better able to bear the costs of having a large ornament than smaller animals, leading to a disproportionate increase in ornament size with overall body size. Behavioral ecologists decided to use this phenomenon to test whether *Pteranodon* head crests and *Dimetrodon* and *Edaphosaurus* sails were ornaments (Tomkins et al., 2010). The researchers also tested the alternative hypotheses relating to rudders and thermoregulation, which biophysics predicted would have their own unique relationships with body size (Figure 12.2).

By comparing the size of head crests and sails in fossils for a range of individuals varying in body size, the rudder and thermoregulation hypotheses were rejected by the magnitude of the allometric slopes (it was too large; Figure 12.2). But these allometric slopes were well within the range for what would be expected for ornaments (Tomkins et al., 2010). By extension, these apparent ornaments—head crests and dorsal sails—implied that male *Pteranodon*, *Dimetrodon*, and *Edaphosaurus* dinosaurs competed among themselves for mating opportunities with females and that those females probably exerted a strong preference for males with the largest ornament.

COMPARE AND CONTRAST TODAY TO RECOVER BEHAVIORS PAST

Carl Linnaeus created a classification scheme based on a nested hierarchy of shared characteristics among organisms, a scheme that remains at the heart of modern taxonomy. This scheme exploited the common observation of naturalists that groups of species often shared physical characteristics. Darwin argued a hundred years after Linnaeus that such shared features reflected the shared ancestry among species (Darwin, 1859). He expanded on this idea to formulate the theory of evolution, encapsulated by the notion of "descent with modification": descendent species inherit features from evolutionary ancestors, with those features becoming modified over evolutionary time through natural selection. Today we understand evolution as a process that is more complex than Darwin could have appreciated in his day. But this idea of common ancestry and its influence on the features expressed by animals—and this includes an animal's behavior—also provides a powerful way to uncover the probable behavior of evolutionary ancestors.

By comparing the similarities and differences among phylogenetic close relatives, it becomes possible to map behaviors onto a phylogeny and retrace their likely origin. In this section, we review examples of some remarkable animal behavior and how comparative biologists have uncovered the evolutionary history of those behaviors with the aid of modern phylogenetic methods.

Ancient Squirrels Exploited Smelly Predators

For a number of North American ground squirrel species, rattlesnakes pose an acute threat to the survival of offspring. At dusk, rattlesnakes use smell to locate burrows in which squirrel pups are sheltering. Adult ground squirrels have evolved a number of strategies to reduce the likelihood of their pups being eaten, such as mobbing a snake before it enters a burrow. Mobbing is meant to harass the snake so much that it is forced to give up hunting and leave the area. It is not always successful.

Some ground squirrel species, and in particular the females and juveniles of those species, add another defense: they smear themselves with the chewed-up remains of shed rattlesnake skins (rattlesnakes molt frequently). This behavior was puzzling to researchers at first. It seemed that the squirrels were willingly covering themselves with the scent of their main predator. Experiments later revealed that this anointing behavior helped to minimize predation. Rattlesnakes avoided the burrows of squirrels that had recently anointed themselves with rattlesnake sheds (Clucas et al., 2008). The scent-application behavior was a novel antipredator strategy. The scent of the rattlesnake not only hid the squirrel's own smell but also gave the false impression that a squirrel's burrow had already been visited by a rattlesnake.

But *what was the evolutionary history of this extraordinary anointing behavior? Did anointing evolve multiple times independently in each squirrel species or just once early in the history of the squirrel family and was retained in those species performing the behavior today?*

An extensive study of different squirrel species throughout North America and Mexico was undertaken to determine which species performed the anointing behavior and which species did not (Clucas et al., 2010). This survey in itself led to some fascinating findings. It revealed that squirrels not only anointed with rattlesnake scent but weasel scent as well; weasels were another key predator of ground squirrel pups in some areas of the Americas. That is, the behavior was not specific to rattlesnakes but general to predators using smell to hunt for squirrel pups.

The researchers then used the phylogenetic relationships among squirrel species to reconstruct the evolutionary history of predator scent application. The behavior was ancient, evolving once some 28 million years ago (Figure 12.3) and possibly even as far back as 75 million years ago (Clucas et al., 2010). Yet, in another twist to the story, the earliest fossils of rattlesnakes and weasels were roughly 15 million years ago. This meant that scent application evolved well before rattlesnakes and weasels even existed. It must therefore have evolved as an antipredator strategy to some other, now extinct predator that also relied on smell to hunt for prey. A good candidate was the ancient North American boa snake that existed during the Oligocene (Clucas et al., 2010).

Further analysis of the relationship between the overlap of rattlesnakes and weasels with living ground squirrels gave other insights as well. Squirrel species that no longer faced predation from rattlesnakes had lost the scent-application behavior. In a couple of cases, squirrels have since come back into contact with rattlesnakes but have not reevolved the behavior. It seems then that applying predator scent was easily lost in the absence of predation, was a highly unusual event in the prehistory of the squirrel family, and has not been repeated since.
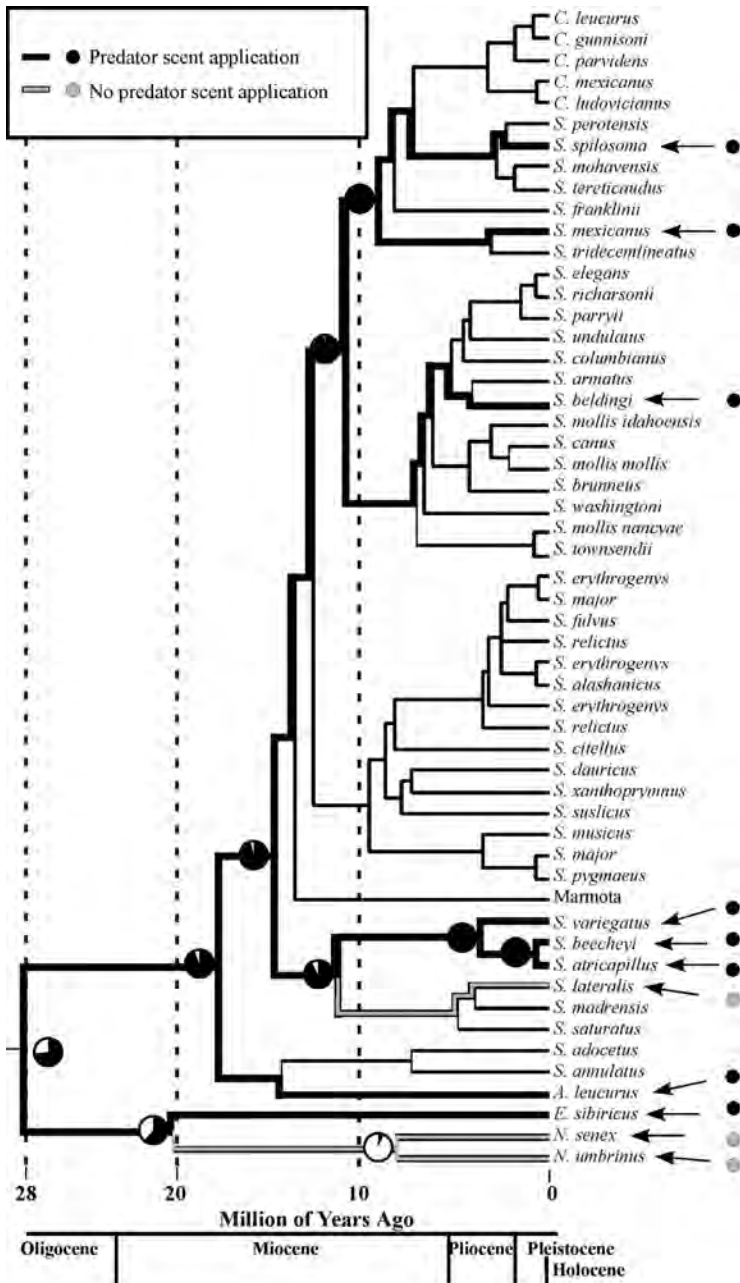
Figure 12.3. Ancestor reconstructions of the predator-scent-application behavior of North American ground squirrels. Filled lines on the phylogeny depict reconstructions using parsimony; pie charts depict reconstructions using maximum likelihood. The phylogeny of scent application indicates that the behavior evolved at least 28 million years ago. Dots at the tips of the phylogeny indicate which species did and did not anoint themselves with predator scent when researchers placed scent out in the environment for squirrels to inspect. (This figure is reprinted from Clucas et al., 2010, by permission of John Wiley & Sons.)

The ground squirrels are a wonderful example of how field studies of behavior on a select number of species and experiments in the laboratory documenting the adaptive significance of initially puzzling behavior can be integrated with evidence from phylogeny and paleontology to show the history of animal behavior. In doing so, researchers were able to not only date the origin of behavior but also show how unusual the evolution of such an odd behavior like predator-scent application might have been.

Reconstructing Past Mating Calls

What the vocal communication of extinct species might have sounded like, such as the calls of the *Archaeopteryx*, has been inferred from the shape of the cochlear preserved in fossils (see "Fatherly, Musical Dinosaurs" above). But there is another way scientists can reconstruct the calls of ancestral species. By exploiting detailed information on the call structure of living species and the phylogenetic relationships of those species, it has been possible to recreate the calls of evolutionary ancestors.

In a remarkable study on Central American túngara frogs (*Physalaemus* spp.) (Ryan & Rand, 1995), phylogenetic methods were used to reconstruct the evolutionary history of mating calls (Figure 12.4). Male frogs in this species group produce a whine to attract females. Each species has a variant on this call, and it has been assumed from this species variation that the whine was also important in species recognition. A female needs to recognize males of her own species as potential mates; otherwise she is in danger of wasting her efforts with a male from the wrong species.

Once researchers had reconstructed the ancestor calls, they synthesized the calls on a computer and played them back to females of living species in mate-choice experiments. The researchers wanted to test how female responses to male calls had changed over evolutionary time.

Females responded to both the calls of conspecific males and those of males from their immediate evolutionary ancestors. This showed that female preferences were not especially tuned to the specific call of males from their own species. Female responses did drop off, however, as evolutionary ancestors became older; the longer females had been separated from ancestors, the longer their preferences have had time to change.

The study indicated in a novel way that changes in male calls were generally accompanied by shifts in female preferences. The match was not perfect, and this was interesting. It revealed that female responses were not the driving force behind changes in the structure of male calls, as would be expected if the differences in male whines among species today were the product of the need for accurate species recognition by females. Rather, shifts in the structure
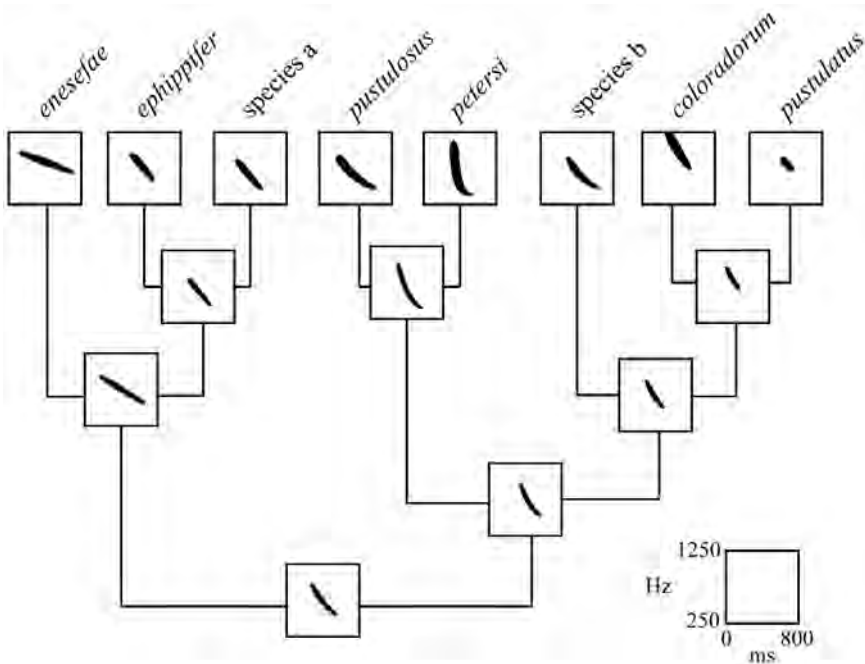
Figure 12.4. Ancestor reconstructions of the mating call of male túngara frogs of the genus Physalaemus. Shown are the sonograms of calls; those reconstructed at phylogenetic nodes were synthesized by researchers and played back to females of living species. (This figure is reprinted from Ryan and Rand, 1995, by permission of the American Association for the Advancement of Science.)

of the male whine were either generated from random mutation, or ***genetic drift***, or in response to some selection pressure other than female preference (e.g., properties of the acoustic environment, male competition, or predation). The fact that female preferences did generally track the evolution of male calls showed that the ***coevolution*** of male calls and female preferences has still been an important aspect of how communication has evolved in the group but just that female preference has not been the engine of change in male calls.

Follow-up studies have since shown this coevolution between signal and receiver extends beyond the whine component of the mating call. It includes the elaboration of this call with a series of chucks added to the end of the call. Not all species add these chucks, but the more complex call that it creates is strongly preferred by females over just the whine by itself. Early reports using phylogenetic reconstructions suggested that the preference for chucks pre-dated the evolution of the chuck (Ryan & Rand, 1993), perhaps because of

a latent sensory bias for complex acoustic stimuli rather than a specific preference for the chucks themselves. This was an exciting prospect because it suggested that sensory biases in receivers could have had an important influence on the evolution of the chuck component in the mating call. There has since been a reexamination of this sensory bias hypothesis using a more detailed phylogeny and broader species survey of female responses to calls that included chucks (Ron, 2008). This later study found no evidence for females preferring calls with chucks before the chuck evolved. Instead, the chuck produced by males and the preference for it in females had coevolved in a similar manner as the whine component of the call (Ryan & Rand, 1995).

This provides an important cautionary note: methods used to extrapolate the evolutionary history of behavior are dependent on the data available at the time the analysis is done. If these data are updated, for example if new information comes to light, conclusions can and should be revised. This should always be kept in mind when considering evidence from fossils or phylogenetic comparative studies.

The Origin of Caterpillar Communication

While Charles Darwin is best known for his ideas on evolution outlined in what are now classic works such as *The Origin of Species* (1859), he was also interested in the origin of social communication. In his book *The Expression of the Emotions in Man and the Animals* (1872) he pondered how some forms of communication might have originally evolved from the grunts of physical exertions or posturings that occurred during aggressive contests among animals. Early ethologists like Niko Tinbergen (1952) and Konrad Lorenz (1966) explored this idea further and postulated that activities not initially associated with communication become social signals through a process of ritualization. For example, the aggressive head-bob displays of territorial lizards might have initially evolved from moving the head up and down to aid depth perception and help gauge the distance of territory intruders before launching an attack. Behaviors like head-bobs that provide cues on an animal's intentions were hypothesized to evolve into social signals through a process in which the behavior becomes simplified and exaggerated in structure and then repeated in a stereotyped sequence. Testing whether this process of **ritualization** explains the evolution of communication has proven difficult. It requires that the initial precursors of a communicative behavior still be in existence today alongside the very signals they are believed to have evolved into. Opportunities to study ritualization are therefore quite limited.

One of the best examples is the territorial vibration signal of caterpillars (Scott et al., 2010). Many caterpillars build shelters out of silk and leaves.

Individuals defend these shelters against interlopers that have either lost or failed to build shelters of their own. In some species, individuals advertise ownership of a leaf shelter using complex vibration signals. The signals consist of an elaborate sequence of leaf scraping using a specialized hardened "oar" on the abdomen and rapid drumming of the mandibles against the leaf surface (Scott et al., 2010). On closer examination, researchers found the abdomen-scraping part of the signal had the same sequence of movements as the crawling cycle of the caterpillar along the leaf. This suggested this part of the signal was derived from crawling behavior.

Researchers then looked at caterpillar species that did not perform vibration signals (Scott et al., 2010). In these nonsignaling caterpillar species, shelter owners are on alert for the vibrations of a potential intruder crawling along the branch. When detected, shelter owners start whipping violently backwards and forwards across the leaf in an attempt to knock the intruder off the leaf. The intruder can feel the vibrations of this flaying behavior and sometimes retreat before reaching the shelter. In many cases, this does not happen, and shelter owners must fight it out with the intruder. (In signaling caterpillars, individuals almost never came to blows, and disputes were resolved through the exchange of vibration signals.) Through careful analysis of the vibrations of the flaying behavior and the vibrations produced by territorial signaling, the researchers found the stylized mandible drumming of the leaf surface in the signal had striking similarities with the flaying defensive behavior.

Through phylogenetic reconstructions and detail species comparisons, it became apparent there had been a progressive ritualization of the crawling and flaying behavior over evolutionary time to produce the synchronized vibrations used by signaling species today. Signal movements were repeated in long bouts, highly stereotyped, and far simpler and more exaggerated in structure than the sporadic movements associated with crawling and flaying defensive behavior (Figure 12.5). This met all the requirements of a ritualized behavior: simplification, exaggeration, repetition, and stereotypy.

There are other possible examples of the ritualization of noncommunicative behaviors into social signals, such as the foot-drumming displays of some mammals, but formal tests are few and difficult to perform. The study of caterpillar communication represents a particularly elegant and rare confirmation of the ritualized origins of a complex communication behavior.

THE DETECTIVE WORK OF EVOLUTIONARY HISTORY

A common theme in evolutionary research is the integration of multiple methods from a range of different disciplines. This integrative study is a general attribute of animal behavior research, but it is especially conspicuous in
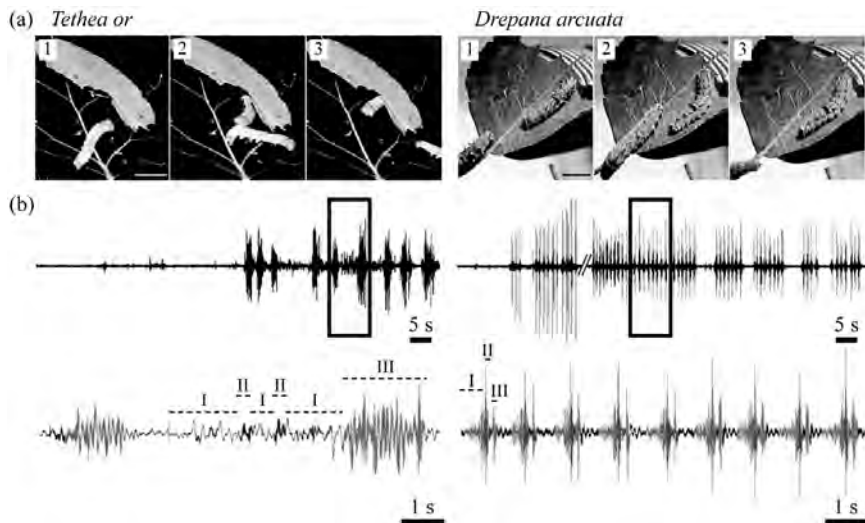
Figure 12.5.   Shown in the upper panel (a) are video frames showing an encounter between a shelter owner and an intruder. On the left is a species that does not use territorial vibration signals, Tethea or, while on the right is a species that uses vibration signals, Drepana arcuata. In the lower panel (b), traces from a laser vibrometer show the vibrations produced by the flaying defensive behavior of the nonsignalling species on the left and the vibrations of the territorial signal from the signaling species on the right. The boxes show areas of the trace that are enlarged to show roman numerals corresponding to components that researchers found to be modified into the ritualized signal. (This figure is reprinted from Scott et al., 2010.)

evolutionary studies of behavior. This is because we are unable to observe the behavior of prehistoric animals directly, so we must infer it by combining various sources of evidence. This evidence comes in a variety of forms. The examples discussed in this chapter used information on morphological characteristics, the histology of bones, allometry, stable isotope signatures, the study of living animals, and statistical analyses that reconstructed changes in behavior into a phylogeny.

With careful consideration of the data that are available, it is possible to study the prehistory of behavior indirectly. Evolution on a smaller scale can also be studied using breeding experiments to identify the genes that regulate behavior and how they are inherited from one generation to the next. Other studies adopt the comparative approach among closely related species to investigate correlated evolutionary changes in behavior with the environment. For example, in the scent-applying squirrels, the hypothesis was that predation by rattlesnakes led to the evolution of squirrels anointing themselves with

scent from shed rattlesnake skins. Another way the researchers examined this hypothesis was by testing whether there was a correlation between squirrel species that applied scent and geographic overlap with rattlesnakes. That is, squirrels that overlapped with rattlesnake ranges should apply scent, while squirrels that did not overlap with rattlesnakes, and therefore did not suffer rattlesnake predation, should not apply scent (given the opportunity when researchers artificially placed shed skins out in the environment for squirrels to inspect). A strong correlation was found and provided yet another piece of evidence that anointing behavior in squirrels was an adaptation to predation (Clucas et al., 2010).

To conclude, the imprint of evolutionary history is apparent in all types of behavior to a lesser or greater degree. By placing animal behavior in a historical context—whether it is through the study of fossils or comparisons among living species—scientists can understand the origin of behavior and in turn better interpret its present-day function (e.g., predator-scent application by squirrels or the role of frog calls in species recognition). This chapter has only briefly touched on the ways in which scientists have studied the evolution of animal behavior. More detailed reviews can be found in Ord (2010) and Ord and Martins (2010) for those readers who would like to delve deeper into this exciting area research.

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