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Social Sounds: Vocal Learning and Development of Mammal and Bird Calls

Janette Wenrick Boughman and Cynthia F. Moss

1. Introduction

First, we hear a rustle in the shrubs, and then a bird whose call sounds like "where are you?" From a short distance away, another bird gives a slightly different call: "oh, where are you?" For simplicity, we will call these WAY calls. In answer, several small gray and white wrens fly toward the first caller, giving WAY calls that sound virtually identical to the first caller's. At the same time, a small flock flies toward the second caller, giving their own WAY calls. A skirmish follows, with much calling on either side. Careful listening picks up distinct WAY calls throughout and another staccato call, which turns out to be a duet. When the dust settles, the small flocks move off in different directions, territory boundaries apparently stable for the day.

The birds are stripe-backed wrens, and this species lives in stable groups composed of a dominant pair and their offspring, who cooperate to care for the pair's brood (Rabenold 1984). Group mates also cooperate to defend their joint territory. The dominant pair advertises boundaries by singing duets, but when a neighbor intrudes, WAY calls provide a means of identifying group mates. All males in a group share a repertoire of about 12 WAY calls that they use both to maintain contact among the group and to identify themselves in territory disputes. Female group members have their own shared repertoire of WAY calls (Price 1998a). WAY calls indicate group membership—a kind of badge to indicate "I belong to this group." All stripe-backed wrens live in social groups, so belonging to a group is critical. But, how do group members come to share calls? Most group mates are closely related, so call similarity based on genetic similarity is one possibility. Yet, calls are passed down along sex-specific lines, and a genetic mechanism for this is difficult to envision. Instead, it seems that calls are learned—sons copy their fathers and daughters copy their mothers, and do so with remarkable precision. Like a surname passed on from father to son, or mother to daughter (Price 1998a), calls convey family identity (Price 1999). The patterns observed suggest that call sharing is essential to call function. Although most males in a group are closely related, occasionally

juvenile males immigrate (Piper et al. 1995) and then learn their new group's call repertoire (Price 1998b). For the occasional immigrants to be able to match the calls of a new social group, call repertoires cannot be hardwired. Learning vocalizations allows both the incorporation of unrelated individuals into groups (which is a way for pairs to increase group size) and sex-specific transmission of calls.

1.1. Detecting Vocal Learning—What Constitutes Good Evidence?

Vocal learning has a fairly clear function in the example above, yet what exactly is vocal learning? Vocal learning refers to changes in vocalizations influenced by social interaction. Here, we focus on vocalizations given by species that live in social groups and organize our discussion around the function these vocalizations serve. This functional focus rests on the premise that vocal learning has evolved to facilitate the social function of some calls. Learning is likely to occur for a specific subset of the vocalizations in a species' repertoire whose function is enhanced by the degree of acoustic similarity to social partners who may or may not be related (e.g., members of a social group, territorial neighbors, competitors, and kin). We discuss the evidence for learning of calls that serve a variety of functions, including affiliative vocalizations, contact calls, food vocalizations, vocalizations used in defending a group or individual territory, and vocalizations that convey individual or group identity. We present evidence for several families of birds and mammals. The taxonomic distribution of various forms of vocal learning supports the hypothesis that it has evolved independently in several taxa. Our review is intended to help develop hypotheses about the social and ecological factors that favor its evolution and to stimulate additional research to test the hypotheses we present.

We distinguish two types of vocal learning: *learned acquisition* and *social modification*. These may differ in the learning process involved, and each type may be the outcome of different forms of selection and rely on different neural mechanisms. However, both are true vocal learning.

Learned acquisition is the adding of new vocalizations to an individual's repertoire. Acquisition is frequently, but not always, age-dependent, and changes are influenced by social interactions. Typically, juveniles require auditory experience to produce adult-form vocalizations. Social interactions are often essential and can be important in identifying who serves as the tutor in this developmental process. Subtle forms of interaction can reinforce the acquisition and retention of specific vocalizations during development (e.g., West and King 1988). The production of abnormal vocalizations in acoustically or socially isolated individuals has long been considered strong evidence for vocal learning. In contrast, vocalizations that are produced normally by deafened, or acoustically or socially isolated individuals are good evidence against learned acquisition. They do not;

however, preclude social modification (see below). Learned acquisition is not restricted to the juvenile phase in all species; adults can acquire new vocalizations, and this acquisition is often guided by social partners (e.g., Slater 1989). This category of vocal learning includes age-dependent learning (Payne and Payne 1997) and selective attrition (Nelson and Marler 1994; Nelson et al. 1996).

Song learning in oscine passerines is an excellent and well-studied example of learned acquisition. We elect not to describe this process here because there are a number of excellent recent reviews (e.g., Catchpole and Slater 1995; Kroodsma and Miller 1996). We refer the reader to these. Instead, our review focuses on call learning in oscines and on less well-studied groups.

Social modification occurs when existing vocalizations are altered in response to social interactions. Frequently, although not necessarily, this results in increased acoustic similarity between the social partners' and target individuals' vocalizations. Occasionally, vocalizations can become more distinct, which may facilitate identification of individuals (Janik and Slater 1997; Janik 1999). In many species, social modification is not restricted to a particular developmental stage. Vocalizations that are acquired developmentally can be subject to later social modification. But even vocalizations that do not require auditory experience for normal production can be socially modified. This category of vocal learning includes social-dependent learning (Payne and Payne 1997).

Changing frequency characteristics of vocalizations through learning may require more complex perceptual and motor mechanisms than changing temporal characteristics. We discuss both frequency and temporal changes because we consider both to be interesting for understanding vocal development. Other authors have limited their definition of vocal learning to frequency changes or learned production (e.g., Janik and Slater 1997, 2000). We elect not to restrict ourselves in this way because we do not think this is the most critical distinction, although we do differentiate frequency from temporal changes in our discussion of evidence for vocal learning, and data on frequency changes are more abundant.

Here, we focus on behavioral and acoustic data. Data on the biophysics of vocal production are reviewed by Fitch and Hauser (Chapter 3), data on ecological constraints are discussed by Bass and Clark (Chapter 2), and data on neural mechanisms underlying call detection are reviewed by Gentner and Margoliash (Chapter 7).

1.2. What Does Vocal Learning Teach us about Acoustic Communication?

Vocal learning involves modification of acoustic signals produced in a social context and requires the coordinated operation of both perceptual and motor systems. For vocal learning to take place, two things must happen.

An animal's perceptual system must support discrimination among conspecific acoustic signals, and its vocal system must support flexible signal production. A well-developed perceptual system that operates independently from a flexible vocal-production system is insufficient. A flexible vocal system that is not guided by socially relevant acoustic input is also inadequate. There must be an audio–vocal interface that allows for adjustments in signal production with changing acoustic input. Without this neural interface, there is no way for acoustic input to influence subsequent vocal production.

Feedback between the study of call function and vocal learning can be productive. Knowing call function can help to focus research on those vocalizations that are likely to be learned. For example, when acoustic similarity among group members facilitates recognition and individuals are not closely related, vocal learning is likely. Similarly, studying the structural features influenced by the social environment can reveal additional subtleties of call function and where vocal flexibility is adaptive. In addition, the extent of modification through vocal learning—whether learned acquisition or social modification is involved—gives us insight into the direct forces that shape vocalizations and points to the perceptual, motor, and neural mechanisms necessary for such vocal flexibility.

Learned vocalizations are by no means the only interesting ones. Study of acoustic structure and usage of genetically determined vocalizations can give great insight into many aspects of a species' social behavior and cognition. Vocal learning is but one way to achieve communicative complexity. Contrasting learned with hardwired vocalizations can tell us much about the conditions favoring cultural inheritance and those favoring genetic inheritance.

1.3. Testing the Vocal Learning Hypothesis

Observational data can provide evidence in support of vocal learning, but only carefully controlled experiments can unambiguously demonstrate it, and experiments are necessary to identify mechanisms and rule out alternative explanations. Important baseline observational data should include descriptions of normal ontogenetic changes in vocalizations and the social contexts in which they occur (e.g., Moss et al. 1997). When ontogenetic change is absent, learned acquisition is unlikely. In addition, interpreting results from many experimental manipulations requires data on normal vocal development. Acoustic data accompanied by data on morphological development are especially valuable, because they facilitate exploration of how morphological changes affect acoustic structure (e.g., Jones et al. 1991). Comparisons of acoustic structure among individuals, territorial neighbors, social groups, and geographic regions help to characterize call function and reveal when call similarity is favored. When individuals copy neighbors or other social partners, both microgeographic and macrogeographic patterns

can emerge. Thus, the occurrence of call sharing at any of these scales implicates vocal learning. However, alternative mechanisms can cause similar patterns (see below), necessitating experimental tests to demonstrate unequivocally that vocal learning does occur. Without this experimental proof, vocal learning can only be conjectured.

A number of experimental protocols have been used to test for both forms of vocal learning and to identify the mechanisms involved. Perhaps the most common and most convincing for learned acquisition are acoustic isolation experiments and deafening (e.g., Winter et al. 1973; Heaton and Brauth 1999). Social isolation experiments provide evidence of when social interaction is essential to normal call acquisition (e.g., Hughes et al. 1998). Many experiments on song learning provide either recorded or live call tutors and then quantify the extent of acoustic similarity between tutor and pupil, which can test either learned acquisition or social modification, depending on the call repertoire at the start of the experimental manipulation (see Kroodsma and Miller 1996); unfortunately, this protocol has seldom been used to study call learning. Data from experiments where pupils copied call tutors who produced aberrant calls (including humans) clearly demonstrate the power of social interactions (e.g., Brittan-Powell et al. 1997). An important experimental protocol to test social modification is to alter the social environment (i.e., create new social groups) and quantify acoustic changes. When convergence or divergence occur in novel social groups, social modification is strongly supported (e.g., Farabaugh et al. 1994; Boughman 1998).

In all of these observational and experimental studies, careful characterization of vocalizations is required to ensure that the acoustic parameters measured capture the relevant variation. Determining the appropriate measurements to make can be complex. Ideally, prior experiments have identified the acoustic features that the animals use to discriminate among individuals, groups, or dialects.

1.4. What Alternative Mechanisms Can Produce Patterns Similar to those Found in Learned Vocalizations?

Alternative mechanisms such as maturation of the vocal tract, body size, genetics, and local ecology can affect the structure and development of vocalizations and can produce patterns similar to those found for learned vocalizations, although these mechanisms do not involve vocal learning. Thus, these mechanisms need to be ruled out when tests of vocal learning are being done.

As animals mature, vocal tract morphology changes and motor control improves. These maturational changes can result in subtle to striking changes in vocalizations (e.g., Scherrer and Wilkinson 1993). However, these changes have a purely biophysical basis and are not influenced by social interactions and thus are not due to vocal learning. Age-related changes in vocalizations can provide substantial information to listeners

about the caller's age and thus may have important functions, even though learning is not involved.

Body size is an important determinant of vocalization frequency in a number of taxa (e.g., Hauser 1993; Fitch and Hauser, Chapter 3). Individuals of similar body size often produce vocalizations of similar frequency; individuals of different size produce vocalizations that differ in frequency. Larger individuals typically produce lower-frequency vocalizations. The effects of body size on call frequency can profoundly influence consequent function of vocalizations and can contribute to individual distinctiveness and to signature function. Size dimorphism can be part of the basis for sex differences in vocalization frequency (e.g., Gouzoules and Gouzoules 1989b, 1990). Combined with maturational effects, body size can contribute to age-specific patterns in vocalizations (Gouzoules and Gouzoules 1995). Dialects can occur as a consequence of populations differing in body size because of adaptation to local environments or genetic differences (Barclay et al. 1999). These differences might be very important for identifying individuals, for classifying social partners and opponents, and even for deciding who to mate with, but vocal learning through social interaction need not be involved. Body size can have large effects on individual fitness; thus, finding that calls indicate body size is an important discovery, even when calls are not learned.

Social groups are often organized along kinship lines. Genetic variation among social groups can generate parallel variation in vocalization characteristics, facilitating recognition of kin (e.g., Rendall et al. 1996). Kin recognition based on vocalizations may function importantly in many aspects of social behavior. However, vocal learning is not necessary to produce these patterns and may even be costly. Learning can introduce copy errors that can decrease similarity among kin. Additional error can result if the individuals who serve as the tutors are unknowingly unrelated. Vocalizations open to learning might be more easily copied by nonkin who usurp a group's resources through their cheating. Selection against cheaters can favor vocalizations that directly reflect underlying genetics—a type of relatedness marker that is uncheatable. Therefore, when groups consist of relatives, genetic explanations need to be carefully considered and tested before vocal learning can be inferred. This is especially true when there is no previous experimental evidence demonstrating that the species under consideration learns vocalizations. In these situations, vocal learning might be a viable hypothesis, but we cannot be sure it occurs without direct experiments that control for the influence of relatedness. Even when vocalizations are not learned, finding that individuals use heritable vocalizations to recognize kin would be extremely important (e.g., Grafen 1990; Medvin et al. 1992).

Dialects can also result from processes that do not involve vocal learning. For instance, species distributions can be disjunct because of geographic barriers that reduce matings between populations, creating population substructure. Sustained isolation can give rise to sufficient genetic differentia-

tion to produce vocalizations that differ systematically among populations. This can be independent of any possible advantages to vocal variation and need not involve vocal learning. In this case, morphological and behavioral traits will also reflect population substructure. This expectation provides one way to test the influence of population substructure on vocal differences. Finding vocal variation without concomitant variation in other traits would refute the population substructure hypothesis.

The same kinds of dialect patterns can result from local adaptation, which can also result in genetic variation among populations. Where population substructure can result from genetic drift generating random differences between isolated populations, the local adaptation hypothesis argues that the action of divergent selection is important. Populations that inhabit areas differing in physical features may produce vocalizations whose characteristics allow for efficient transmission in their respective habitat (Slobidchikoff and Coast 1980; Rydell 1993; Barclay et al. 1999; Bass and Clark, Chapter 2; Ryan and Kime, Chapter 5). Characteristics can include frequency shifts, changes in the proportion of tonal, trilled, and noisy elements, and temporal pattern (Wiley and Richards 1982). In captive studies, the physical characteristics of housing facilities can influence frequency and temporal characteristics of vocalizations. Individuals or groups housed in different facilities can produce vocalizations that differ systematically, whereas those housed in similar facilities can sound similar, independent of actual vocal learning. Changes in housing can induce changes in vocalizations, again independent of social influences and vocal learning. Predation can also exert selection on signal structure by selecting for vocalizations that are hard for predators to detect, localize, or recognize. Consequently, vocalizations can vary among areas that vary in predation risk or predator identity.

To unequivocally demonstrate vocal learning, the alternative mechanisms described above must be ruled out. When a species' biology implicates one or more as possible explanations for observed patterns, observational studies are not conclusive. Descriptions of dialects are especially vulnerable to this. Demonstrating that vocal learning produces the patterns observed is especially challenging in animal systems where experimental manipulations are difficult and direct observations of behavioral interactions and context are not possible. However, we suggest possible approaches and point out those that have been successfully used. Experiments are necessary, and these should be carefully designed to control or directly test the likely alternatives. Determining which of these alternatives is involved is difficult because they can predict the same kinds of patterns—in many cases only the process differs.

In the next sections we begin by describing vocal learning in the context of individual signatures, group signatures, and dialects. We specifically focus on expected patterns of vocal variation at each of these levels and with respect to call function to highlight potential sources of selection

that may favor vocal learning. We follow with case studies of birds and mammals. These in-depth case studies are mostly in the bird groups oscines, psittacines, and trochilids and in the mammalian groups chiropterans, cetaceans, and primates because that is where research has focused or evidence suggests vocal learning may occur. We recognize that different sources of selection may favor vocal learning at each level and so divide the following sections into three functional levels: individual signatures, group signatures, and dialects. However, in some taxa, data at multiple levels indicate that vocal learning occurs. In these cases, it may be difficult to determine where the primary function for vocal learning resides. For instance, dialects may be a by-product of vocal learning that has evolved to serve a function on a smaller scale. We include studies at the level we believe is most important or where the system has been best studied, and we also describe evidence at other levels.

2. Individual Signatures

Individually distinctive vocalizations have been described in many birds and mammals. In fact, individual distinctiveness is ubiquitous and has been found in almost every taxon in which it has been explored. Individual distinctiveness is enhanced when differences between individuals are large and variation within individuals is minimal, so that each individual produces a consistently unique vocalization. Distinctly different call types are the most noticeable individually distinctive vocalizations (e.g., whistle signatures in bottlenose dolphins, *Tursiops truncatus*; Caldwell and Caldwell 1965). However, large differences are not essential; even subtle acoustic differences can generate sufficiently distinctive voices for individual identification in some species (e.g., Weary and Krebs 1992). This is especially true when individuals differ on several acoustic dimensions, but subtle differences on a single acoustic dimension can be sufficient for individual identification. Nor does variation within individuals necessarily obliterate distinctive voice characteristics. Differences in several acoustic dimensions are more likely in complex, frequency-modulated, or noisy calls, whereas tonal calls may differ in a single acoustic dimension.

   Individual distinctiveness is necessary but insufficient for vocalizations to function as individual signatures. Conspecifics must be able to use vocalizations to discriminate between individuals. This is a more demanding criterion. Although many taxa have individually distinctive calls, far fewer cases of individual signatures have been demonstrated, in part because recognition is difficult to test. Yet, individual signatures are defined both by their structure and their function. Individual signatures need not be learned to serve their function. Individual distinctiveness can arise in two ways: by *designed individual signatures* or *by-product distinctiveness*. Only designed individual signatures are likely to rely on learning.

Vocalizations can be specifically designed by learning or by natural selection to enhance individual distinctiveness and facilitate individual recognition. These *designed individual signatures* appear to be relatively rare. They include the cases where individuals produce distinct call types. The more common mechanism is for individual distinctiveness to arise as a by-product of individual variation in vocal tract morphology and body size. Such variation has a purely biophysical basis and appears to be sufficient in many cases to generate a large number of unique signatures or distinct voices. Such *by-product distinctiveness* can serve the signature function quite well, although it is unlikely to involve learned acquisition. Individual distinctiveness is a simple consequence of morphological variation that may have other functions when by-product distinctiveness is involved. In contrast, selection must directly favor individual distinctiveness, or learning must occur specifically to enhance it to produce designed signatures. Designed individual signatures are likely to be found primarily when by-product distinctiveness is insufficient or unreliable. Even taxa that have repertoires of call types may rely, in part, on by-product distinctiveness. For example, call types usually fall into classes so that some individuals sound roughly similar. Individuals that share call types may be differentiated on the basis of by-product distinctiveness (e.g., Weary and Krebs 1992).

Understanding how selection has shaped vocalizations to serve as individual signatures requires knowledge of the potential benefits to conveying individual identity offset against the costs that might arise. From the signalers' point of view, indicating identity could be beneficial to facilitate interactions between social partners. Good examples are isolation calls that infants give to facilitate reunions with caregivers in many species of bats (e.g., Scherrer and Wilkinson 1993). However, indicating identity might not always be favored. A signaler might also benefit from concealing identity or from imitating another individual. Vocal learning can facilitate both of these kinds of cheating, making it costly from the receivers' point of view. Vocal learning will only be favored if its benefits outweigh its costs. In developing and testing hypotheses for the evolution of vocal learning these potential costs should not be overlooked. Costs can be a powerful force shaping signal design and development (see Fitch and Hauser, Chapter 3).

Vocal learning is one mechanism to enhance differences between individuals (e.g., Janik 1999), and this mechanism operates on the time scale of individual lifetimes. However, individual signatures need not be learned, and in fact several demonstrated cases have a strong heritable component (e.g., Scherrer and Wilkinson 1993). Heritable individual signatures reflect the action of selection over evolutionary time to enhance differences between individuals. As an example, learning plays almost no role in structuring squirrel monkey calls, but individuals vary in voice (Winter et al. 1973; Symmes et al. 1979) and are likely to be recognized by their calls (Snowdon et al. 1985; Boinski and Mitchell 1997), so the calls function as individual signatures. Studies of vocalizations in several taxa have shown

significant heritabilities for multiple features of calls that serve as individual signatures, especially in bats (Jones and Ransome 1993; Scherrer and Wilkinson 1993; G.S. Wilkinson and D. Lill unpublished data). The distinctiveness in these species' calls has a strong genetic basis. Indeed, Scherrer and Wilkinson (1993) calculated that sufficient heritable variation exists in the isolation calls of evening bat pups (*Nycticeius humeralis*) for more than 1,800 pups to produce unique calls; the largest colonies consist of 1,000 bats. This is a huge amount of variation, none of which is due to learning, and these calls indicate individual identity (100% correct classification in a discriminant analysis) and relatedness (significant heritability) quite well. A strong inherited component will lead to acoustic similarity among relatives; thus, when relatives need to identify each other, heritable individual signatures should be favored.

We expect vocal learning of individual signatures to play a role in the following cases: (1) determining which call types to include in an individual's repertoire, and (2) increasing distinctiveness of voices among a specific set of individuals (for instance, a social group, set of relatives, or territorial neighbors) to allow for greater precision in individual identification within that group. In both cases, mechanisms to detect cheaters should be built in. Determining which call types to produce, especially when the calls are designed signatures, is likely to rely on learned acquisition. In contrast, social modification is likely to be the predominant form of vocal learning for increasing distinctiveness of individual voices. Group mates provide a benchmark against which to gauge distinctiveness. Learned acquisition is unlikely here because group mates are the most likely models, and copying call types from them makes it difficult to achieve the desired outcome of sounding different from social partners.

Although the specific function of repertoires is not clearly known for many taxa, learning repertoires may provide different benefits than learning a single, variable call type and may rely on different neural and behavioral mechanisms. The form of selection that has molded designed signatures is also likely to differ from that underlying individual voices arising from by-product distinctiveness. Identifying the selective factors that generate these different vocal systems promises to be a difficult but exciting area of research.

In the case studies described below, we begin by describing the social biology and the context in which calls are produced and identification of individuals favored for each species. We present information on call patterns to demonstrate that calls are individually distinctive and are used by conspecifics in identification. We follow with a discussion of the evidence that vocal learning produces individual signatures and conclude with a consideration of alternative mechanisms. Little information is available on the process of vocal learning for individual signatures, but we include it where we can. In addition to these case studies, we briefly review other taxa where vocal learning has been studied for calls that are individually distinctive (Tables 4.1 and 4.2).

TABLE 4.1. Selected bird species for which vocal learning of calls has been studied.

Bird group	Species	Social structure	Call	Function	Genetics and relatedness	Vocal learning evidence	LA SM*	Alternative explanations	Exp‡	References
Oscines	*Campylorhynchus nuchalis* (stripe-backed wren)	stable family groups that defend long-term territories	family- and sex-specific call repertoires	maintain contact among group mates; territorial defense; identify group members	primarily related males; females disperse from neighboring territories; some males disperse to neighboring territories	all males share sex-specific repertoire; females share sex-specific repertoire; unrelated juvenile males learn new groups' repertoire	U	repertoires reflect patrilineal or matrilineal kinship; therefore, genetics could contribute	N	Price 1998a, 1998b, 1999
	Cacicus cela vitellinus (yellow-rumped caciques)		colony-specific songs	unknown	unknown	shared song types among males in colony; differences between colonies; distance effect	U		N	Feekes 1977, 1982; Trainer 1987, 1988, 1989

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Group	Species	Social structure	Call	Function	Who learns	Vocal characteristics	Type*	Notes	‡	References
	Gymnorhina tibicen (Australian magpie)	social groups	duets; communal chorus; carol	territorial defense; within-group cohesion	unknown	song sharing within group; sex differences; individual differences; mimicry of human whistles	SM		N	Brown et al. 1988; Farabaugh et al. 1988; Brown and Farabaugh 1991; Farabaugh et al. 1992b
	Taeniopygia guttata (zebra finch)	breeding colony and pairs	distance call	maintain contact with pair mate	fathers and sons; unknown for pairs	individual differences; sex differences; no dialects; sons copy fathers or other adults	LA		Y	Zann 1984, 1985, 1990
Phasianids	*Colinus virginianus* (bobwhite quail)	family groups	hoypoo call	contact calls	family groups	coveys of unrelated birds differ in hoypoo calls; dialects based on temporal characters; individuals differ in frequency	SM	coveys differ only in temporal variables	Y	Bailey 1978; Goldstein 1978; Bailey and Baker 1982; Baker and Bailey 1987

* LA = learned modification; SM = social modification; U = unknown.

‡ This column indicates whether an experiment has been conducted to test vocal learning.

TABLE 4.2. Selected mammalian taxa for which vocal learning has been studied.

Mammal group	Species	Social structure	Call	Function	Genetics and relatedness	Vocal learning evidence	LA SM*	Alternative explanations	Exp‡	References
	Individual signatures									
Bat	*Rhinolophus ferremuquinem* (horseshoe bat)	maternity colony; mother–pup	CF echolocation pulse	navigation	mother–offspring	age changes in mother's resting frequency mirrored by pups; heritability greater than 1 suggests possibility of learning	SM	body size effects potentially confound analysis	N	Jones and Ransome 1993
	Nycticeius humeralis (evening bat)	maternity colony; mother–pup	pup isolation calls	facilitate reunions	mother–offspring; half sibs	none	N	strong heritable component suggests calls are genetically coded	N	Scherrer and Wilkinson 1993
	Eptesicus fuscus (big brown bat)	maternity colony; mother–pup	FM echolocation pulse	navigation	mother–offspring	calls vary by age, sex, and individual; geographic differences	U	probably genetic and maturational; geographic differences reflect different foraging strategies	N	Moss 1988; Rydell 1993; Masters et al. 1995

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Species	Social group	Signal	Function	Social context	Description		Notes		References
Myotis lucifugus (little brown bat)	maternity colony; mother–pup	FM echolocation pulse	navigation	maternity colonies; mother–offspring	colony differences	U	primarily ontogenetic changes	N	Pearl and Fenton 1996; Moss et al. 1997
Primate *Cercopithecus aethiops* (vervet monkey)	social group	alarm calls; social calls	predator warning; intergroup encounter	group mates; variable relatedness including parent–offspring and matrilineal	correct usage learned	N	no evidence for learning of acoustic structure	Y	Seyfarth and Cheney 1980, 1986
Pan troglodytes (Chimpanzee)	fission–fusion social groups	pant–hoot	contact call; recruit social partners; intergroup spacing; mating	group mates; territorial neighbors; potential mates; unknown relatedness	populations differ; call matching among chorusing partners; novel element included in one group's calls	SM ?	genetic differences between populations; calls recorded in different contexts in each population	N	Marler and Hobbett 1975; Mitani et al. 1992; Mitani and Nishida 1993; Clark and Wrangham 1999 1993; Mitani and Brandt 1994; Mitani and Gros-Louis 1995; Marshall et al. 1999

TABLE 4.2. *Continued*

Mammal group	Species	Social structure	Call	Function	Genetics and relatedness	Vocal learning evidence	LA SM*	Alternative explanations	Exp‡	References
	Individual signatures									
Rodent	*Dipodmys* spp. (kangaroo rat)	territorial neighbors; parent–offspring	foot drums (nonvocal)	territorial advertisement	unknown relatedness between neighbors; parent–offspring	greater than expected distinctiveness between neighbors	SM		N	Randall 1989a, 1989b, 1994, 1995
	Group signatures									
Cetacean	*Physeter macrocephalus* (sperm whale)	stable matrilineal groups of 10–12; temporary association with other groups and individuals	coda	not known	matrilineal	codas are specific to matrilineal groups	U	groups are not very stable; some group members are related, which could indicate that genetic similarity underlies vocal similarity	N	Whitehead et al. 1991; Weilgart and Whitehead 1993, 1997; Richard et al. 1996; Lyrholm and Gyllensten 1998; Christal et al. 1998
Primate	*Macaca nemestrina* (pigtail macaque)	social groups	screams	recruit allies in dominance interactions	matrilines within groups	screams indicate maternal lineage; learned usage suggested by increasing accuracy of contextual use with age	N	analysis to test contextual usage confounded by body size effects, which are known to affect vocalization frequency	N	Gouzoules and Gouzoules 1989a, 1989b, 1990, 1995

Dialects										
Bat	*Saccopteryx bilineata* (white-lined bat)	harems	male tonal calls	attract females; advertise and defend territory	males within a colony are likely to be related	individual differences; differences between colonies	U	relatedness of males within colonies could mean colony differences have a genetic basis	N	Davidson 1999
Primate	*Hylobates* sp. (gibbon)	territorial social groups	great call; mother–daughter chorus; female–male duet	advertise and defend territory; pair-bond maintenance	mother–daughter; mated pairs; primarily monogamous	groups respond to own group's call; daughters sing with mothers, which could indicate that practice is necessary for call development; hybrids give calls intermediate between parental species	N	intermediacy of hybrids suggests genetic basis; bulk of evidence suggests calls are not learned	N	Marshall and Marshall 1976; Chivers and Raemaekers 1980; Brockelman and Srikosamatara 1980; Deputte 1982; Brockelman and Schilling 1984; Raemaekers et al. 1984
	Microcebus murinus (grey mouse lemur)	family groups	trilled loud calls	territorial maintenance; mate attraction	males within groups related; females within group likely related	individual differences; differences between captive groups	U	individually distinctive calls of few males in a group would give appearance of dialects; males within groups related, making genetic basis likely	N	Zimmermann and Lerch 1993; Zimmermann 1995; Hafen et al. 1998

TABLE 4.2. *Continued*

Mammal group	Species	Social structure	Call	Function	Genetics and relatedness	Vocal learning evidence	LA SM*	Alternative explanations	Exp‡	References
Seals	*Dialects*									
	Leptonychotes weddelli (Weddell seals)	population	underwater calls	unknown; possibly mating	probable discrete populations	differences between geographic regions in repertoires; occurrence of "unique" call types; differences between populations in frequency characteristics of shared calls	U	genetic differences between populations could give rise to differences; incomplete sampling or repertoires makes designation of "unique" call types premature	N	Thomas and Stirling 1983; Green and Burton 1988; Thomas et al. 1988; Morrice et al. 1994
	Erignathus barbatus (bearded seal)	population	underwater calls	unknown; possibly mating	probable discrete populations	differences between geographic regions	U	genetic differences between populations could give rise to differences	N	Cleator et al. 1989
	Mirounga angustirostris (Northern elephant seal)	population	threat calls	deter rivals	breeding populations	differences between breeding colonies; individual bulls differ	U	differences between populations deteriorate over time	N	Le Boeuf and Peterson 1969; Le Boeuf and Petrinovich 1974; Shipley et al. 1981, 1986

Rodent	*Cynomys gunnisoni* (prairie dog)	population	alarm calls	predator warning	unknown	N	variation in temporal characteristics	N	divergent characteristics correlated with local habitat; possible genetic differences	Slobidchikoff and Coast 1980
Lagomorph	*Ochotona princeps* (pika)	population	alarm calls; songs	predator warning; territorial maintenance and mate attraction	unknown	N	variation among populations in duration and maximum frequency of fundamental frequency	N	no evidence of learning; geographic variation correlates with pelage and body size variation, suggesting genetic basis	Somers 1973

* LA = learned modification; SM = social modification; U = unknown.

‡ This column indicates whether an experiment has been conducted to test vocal learning.

2.1. Mammals

2.1.1. Bats—Lesser Spear-Nosed Bat Pup Isolation Calls

Lesser spear-nosed bats (*Phyllostomus discolor*) roost in hollow trees in large colonies of 50–300 bats. These colonies are composed of several smaller groups of 4–14 females and a single male. Colonies move from roost tree to roost tree as a unit and thus appear to be relatively stable, whereas the composition of groups within colonies is dynamic (C. Kagarise, J. Bradbury, and L. Emmons unpublished data). Adult females leave their infants in the roost each night when they go out foraging and must find their pup when they return. Finding their mothers has immediate fitness consequences for pups who depend on their mothers for sustenance, grooming, thermoregulation, and protection. Identifying her own pup affects adult female fitness as well. Females produce a single pup each year, so losing a pup can seriously depress reproductive success. Misdirecting maternal care is also costly because it decreases the amount of care a mother can provide her own offspring. These costs should favor a mechanism for mothers to identify offspring and for offspring to find mothers.

Like many bat species, when separated from their mothers, *P. discolor* infants give sinusoidally frequency-modulated (FM), multiharmonic calls, termed isolation calls (Fig. 4.1A). Mothers produce maternal directive calls whose frequency structure is quite similar to infant isolation calls. Isolation calls and maternal directive calls vary individually in the pattern of sinusoidal FM and duration (Esser and Schmidt 1989). Adults can discriminate modulation frequencies that differ by as little as 2 or 3 Hz, more than sufficient to discriminate individuals whose modulation frequencies differ by as much as 49–100 Hz (Esser and Lud 1997). Infants appear to recognize the directive call of their own mother (Schubert and Esser 1997), and mothers respond to their own pup's calls. Reciprocal calling facilitates reunions between pups and their mothers when pups fall or fly from the roost site or when mothers return from foraging (Gould 1983). We focus here on data concerning vocal learning of pup isolation and maternal directive calls.

Research on vocal learning in *P. discolor* includes observational information on normal development (Esser and Schmidt 1989), descriptive work on geographic variation (Esser and Schubert 1998), and experimental tests of social modification (Esser 1994). In addition, psychophysical work has described auditory thresholds in infants (Esser and Schmidt 1990) and adults (Esser and Daucher 1996), and detection of frequency modulation (Esser and Kiefer 1996), which may be important for individual discrimination of these FM calls.

Newborns produce isolation calls at birth, suggesting that learned acquisition is not necessary for normal production. However, pup isolation calls do undergo progressive changes during development (Fig. 4.1A). Calls given by newborns show little FM and the pattern of sinusoidal FM increases with age. In addition, some calls given by newborns drop out of
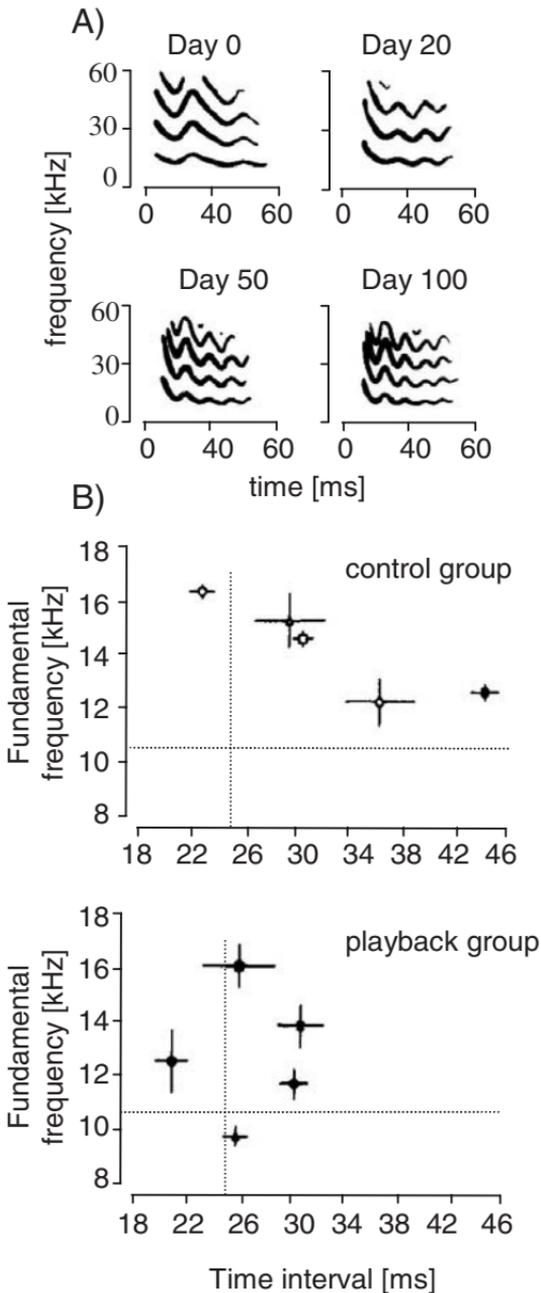
FIGURE 4.1. Lesser spear-nosed bat infant isolation calls. (**A**) Sonograms showing changes during development for one infant. (**B**) Sinusoidal frequency-modulation rate at day 50 for control and playback groups. Time interval between the first and third frequency minima on the *x*-axis, fundamental frequency on the *y*-axis. Values of maternal reference call are indicated with dotted lines. (From Esser 1994. Reprinted with permission from Lippincott, Williams & Wilkins.)

the repertoire during the first weeks of life (Esser and Schmidt 1989; Esser 1994). Esser and Schmidt (1989) suggest that a female infant's isolation calls develop into maternal directive calls. Social modification is possible, but these developmental changes could simply be due to maturation of the vocal tract and increasing motor and respiratory control.

One piece of evidence that the fine structure of vocalizations is modified by learning is the suggestion of dialects in maternal directive calls (Esser and Schubert 1998). Captive adult females from two regions show differences in carrier frequency, modulation frequency, and the number of FM peaks, which separates them into two partially overlapping multivariate clusters in a multidimensional scaling analysis. The authors present no direct data that dialects result from learning; rather, they draw parallels between their findings and dialects in oscine birds to suggest learning. They also cite the experimental evidence for social modification described below. Alternative explanations have not been ruled out. Groups from the two regions are likely to have been genetically isolated, so genetic differences could contribute to the differences described. Variation among captive groups in body size or age could also contribute to differences in the frequency measures. Testing for the influence of these factors should be straightforward and would greatly strengthen claims for learning-based dialects.

One experiment supports the importance of social modification in this species' vocalizations (Esser 1994). Four individually housed, hand-reared bats were presented with one maternal directive call as a reference vocalization, and changes in the isolation calls of these pups over the first 100 days of life were monitored. The playback group was compared with a control group of hand-reared pups that heard no maternal directive calls (Fig. 4.1B). Both groups increased the amount of sinusoidal FM in their calls during development; however, the playback group showed a larger amount of FM at 100 days, coming close to the value of the maternal directive call. The rate of sinusoidal FM in the playback group's calls showed some convergence with the maternal directive call as compared with the control group, although the extent of convergence was not great. No apparent convergence in fundamental frequency of the first FM peak was found. Bandwidth of both control and playback groups overlapped the distribution of the reference call (Esser 1994). The observed convergence was interpreted as evidence for vocal learning; clearly, social modification is the relevant form. For *P. discolor*, vocal learning functions to increase vocal similarity to promote mutual recognition and facilitate reunions.

There may be two opposing forces at work shaping isolation calls. Pups that sound similar to their mother may facilitate recognition and reunion. But pups that sound different from infant roost mates should also facilitate recognition. The extent of convergence on the reference call that Esser (1994) observed may have been constrained by the need for pups to distinguish themselves from other infants. This theme runs through other studies on learned individual signatures—similarity to some individuals may be favored simultaneously with increased distinction from other individuals.

2.1.2. Cetaceans—Bottlenose Dolphin Whistles

Bottlenose dolphin (*Tursiops truncatus*) social structure is characterized as fluid, meaning individuals interact with many others during their long lives. However, two types of long-term associations occur: mother–calf pairs and male coalitions (Wells et al. 1987; Smolker et al. 1992). Presumably, identifying individuals in these long-term associations is important, although little data are available to test this hypothesis. Calves are dependent on their mothers for three to five years and may remain with mothers for up to ten years, and females of reproductive age associate with other females in their matriline (Wells et al. 1987). Benefits of long-term associations vary. Female matrilines may receive aid in caring for and protecting calves against predators and may gain feeding benefits from associating with conspecifics (Hoese 1971). Males form long-term coalitions (Smolker et al. 1992; Connor and Smolker 1995) that aggressively herd and consort with females in reproductive condition (Connor et al. 1992b) and compete with other males and coalitions for access to these females. Long-term and large coalitions tend to be more successful in these competitions (Connor et al. 1992b).

Bottlenose dolphins produce a variety of social calls in addition to echolocation calls, including pulsed, tonal, and whistled sounds. The specific function of pulsed and tonal sounds has not been thoroughly investigated, but whistles have been studied in some depth. Adults produce a repertoire of three to nine FM whistles (McCowan and Reiss 1995a). Usually one of these (but up to three) is unique to an individual and is termed that individual's signature whistle (Caldwell and Caldwell 1965). Signature whistles can make up from 5% (McCowan and Reiss 1995a) to 95% (Caldwell and Caldwell 1965) of an individual's call production. The primary function of signature whistles is thought to be individual identification (Caldwell and Caldwell 1965; Caldwell et al. 1990). The combination of small, stable groups such as mother–calf pairs and male coalitions, and the fluid and repeated association of these groups with other individuals over many years is thought to favor individual identification (Janik 1999). Whistles are somewhat variable within individuals (Sayigh et al. 1990), but tend to have a greater amount of variation between individuals (P.L. Tyack unpublished data), so their structure is appropriate to serve as individual signatures. Statistical analysis can classify calls to the correct individual (Buck and Tyack 1993), and dolphins have sufficiently good discrimination abilities to differentiate among whistle variants, although no study has tested for recognition of individuals by whistles (Tyack 1997). This is a case where data on signal structure have been taken as proof of signal function. Calves who are separated from their mothers whistle as they initiate reunions (McBride and Kritzler 1951; Smolker et al. 1993). The exact function of whistling in this context is unclear. It seems doubtful that whistles facilitate reunions in a manner similar to isolation calls given by bat pups because the calf approaches the mother and mothers rarely call in response to calves. Also, calves have usually oriented to the mother prior to calling.

The signature hypothesis has been reassessed recently (Caldwell et al. 1990; McCowan and Reiss 1995a, 2001). McCowan and Reiss (1995a) argue that repertoires include many whistles shared among the members of a social group or even across social groups. These whistles are not likely to be individual signatures; rather, hypotheses suggest they may be referential (Tyack 1997) or affiliative (Smolker 1993; Tyack 1997). McCowan and Reiss (1995a) also provide data indicating that the proportion of whistles unique to an individual can be quite low. They suggest that the preponderance of signature whistles documented by some researchers is due to recording context. When restrained and isolated from others, both adults and infants produce many signature whistles (McCowan and Reiss 1995a; Janik and Slater 1998). When freely interacting with others, dolphins produce many shared whistles (McCowan and Reiss 1995a, 1995b). Thus, defining a signature as the whistle most commonly produced is problematic.

Much of the evidence for vocal learning in *Tursiops* comes from observational studies of captive animals (Tyack 1986; Reiss and McCowan 1993; McCowan and Reiss 1995a, 1995b). Observational studies of communication are being incorporated into long-term studies of two wild populations, one in Sarasota, Florida (Wells et al. 1987; Sayigh et al. 1990, 1995; Wells 1991), and the other in Shark Bay, Australia (Connor et al. 1992a; Smolker 1993; Connor and Smolker 1995, 1996). Experimental work on vocal learning is restricted primarily to eliciting specific whistles by operant conditioning (Richards et al. 1984; Reiss and McCowan 1993). Experimental work is hampered by two factors: small sample sizes due to difficulties keeping animals in captivity, and neither social and acoustic isolation nor deafening are possible due to ethical considerations or because they induce abnormal social and acoustic behavior.

Vocal development has been studied for both captive and free-living dolphins. Infant bottlenose dolphins produce whistles when they are only a few days old (Caldwell and Caldwell 1979), suggesting that auditory experience is not required for whistle production. Like adults, calves give some whistles that are unique to each individual (73% of whistle types produced during the first year), but do not retain one particular whistle as their individual signature (McCowan and Reiss 1995b). A high proportion of whistles are shared within social groups (23%), and many whistles are shared by calves in the three groups studied (17%). Certain whistle types are produced only by very young infants, and the same type is given by all infants. The proportion of this infant whistle gradually decreases and the proportion of other whistles increases as the calves age, resulting in a turnover in the repertoire. Calves continue to acquire new whistle types even as they discontinue use of earlier types. This process continues past the first year, as repertoires of 12-month-old calves differ from adults. At any one developmental stage, calves have larger repertoires than adults and by 12 months have given as many as 22–55 different types of whistles (McCowan and Reiss 1995b). This suggests that individual repertoires can

be very large. This overproduction suggests that a process of selective attrition (Nelson et al. 1996) may be involved in shaping adult repertoires of three to nine whistles. Calves' acquisition of this large number of whistle types may depend on auditory and social experience, although published data are lacking to determine the importance of either factor in the initial acquisition of whistles or the process of selecting which types to retain.

The contextual use of some whistles changes during development (McCowan and Reiss 1995b). Calves call more when separated than in socializing or other contexts until about 8 months of age. Their use of signature whistles in social contexts increases after this point. This pattern is similar for signature and shared whistle types. The function of these whistle types is uncertain, making it difficult to know whether developmental changes arise from increasing accuracy of use or from changing social relationships and behavior as calves mature.

The ontogeny of whistle repertoires and production is more difficult to study in free-living dolphins. Sayigh et al. (1990) repeatedly recorded 12 pairs of mothers and their one year or older calves during captures. Dolphins were lightly restrained in shallow water and recorded with a suction cup hydrophone attached to the melon. Within a single recording session, renditions of individual calls varied in such acoustic parameters as duration and absolute frequency even though whistle contour varied little. The most commonly produced whistle of calves (presumably their signature whistle) was stable, undergoing little systematic modification in contour over the course of their 3-year study. Slight modifications to whistle contour took place in a few individuals' calls, but for most individuals, calls did not vary more across years than within a recording session. Adult signature whistles were consistent over even longer time periods of up to 12 years. This study focused on stability of the signature whistle rather than cataloging the entire repertoire. Signature whistles were recorded almost exclusively—only 8% of calls recorded from female calves and 27% from male calves were other whistle types. This finding contradicts the finding of large repertoires (McCowan and Reiss 1995a, 1995b), perhaps because of the different recording contexts. Although McCowan and Reiss (1995a, 1995b) worked in captivity, which can itself introduce artifacts, they recorded in a variety of behavioral contexts, whereas Sayigh et al. (1990) recorded only loosely restrained dolphins during captures.

Sayigh et al. (1990) found sex differences in the apparent acoustic model used by males and females. Female calves produced signature whistles that differed from their mothers', whereas male calves were more likely to produce whistles similar to their mothers'. This sex difference was less pronounced in a later study (Sayigh et al. 1995), where many male whistles differed from their mothers'. Sayigh et al. (1990) suggested that vocal learning underlies this sex difference; however, their data cannot be used to determine directly whether learned acquisition or social modification occurred. They studied calves older than one year and found little change in whistle

contour; therefore, the processes that influenced contour development had clearly taken place before the end of the first year and the start of their study, which agrees with McCowan and Reiss (1995b). Sayigh et al. (1990) hypothesized that because females may continue to associate with their mothers for many years, distinctive signature whistles may facilitate accurate individual identification. Males disperse and thus may not face the same constraints; rather, they suggested that similar whistles may facilitate kin recognition. For this latter interpretation to be plausible, all males should have imitated their mothers, and this was not the case (Sayigh et al. 1990, 1995). The occurrence of shared whistles in captive repertoires further complicates interpreting the results of these two studies. It seems quite likely that both females and males shared some whistles with mothers and produced others that were individually distinctive. Individuals need to be recorded in a large number of sessions, preferably in multiple contexts, before one can be sure that the entire repertoire is cataloged.

Data on sharing of whistles among social companions are somewhat conflicting. Most studies suggest that infants only occasionally copy their mother, who is their primary social partner during the first few years of life (Sayigh et al. 1990, 1995; Reiss and McCowan 1993; McCowan and Reiss 1995b). Yet other studies show sharing of whistles among other types of companions (Connor and Smolker 1995; McCowan et al. 1998) and even apparent imitation of a trainer's whistle (Tyack 1997). Currently, it is unclear who serves as the primary tutor and why.

Three males in a coalition increased the similarity of their whistles as the tenure of their coalition lengthened (Fig. 4.2; Smolker 1993; Smolker and Pepper 1999). Given the information on the potential size of repertoires and the extent of shared calls, it is unclear whether males socially modified existing whistles to increase similarity, acquired novel whistle types, or increased their use of a particular whistle already in their repertoire. Because of the possibility that convergence results from changing use rather than the generation of novel whistles, Smolker and Pepper (1999) did not demonstrate vocal learning in the sense outlined by Janik and Slater (1997) (e.g., acquisition of novel calls or modulation of call frequency characteristics). However, it seems quite likely that the whistle type these males used depended on their social affiliation, which meets the criterion for vocal learning that we use. The contribution of by-product distinctiveness to variation among individuals in these shared whistles should be studied.

Dolphins have been trained operantly to match a whistle of a particular contour presented as a stimulus (Richards et al. 1984; Reiss and McCowan 1993). This requires vocal flexibility and auditory–vocal feedback to achieve matching. Such work demonstrates remarkable intrinsic cognitive and vocal abilities, but does not tell us much about the context, function, or extent of vocal flexibility in nature.

The work on dialects in dolphins has produced conflicting results. One study found evidence of geographic variation at both the microgeographic
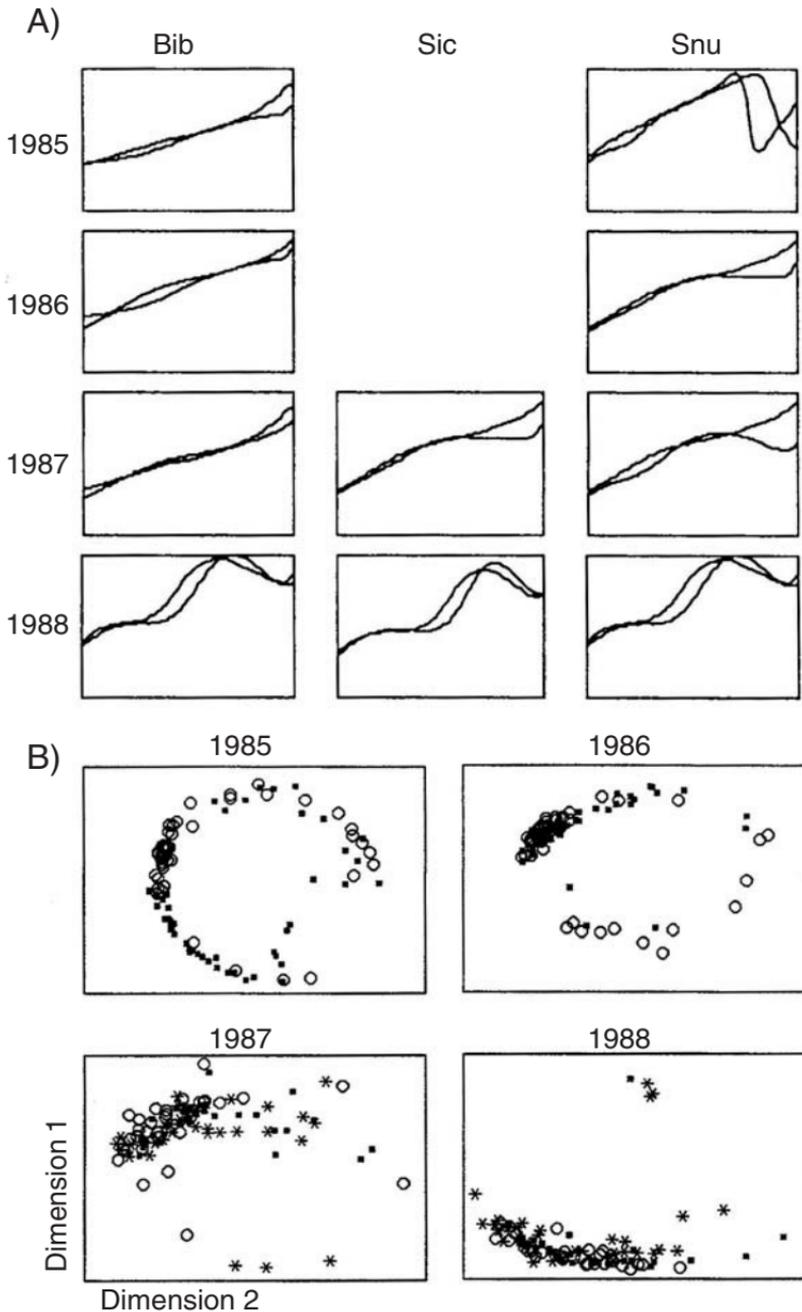
FIGURE 4.2. Whistles used by allied male bottlenose dolphins. (**A**) Average frequency contours of the two most commonly used whistles for three allied males over four years. (**B**) Multidimensional scaling of whistles for each male. Individuals noted by different symbols. Note that the scatter in multidimensional space is reduced over time, indicating acoustic convergence among individuals. (From Smolker and Pepper 1999. Reprinted with permission from Blackwell Wissenschafts-Verlag Berlin, GmgH.)

and macrogeographic scales (Ding et al. 1995). Whistles from three sub-populations in the Gulf of Mexico differed. Comparisons among populations in the Gulf of Mexico, the Gulf of California, Argentina, Japan, and Australia also indicated that these populations differed from one another. Other studies failed to find such evidence (Evans and Dreher 1962; Graycar 1976; Steiner 1981). Additional work is necessary to determine the prevalence of dialects in dolphins.

A primary factor favoring vocal learning in dolphins may be individual identification (Janik and Slater 1997; Janik 1999). In terrestrial animals, differences in vocal tract morphology and body size often result in individually distinctive vocalizations. Dolphins may not be able to rely on these by-product mechanisms because the shape of air sacs involved in whistle production is influenced by pressure, which changes when they dive. Thus, dive-induced variation may undermine the consistency of individual voice characteristics (Tyack and Sayigh 1997). Janik (1999) suggests that this constraint favored individual identification via distinctly different whistle contours. He argues that vocal learning was therefore favored—individuals could listen to social companions and develop a whistle contour that differentiated them. This idea is intriguing, but no data exist to test it directly. Some of the information described above seems consistent with this hypothesis, but the existence of shared whistles in dolphin repertoires (McCowan and Reiss 1995a, 1995b) and the occasional matching of mothers' whistles by sons (Sayigh et al. 1990, 1995) contradict it. Further work to test this hypothesis is warranted.

It is clear that dolphins can imitate other sounds and this imitation may require both forms of vocal learning—learned acquisition and social modification. What is unclear is how often they use imitation in nature, what induces them to copy a particular individual or sound, and the functions of such copying. Perhaps these questions are difficult to address because whistles from known individuals can only be recorded in limited contexts, and these contexts may not adequately elicit the full repertoire nor allow identification of who serves as tutor from the potentially large pool of individuals. More thorough sampling of free-living dolphins, although logistically difficult, would be extremely useful for clarifying the pattern of sharing among individuals in social groups, across populations, and the extent to which signature whistles are individually specific. Captive studies are likely to continue to provide important information on ontogeny, yet they cannot adequately address some important questions with respect to vocal learning because of constraints in composition of social groups, the small number of individuals in captivity, and the absence of ecological context.

2.1.3. Primates—Macaque Food and Contact Calls

The vocal behavior of several species of macaques (*Macaca* spp.) has been studied to test whether vocalizations are learned. Most macaques live in large, multimale social groups with strong dominance hierarchies among

matrilines. Matrilineal groups are genetically differentiated (Olivier et al. 1981). Females remain in their natal group, whereas males disperse. Female offspring assume the dominance rank of their mothers; members of a matriline assist one another in agonistic interactions to actively defend their dominance rank. Social groups generally avoid one another rather than actively defend territories. Aggressive encounters do occur, and females usually focus their aggression on other females when defending a clumped food source. Females sometimes act aggressively toward immigrant males, and males almost always do so (Cheney 1987).

Japanese (*M. fuscata*) and rhesus (*M. mulatta*) macaques give calls, termed "coos," in various social contexts and when encountering food (Hauser 1996). Coos can be used to recognize individuals (Hansen 1976; Masataka 1985). Studies of call structure provide conflicting results with respect to vocal learning. Green (1975) argues that social transmission has produced differences in frequency modulation of coos in three troops of Japanese macaques (*M. fuscata*). Unfortunately, he provides no analysis of acoustic features and illustrates single examples from each troop, which makes quantitative assessment of troop variation impossible. The vocal differences he describes are related to the provisioning context and are the only acoustic differences among troops noted. Individuals give some coos with the "locale-specific" features and some without. Other vocalizations do not differ among troops.

Subsequent work to investigate vocal learning has used cross-fostering among two species, the Japanese macaque, *M. fuscata*, and rhesus macaque, *M. mulatta* (Masataka and Fujita 1989; Owren et al. 1992, 1993). These studies ask whether offspring raised by heterospecifics produce coos like those of their foster mothers. Masataka and Fujita (1989) cross-fostered a single Japanese and two rhesus macaques. They describe differences in peak frequency of the fundamental frequency, but not in duration, of the two species' calls, and they claim that cross-fostered infants produce coos with frequency characteristics similar to their adoptive mothers'. They also present playback data suggesting that others respond to the cross-fostered monkeys as though they are conspecifics. These data are interpreted as providing strong evidence of vocal learning.

However, Owren et al. (1992, 1993) challenge these results. Although calls of infants raised by conspecifics are individually distinctive and differ between species, there are no statistically significant differences between calls given by adults of the two species for peak frequency or duration, nor for five other frequency variables related to fundamental frequency (Owren et al. 1992). Each species shows substantial variability and overlaps the frequency range of the other. Rather than being species-specific, adult coos differ among individuals, although classification accuracy in a discriminant analysis is low. Coos are not particularly good vocalizations to use in a cross-fostering study because there are no consistent differences between species in adult calls (Owren et al. 1992). Thus, they cannot serve as distinctive models for developing species-specific characteristics. In addition, similar-

ity between mothers and infants has not been described, and such similarity may not enhance the calls' function. If similarity is not favored, there is no reason to expect convergence between calls given by cross-fostered infants and their mothers. This lack of functional consideration may have interfered with progress in testing vocal learning in these and other primate species.

The use of cross-fostering to test vocal learning requires differences in vocalizations among species. Japanese and rhesus macaques differ in their use of several calls. Japanese infants give coos during play almost exclusively, whereas rhesus infants use coos and gruffs (Fig. 4.3). Rather than focusing on changes in acoustic structure, Owren et al. (1993) compare the proportion of coos and gruffs given by cross-fostered infants to proportions given by normally raised infants of each species. Cross-fostered Japanese infants continue to give coos almost exclusively, in proportions indistinguishable from normally raised Japanese infants. Cross-fostered rhesus infants give more coos than normally raised rhesus infants in two contexts but fewer coos than normally raised Japanese infants in two other contexts (Fig. 4.3B). Owren et al. (1993) interpret these results as very limited modification of usage. Even when interacting with others producing gruffs, cross-fostered Japanese infants almost never give these calls. Furthermore, rhesus infants give gruffs even though they almost never hear their mothers or social companions produce such calls. This result is particularly surprising because both species are capable of producing both coos and gruffs (Owren et al. 1993), so very little modification is necessary to mimic the calling behavior of social companions. New vocalizations do not need to be learned. Perhaps modification does not occur because there is no strong inducement to produce calls similar to those of social companions. Cross-fostered infants interact normally with peers, despite their unusual vocal behavior. Selection for call similarity seems to be lacking in these species and may be overridden by other social cues such as facial displays and gestures that facilitate social interactions. Thus, vocal learning may simply not be necessary.

3. Group Signatures

Group signatures are signals that indicate an individual belongs to a particular social group. They are likely to be found in species where stable social groups control access to limiting resources, such as food, mating and nesting sites, or territories. In this context, discriminating between group mates and others facilitates both cooperation within the group and exclusion of outsiders who compete for the same resources. Typically, signal structure is shared among group mates, and groups are distinct from one another, although group members can learn to recognize each others' individually distinctive calls. Groups can share call types that are distinct from the types
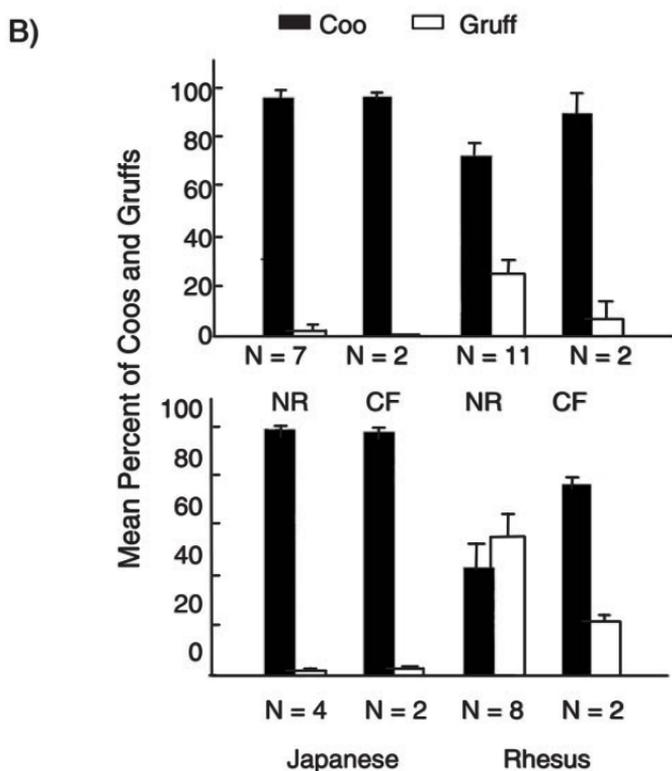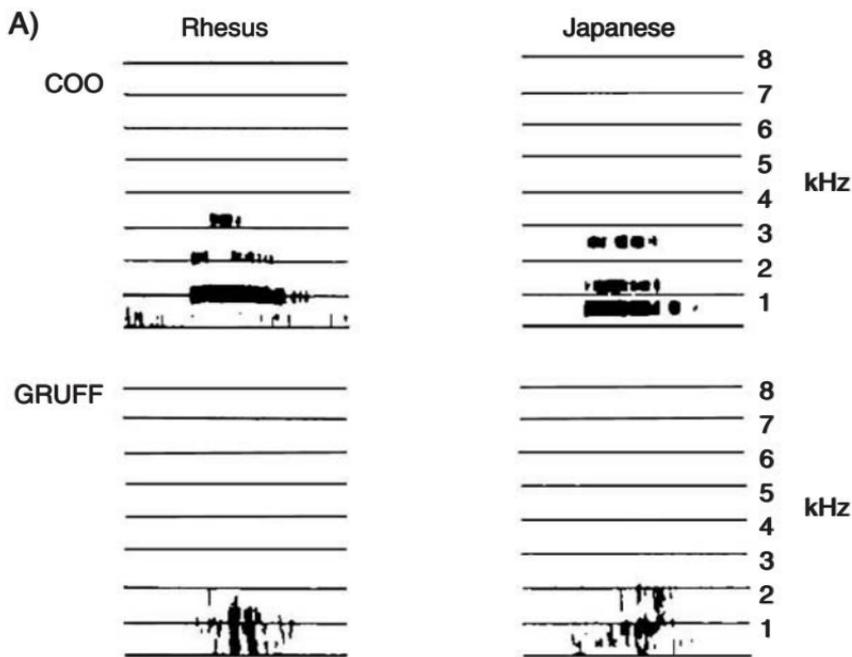
FIGURE 4.3. Coo and gruff calls for Japanese and rhesus macaques. (**A**) Sonograms of each call type for both species. (**B**) Usage by normally raised (NR) and cross-fostered (CF) juveniles during the first two years of life. (From Owren et al. 1993. Copyright © 1993 John Wiley & Sons, Inc. Reprinted with permission from Wiley-Liss, Inc., a subsidiary of John Wiley & Sons, Inc.)

of other groups (likely to involve learned acquisition), or can share more subtle acoustic features of a single call type (likely to involve social modification). As with individual signatures, to demonstrate that calls are group signatures requires demonstrating convergent call structure and recognition of group mates by call.

Using a repertoire that is partially shared with other groups is an inefficient way to convey group identity. If repertoires are shared, to unequivocally identify the group affiliation of a caller requires hearing much of the repertoire or just the few calls unique to that group. In this situation, the function of shared call types appears to be something other than group identity. That function is currently unknown.

As with individual signatures, potential benefits of indicating group identity need to be considered in conjunction with potential costs and the possibility of cheating. Imitating a group's signal can allow an outsider to gain access to group resources. Therefore, mechanisms for cheater prevention—a means of detecting imitators and preventing their access to resources—should evolve in concert with group signatures.

Group signatures need not be learned to serve their function. In species where social groups are formed of relatives, heritable signals can effectively indicate group affiliation and may also be used to determine the level of relatedness between individuals. Heritability of group signatures has not been studied directly, but studies described earlier in several taxa have shown a strong genetic basis for individual signatures (Jones and Ransome 1993; Scherrer and Wilkinson 1993). When social groups are organized along kinship lines, acoustic similarity among group mates can result from shared genetics. Thus, a pattern of convergence within groups or differences between them is insufficient to demonstrate that vocal learning occurs if group mates are close relatives.

When call similarity is favored, we expect vocal learning in two cases: when groups are composed of unrelated individuals who cannot rely on genetics to produce similarity in calls, or when group composition changes slowly over time and group members use calls to indicate group affiliation. In the latter case, the immigrants may change their vocalizations to match the new group, or the entire group may accommodate the new group composition by changing call characteristics. In both of these instances, the most relevant type of vocal learning is social modification. Learned acquisition can occur, but is unnecessary unless new call types are added to an individual's repertoire. Certainly, vocal learning can occur in groups of relatives and may increase similarity or increase distinctiveness depending on the primary function of calls. Separating the effects of heredity from those of vocal learning in such taxa is likely to be a difficult but fruitful task.

In the examples that follow, we begin by describing the species' social biology and the benefits of group living, and consider when learned group signatures are expected. Then, we describe evidence that calls are group-distinctive and present data on call function. We conclude each example by discussing the evidence for vocal learning and discuss alternative hypo-

theses where appropriate. We also describe evidence of the vocal learning process when that information is available. We briefly describe vocal learning of group signatures in taxa not covered in case studies in Tables 4.1 (birds) and 4.2 (mammals).

3.1. Birds

3.1.1. Oscines—Chickadee Flock Signatures

Black-capped chickadees (*Parus atricapillus*) associate in small, fairly stable flocks of four to eight birds during nonbreeding months. Breeding pairs form within these flocks and defend breeding territories (Ficken et al. 1981). Flocks defend shared feeding territories. The composition of flocks is relatively stable throughout each year, but changes from one year to the next due to adult mortality and recruitment of dispersing juveniles (Weise and Meyer 1979; Nowicki 1989). Flock mates are probably not closely related to one another, but the degree of relatedness is unknown.

Song and call distinctions are not particularly clear in chickadees, and the complexity of some call types exceeds that of song. Many call types are given by both sexes (Ficken et al. 1978). Here, we focus on two call types that have been well-studied: the gargle and the chick-a-dee. The gargle is a variable series of two to nine notes given primarily by males (Ficken et al. 1978; Ficken and Weise 1984). Gargles are given in agonistic encounters between flock mates, during territorial encounters, and prior to copulation. They are not used to advertise flock territories but rather to defend those territories against intrusion and to maintain dominance hierarchies within flocks (Ficken et al. 1978). The chick-a-dee call consists of four note types (Fig. 4.4A). Each note type is given a variable number of times in an invariant sequence: A, B, C, D. Chick-a-dee calls are given by both sexes throughout the year and function as contact calls—to coordinate movements of pairs and flocks (Ficken et al. 1978; Nowicki 1983) and facilitate recognition of flock mates (Nowicki 1983). Birds also give chick-a-dees during interflock encounters and when mobbing predators. Flocks differ in call characteristics, primarily of the D note, and calls of individuals within flocks are convergent (Mammen and Nowicki 1981; Nowicki 1989). Recognition of flock mates could be based on both flock and individual differences (Nowicki 1983).

Observational and experimental evidence for vocal learning supports the role of social modification and, to a lesser extent, learned acquisition of both gargle and chick-a-dee calls. Social modification is implicated in gargle development on the basis of observational data on dialect variation (Ficken and Weise 1984; Ficken et al. 1985; Ficken and Popp 1995; Hailman and Griswold 1996). Hand-reared birds produced calls similar to individuals with which they were raised and different in subtle ways from free-living birds (Ficken and Weise 1984). The chick-a-dee call is better studied and suggests both learned acquisition and social modification. Observational
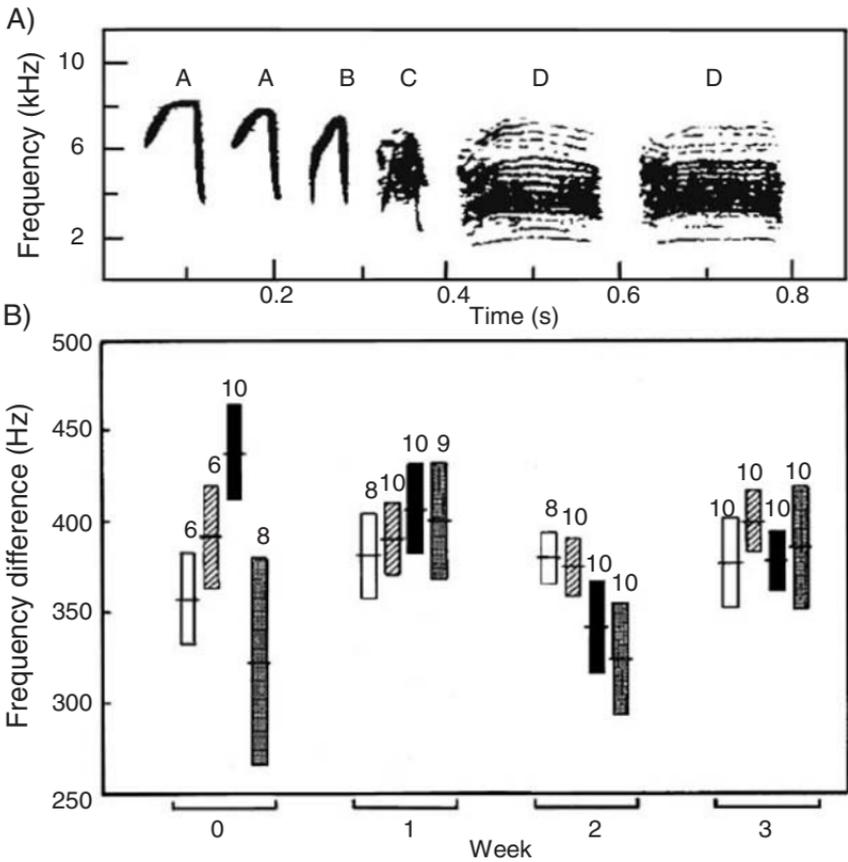
FIGURE 4.4. Chickadee calls. (**A**) Sonogram showing the four note types, marked A, B, C, D. The study focused on convergence among group mates in D notes. (**B**) Changes in frequency structure of D notes during the three-week experiment. Means are indicated by a horizontal line, SD by the vertical bars, and sample size by the numbers above bars. (From Nowicki 1989. Reprinted with permission from Academic Press.)

data (Clemmons and Howitz 1990) and one experiment (Hughes et al. 1998) support the hypothesis that vocal learning is involved in the acquisition of normal chick-a-dee calls. Clemmons and Howitz (1990) described the normal process of call development and found that approximate renditions of adult-like chick-a-dee calls are first given by fledglings at 28 days. These calls were highly variable, especially in the introductory A, B, and C notes, and did not acquire fully adult-like characteristics for another week. Acquisition of normal chick-a-dee calls required auditory and social experience (Hughes et al. 1998). The A note developed normally in isolated individuals, but birds who did not hear normal adult vocalizations produced abnormal B and C notes. Hughes et al. (1998) did not study development of the

D note. Social experience appears to be a powerful determinant of call development because birds who were socially but not acoustically isolated produced B and C notes that were at least as aberrant as those of totally isolated birds.

Social modification also occurs and produces convergence within flocks (Fig. 4.4B; Nowicki 1989). Birds who had no prior contact with one another gave calls that initially differed in several parameters of the D note (week 0). Calls converged rapidly. This is shown by the reduction in variation and increased similarity in means by week 1. No single bird appeared to serve as the model; instead, calls converged on the mean spectral characteristics of the flock. Convergence was observed in several frequency measures, including the bandwidth, maximum frequency, and difference between the minimum frequencies produced by each side of the syrinx. No convergence was observed in temporal measures or proportions of note types in calls. Calls began changing within a week, and by four weeks substantial convergence occurred. Both juveniles and adults changed calls, indicating that social modification is not limited to a sensitive phase in this species. Both types of vocal learning occur in *P. atricapillus* calls. This oscine species is a good counterpoint to studies of song learning in other oscines because it challenges some of our notions about the distinction between song and calls, and the importance of vocal learning to these two kinds of vocal signals.

3.1.2. Parrots—Budgerigar Flock Signatures

Budgerigars (*Melopsittacus undulatus*) are a highly social, nomadic parrot from inland Australia. Budgerigars live in flocks of 20–30 birds that associate seasonally with other flocks in very large assemblages. Both sexes provide parental care, and mated pairs may remain together over several breeding attempts. The arid environment has highly variable productivity both spatially and temporally, and budgerigars are opportunistic feeders that will move great distances to find productive areas. Flock living is thought to provide several benefits in food finding and predator protection (Farabaugh and Dooling 1996). Budgerigars are opportunistic breeders as well, initiating breeding when ecological conditions are favorable (Brockway 1964; Wyndham 1980a). Little is known of the composition of budgerigar flocks in regards to relatedness or stability. However, much is known of their vocal behavior.

Budgerigars give several types of calls, and complex, variably structured song. Most work on vocal learning has examined the most frequently used call, the contact call (Fig. 4.5), but all calls and song are thought to be learned. Contact calls seem to function to maintain social cohesion. Adults give them in flight and when separated from mates or other individuals in the flock (Wyndham 1980a). Contact calls also facilitate reunions between parents and their fledged offspring. Once fledged, offspring live in a creche. Parents visit the creche to feed their fledglings until they reach full independence
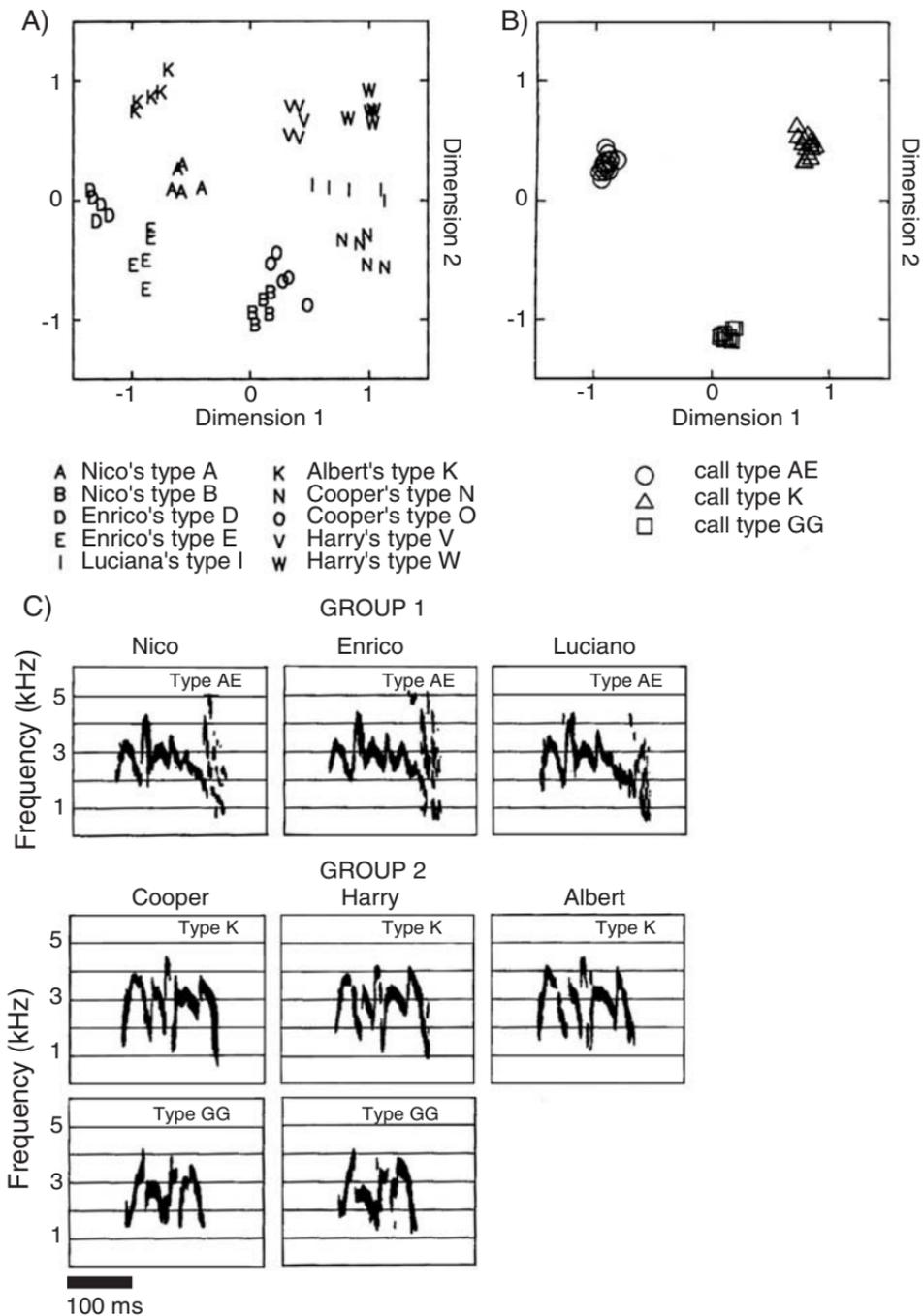
FIGURE 4.5. Contact calls from two social groups of male budgerigar. (**A**) Multidimensional scaling of five renditions of each bird's dominant contact call before contact and (**B**) after 8 weeks of social interaction. (**C**) Sonograms of dominant contact calls for each male after 8 weeks of contact have similar structure and thus show convergence within each group. (From Farabaugh et al. 1994. Copyright © 1994 by the American Psychological Association. Reprinted with permission.)

about two weeks later (Brockway 1964; Wyndham 1980b). Individual birds have a repertoire of contact calls, but use one or two most of the time (Farabaugh et al. 1994). Flock mates share call types (Farabaugh et al. 1994), resulting in flock-specific repertoires of contact calls. Budgerigars can discriminate between very similar contact calls given by their flock mates, suggesting that calls can be used to identify individuals within flocks. This perceptual discrimination appears to be learned because birds can only make these finely detailed discriminations when they are familiar with the individuals from whom the calls are recorded (Brown et al. 1988).

During normal vocal development, juveniles increase the extent and complexity of FM, decrease peak frequency, decrease bandwidth, and increase duration (Brittan-Powell et al. 1997). Contact calls appear to develop from a call given late in the nesting phase, the food-begging call. Broods show few differences and sexes develop similarly early on. However, evidence of call sharing emerges within a month of fledging (Brittan-Powell et al. 1997).

Direct evidence demonstrated that contact calls are learned and that both acquisition and social modification occur. Manipulations of auditory experience demonstrated its fundamental importance. Birds deafened at birth developed abnormal calls (Dooling et al. 1987; Heaton and Brauth 1999). Contact calls of deafened birds retained some features of the species' calls, including maximum and minimum frequency, bandwidth, and duration, but differed in tonality, number of tonal elements, and extent of frequency modulation (Dooling et al. 1987). Deafened birds produced normal food-begging calls but abnormal contact calls (Heaton and Brauth 1999), so vocal learning was confined to calls whose function was enhanced by similarity to social partners. Hand-reared birds gave contact calls that were simpler than typical budgerigar calls and that differed in bandwidth and frequency modulation (Brittan-Powell et al. 1997). Hand-reared birds had more acoustic experience than deafened birds, and their calls resembled typical budgerigar contact calls far more than those of the deafened birds. Contact calls and the song of deafened adults became abnormal within 6 months, indicating that auditory input is required to maintain normal call structure, and demonstrating the absence of a critical period. These studies showed that acoustic experience was essential for normal vocal development in budgerigars and revealed a continuum of effect.

Social experience had a powerful influence on which call types were acquired and how existing calls were modified. Learned acquisition and social modification occurred throughout development and into adulthood. Young birds learned from adults with which they were housed even when those adults produced abnormal contact calls or were heterospecific (Brittan-Powell et al. 1997). Abnormal features included bandwidth, degree of frequency modulation, and duration. Juveniles housed with zebra finches gave contact calls that resembled zebra finch calls but that showed less harmonics and more frequency modulation than the heterospecific call.

These birds also gave contact calls that were more typical of their species. Once abnormally reared birds were exposed to normal song at about 6 months of age, they developed more normal contact calls (Brittan-Powell et al. 1997), indicating that substantial ability for vocal learning persisted to this age. These data suggested that social interactions were very powerful at sculpting young birds' calls. Adults also learned the calls of the birds with which they interacted (Farabaugh et al. 1994; Bartlett and Slater 1999) and formed social bonds (Hile et al. 2000), providing further evidence that vocal learning was not limited to a sensitive phase in this species. Farabaugh et al. (1994) showed that adult birds whose contact calls were initially distinct converged on flock mates' calls within two months' time, with the first changes occurring in a week (Fig. 4.5). Mutual imitation seemed to be the mechanism because the final contact call was composed of call elements from different birds. The importance of social interaction was demonstrated because birds that could hear but not interact with each other did not share contact calls. When a single bird joined a group, that individual altered its call to match the group (Bartlett and Slater 1999). Call convergence occurs between males and females forming pair bonds due to males imitating their mates' calls (Hile et al. 2000).

Vocal learning is not limited to contact calls. Birds reared in acoustic and social isolation developed abnormal warble songs (Farabaugh et al. 1992a), indicating that acquisition of song was learned. In addition, males within social groups had similar warble songs, suggesting that social modification occurred. In support of this hypothesis, one male apparently copied syllables from a cage mate that sang abnormal songs, even though he could hear other birds whose song was typical for budgerigars (Farabaugh et al. 1992a). Birds whose tutor gave abnormal or heterospecific vocalizations continued to include some species-typical characteristics in their song and calls. This result argues that some features of vocalizations rely on underlying genetics. On top of this genetic basis is substantial vocal flexibility and social dependency.

3.2. Mammals

3.2.1. Bats—Greater Spear-Nosed Bat Group Signatures

Female greater spear-nosed bats (*Phyllostomus hastatus*) live in stable social groups that are attended by a single male who maintains nearly exclusive reproductive access to all females in the group (McCracken and Bradbury 1977). Consequently, in a given year, offspring of most females in a group are paternal half-sibs (McCracken and Bradbury 1981). However, adult females in these groups are not close relatives (McCracken and Bradbury 1981), a pattern that results from juvenile dispersal patterns. All offspring disperse from their natal group during their first year. When reproductively mature, at about two years of age, females join an existing female social group. Females obtain several benefits from group living.

Female group mates forage together (Wilkinson and Boughman 1998), which results in faster food finding and better defense of food resources (Wilkinson and Boughman 1999; Boughman unpublished). Group living and group foraging enhance reproductive success (Boughman unpublished). Reproduction is synchronous within a group (Porter and Wilkinson 2001), which may facilitate thermoregulation by young pups and allomaternal care (Porter unpublished).

Females use vocalizations, termed screech calls (Fig. 4.6A,B), to coordinate group foraging (Wilkinson and Boughman 1998), and these vocalizations differ among social groups (Boughman 1997). Screech calls differ among groups in a number of frequency and temporal features, yet calls from individuals within social groups are not statistically distinguishable. Such group-distinctive calls provide an effective mechanism for finding group mates outside the roost cave (Wilkinson and Boughman 1998). In addition to the variation among social groups within caves, variation exists between cave populations (Boughman and Wilkinson 1998). Little migration between caves occurs (McCracken et al. unpublished), yet this does not result in genetic differences between cave populations (McCracken 1987). Thus, geographical variation in screech calls is more likely to result from social modification than from population substructure.

Screech calls convey group membership (Boughman and Wilkinson 1998). Bats discriminate between calls given by group mates and other bats. Bats also differentiate between calls from their own cave and other caves. However, bats reveal no ability to discriminate among calls given by individuals within their group (Boughman and Wilkinson 1998). Screech calls function as contact calls that enable group mates to find one another outside the roost cave. Bats give them when departing on foraging flights, en route to, and at feeding sites (Wilkinson and Boughman 1998). Bats approach when hearing familiar calls but fly away when hearing unfamiliar calls (Boughman and Wilkinson 1998). This result and a lab experiment suggest that screech calls may facilitate group defense of resources. Bats increase their rate of calling when a large number of intruders are present (Boughman unpublished).

Unrelated females give acoustically similar calls (Boughman 1997). Genetics cannot explain this pattern, because group mates are not close relatives. Ontogeny of screech calls has not been studied, but because females join social groups as adults, ontogenetic change is unlikely to give rise to group-distinctive calls. Experimental evidence demonstrated that convergence within groups results from social modification (Boughman 1998). Juvenile and adult bats were transferred reciprocally between social groups that initially differed in call characteristics. Bats gradually changed calls (Fig. 4.6C–F). The first changes occurred within one month, and by five months calls given by transfers and residents showed strong convergence in both frequency and temporal characteristics. Both residents and transfers changed calls. Results showed that the social environment was the primary determinant of acoustic change. Comparisons with age-matched
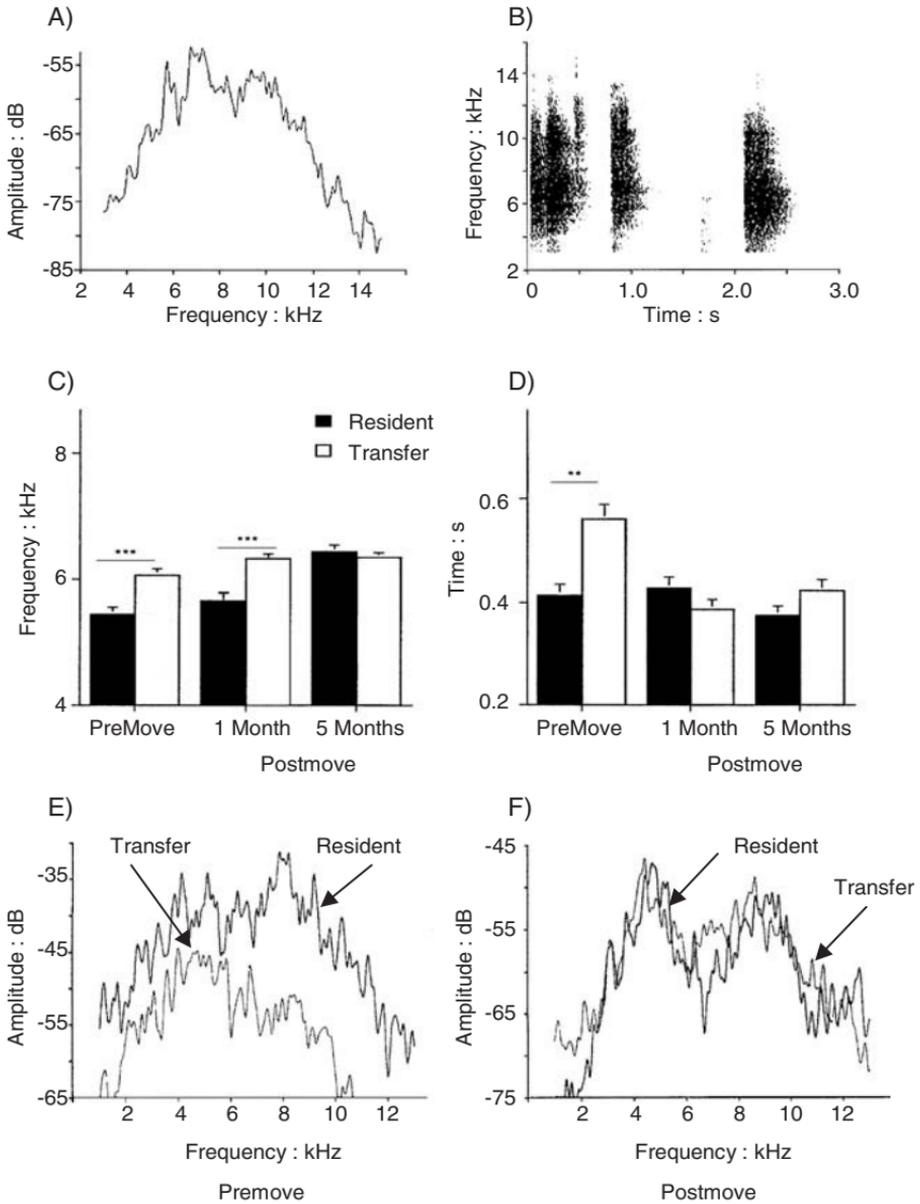
FIGURE 4.6. Greater spear-nosed bat screech calls and changes in acoustics after bats were moved between social groups. (**A**) Power spectrum and (**B**) sonogram of screech call. (**C**) Mean bandwidth and (**D**) repetition rate for group 2 residents (solid bars) and transfers (open bars) before and after social contact. Residents remained in their natal group, whereas transfers immigrated from another social group during the experiment. Premove periods are before this immigration event; postmove periods are after it. (**E**) Power spectra for group 2 residents and transfers before and (**F**) after social contact. (From Boughman 1998. Reprinted with permission from The Royal Society.)

half-sib controls demonstrated that call convergence did not result from maturational processes, acoustic adaptation to the physical environment, or heredity. Instead, half-sibs who transferred to new groups were more similar to their new, unrelated group mates than to relatives in their natal group (Boughman 1998). Call modification was not immediate, and the time required for individuals to match a new group could provide protection against outsiders who might feign identity to obtain access to food resources controlled by groups. Thus, in this species, cheater-protection mechanisms appear to have evolved in concert with group signatures.

3.2.2. Cetaceans—Killer Whale Pod Signatures

Killer whales (*Orcinus orca*) live in stable social groups called pods. Both transient and resident whales are found in the coastal waters of western North America. These types differ in foraging strategy, social structure, and vocal patterns, and they are reproductively isolated (Barrett-Lennard et al. unpublished). Here, we focus on the resident killer whales off the British Columbia (BC) and Alaska coasts, for which the bulk of work on vocal behavior has been done. Residents feed primarily on fish and live in extremely stable matrilineal groups. Neither males nor females disperse out of their natal pods (Bigg et al. 1990; Olesiuk et al. 1990; Hoelzel et al. 1998), so pods are composed of close relatives organized along matrilineal lines. Mating occurs between members of different pods (Barrett-Lennard unpublished). Pod members travel, feed, and socialize together. There is some suggestion that pod members cooperate in finding and capturing prey (Bigg et al. 1987; Hoelzel 1993), and foraging benefits may be one factor that favors living in stable groups.

Like other odontocetes, killer whales use echolocation to find prey. They produce several types of calls, but most work on vocalizations has focused on social calls, which combine tonal and pulsed elements (Fig. 4.7A). Resident pods have a repertoire of 3–16 discrete calls, with an average of nine calls (Ford and Fisher 1983; Ford 1989, 1991). Similar patterns were found for whales in coastal waters off Norway, which appear to have social structure and call patterns similar to BC residents (Strager 1995). Pods differ in their call repertoires. Although most calls are shared by several pods, some are unique to a particular pod (Fig. 4.7). The degree of call sharing between pods may depend on geographic distance, the amount of contact, or genetic similarity. Pods that rarely encounter one another share almost no calls, whereas those that interact frequently share some calls (Ford and Fisher 1983). The function of such call sharing has not been investigated. In addition to variation among pods in the type of calls given (termed repertoire variation), more subtle structural variation is present. Pods differ in frequency and temporal features of several calls, with those pods that associate least and least closely related showing the largest differences (Deecke 1998). An additional class of graded calls appears to be used at close range

A)
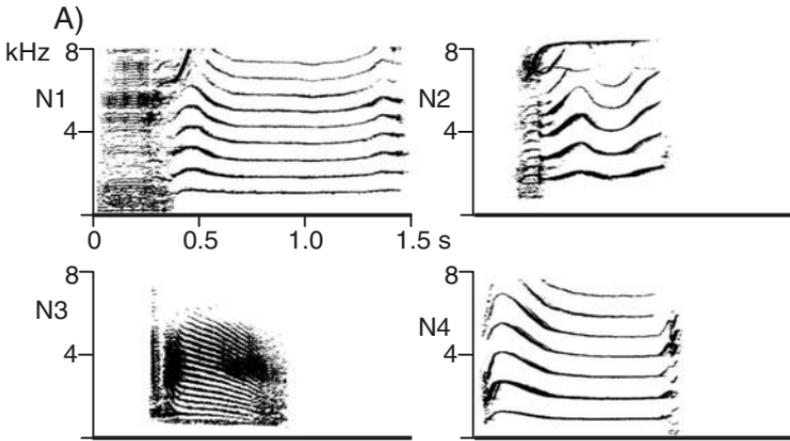
B)

Calls		Pods								
		A1	A4	A5	B	C	D	H	I1	I11
N1		X	X							
N2		X	X	X						
N3		X	X	X	X	X	X	X	X	
N4		X	X	X						
N5		X	X	X	X	X	X	X	X	
N6		X	X	X						
N7	N7I	X	X	X						
	N7II	X	X	X				X	X	
	N7III				X					
	N7IV					X	X			
N8	N8I	X	X	X	X				X	
	N8II					X	X			
	N8III							X		
N9		X	X	X						
N10		X	X	X						
N11		X	X	X	X					
N12	N12I	X	X	X						
	N12II				X	X	X	X	X	
N13		X	X	X						
N14					X	X	X		X	
N15					X	X	X	X	X	
N16	N16I				X				X	
	N16II					X	X			
	N16III							X		
N18					X	X				
N20					X	X	X		X	
N21					X					
N22					X				X	
N23										X
N24										X
N25										X
N26										X
N28										X
N29								X	X	
N31						X	X			
N36										X
N40										X
N41										X
Total		14	14	13	13	11	10	8	11	8

during intense socializing (Ford 1989). These calls do not differ among pods in a consistent way (Ford and Fisher 1983).

The exact function of discrete calls is unclear. They are given in various social situations, and Ford (1989) hypothesized that they function as contact calls, enabling pod mates to stay in acoustic contact while traveling and foraging. Ford speculated that calls might be important in coordinating foraging efforts during group hunts. Presumably, whales can use call differences among pods to determine the pod to which the caller belongs, although call repertoires overlap substantially (Fig. 4.7) and playback studies to test the group signature and contact-call hypotheses have not been conducted. The high degree of repertoire congruence among pods suggests that group identification might be based on structural variation between pods. Ford (1991) hypothesized that shared calls indicate the level of relatedness between pods or maternal lineage and might facilitate outbreeding (Ford and Fisher 1983). Unfortunately, there are no data to test most of these hypotheses. Testing hypotheses for call function with playback experiments is critical for establishing function and could also illuminate the selective pressures that might favor a learned or genetic basis to calls. A single call type is sufficient to identify group membership; the occurrence and function of repertoires remain unexplained, but the pattern suggests additional functions for repertoires. Genetic data indicate that mating usually occurs outside the pod and clan, so mates are likely to differ acoustically (Barrett-Lennard unpublished). This provides indirect support for the hypothesis that whales base mate choice on the degree of acoustic similarity.

No direct published evidence that calls are learned exists. One observation of captive whales is consistent with the learning hypothesis. In this case, a single Icelandic female produced calls similar to the BC whale with which she was housed for many years (Bain 1988).

Despite this lack of direct evidence. Ford (1989, 1991) proposed that calls are learned and that call sharing arises because pods that come into frequent contact imitate each others' calls. Deecke (1998) investigated this latter hypothesis with respect to structural variation, but not repertoire variation, by comparing the association patterns and vocal similarities of nine matrilineal units in three pods. He tested four call types, two of which showed some support for the hypothesis; however, the pattern was not particularly strong. Even though a significant correlation existed between acoustic similarity and association, dendrograms for acoustic similarity for

---

FIGURE 4.7. Killer whale social calls. (**A**) Sonograms of four call types. (**B**) Call types in the repertoire of the pods studied. Three closely related pods have almost identical calls (1, A4, A5) but produce calls that other more distantly related pods do not (B through Ill). Pods B through H have very similar repertoires. All pods except Ill produce call N3, N5, and a variant of N7 and N8. (From Ford and Fisher 1982. Reprinted with permission from the International Whaling Commission.)

each of these two calls were not congruent with dendrograms for associa-
tion. The pattern does not seem to be particularly strong for repertoire
variation either because Bigg et al. (1990) found no significant relationship
between association patterns and repertoire variation. Thus, the call-sharing
hypothesis is not strongly supported, but neither is it refuted. More data are
needed. In any case, congruence between association and call repertoire
or structure is insufficient to prove vocal learning because association can
allow for both genetic and cultural exchange.

Even though the pattern of shared calls within pods (Ford and Fisher
1983; Ford 1989, 1991; Strager 1995) and the stable social structure are con-
sistent with a learning hypothesis, high levels of relatedness within pods also
argue for a strong genetic component. A significant correlation was found
between acoustic similarity and genetic distance (Barrett-Lennard unpub-
lished). We cannot yet determine whether this pattern results from cultural
or genetic inheritance or a combination of the two modes. Genetically
encoded calls would serve their presumed function quite well, indicating
kinship and social affiliation simultaneously. Several authors presume that
insufficient genetic variation exists to produce complex call repertoires
and thus argue that pod-specific calls are unlikely to have a genetic basis.
In marked contrast to this view, studies cited earlier (Jones and Ransome
1993; Scherrer and Wilkinson 1993) have shown that calls with heritable
acoustic components can effectively serve as signatures, especially when the
relevant information is kinship. Determining the contributions of learning
and genetics to the pattern of pod-specific calls in *O. orca* requires experi-
mental tests and additional genetic data. Analysis of both nuclear DNA and
mtDNA is ongoing (Barrett-Lennard unpublished), and the results can be
correlated with information on the degree of distinctiveness and overlap
of calls to determine how well genetic similarity predicts call similarity for
individuals and the potential role for learning. A critical test of vocal learn-
ing must control for relatedness.

3.2.3. Primates—Pygmy Marmoset Contact Calls

Pygmy marmosets (*Cebuella pygmaea*) are small primates that live in family
groups composed of a breeding pair, their offspring, and an occasional un-
related adult (Soini 1993). Offspring care is communal (Kinzey 1997a),
and this cooperative care may improve offspring survival although it is not
essential (Rothe et al. 1993). *Cebuella* inhabit mature forests in the upper
Amazon region that are seasonally flooded (Soini 1993), and they feed
heavily on gum and insects. Groups defend small, exclusive territories
centered around a primary feeding tree, but change their home ranges in
response to food abundance (Soini 1993).

Pygmy marmosets give two types of trilled contact calls, termed the
closed mouth trill (Fig. 4.8A) and the J-call. Closed mouth trills are used
when animals are in close range or within visual contact, whereas J-calls are
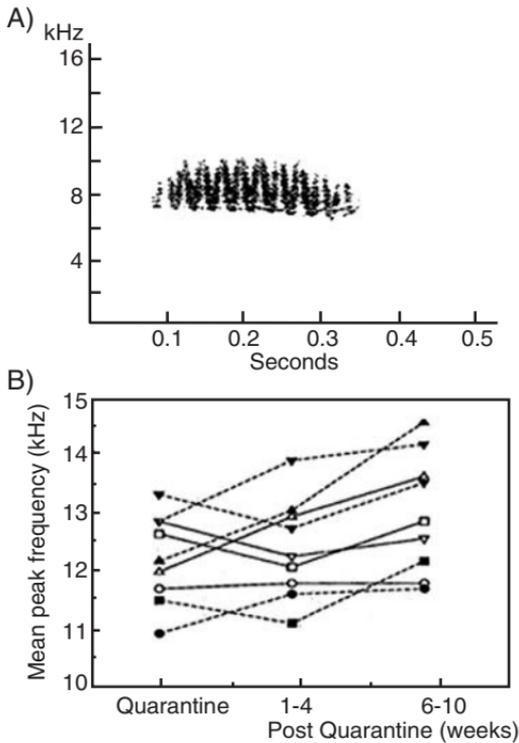given when animals are some distance apart or unable to see one another.

FIGURE 4.8. Pygmy marmoset trills. (**A**) Sonogram of a trill call. (From Pola and Snowdon 1975. Reprinted with permission from Academic Press.) (**B**) Changes m peak frequency of trills for residents (open symbols) and introduced animals (closed symbols) during the ten-week experiment. Groups had no auditory contact during the quarantine period. After quarantine, they had auditory but not social contact. Females (circles), subadult males (squares), juveniles (upward triangles), and infants (downward triangles). (From Elowson and Snowdon 1994. Reprinted with permission from Academic Press.)

The structure of J-calls makes them easy to localize (Snowdon and Hodun 1981). Group mates respond antiphonally to both types of contact calls and may also orient toward and approach an animal producing J-calls. The calls are used primarily in intragroup situations, but may also be used in encounters between groups. Thus, both calls are used to maintain contact between the members of a family group (Snowdon and Hodun 1981). These calls function as group signatures, yet most variation is among individuals. Individual vocalizations differ in several temporal and frequency characteristics for both types of contact calls. These differences do not appear to depend on either familial relationships or sex (Snowdon and Cleveland 1980). There is some evidence that individuals are recognized by their calls, although this conclusion is weakened because of small sample size and because statistical significance rests on responses of two males to their own calls (Snowdon and Cleveland 1980). Calls played from an unfamiliar location elicit very low responses, suggesting that a combination of vocal

characteristics and context are involved in recognizing others (Snowdon and Cleveland 1980).

Infant call repertoires differ from adult repertoires both in types of calls and acoustic structure of adult-like calls (Elowson et al. 1998a). In addition, correct usage of call types appears to be learned (Elowson et al. 1998a). Several features of contact trills change with time, although stereotypy does not increase so the cause is unclear. J-calls show even less age-related modification (Elowson et al. 1992). Individuals' contact calls differ extensively in acoustic structure and the pattern of ontogenetic changes. Such high individual variance makes finding ontogenetic patterns difficult. However, one pattern that emerges is that infants go through a stage of vocal production reminiscent of human infant babbling (Elowson et al. 1998b). Similarities to human babbling include repetition of call types and use of a subset of the adult repertoire in modified infant form. Babbling infants are responded to by caregivers more than their silent counterparts, suggesting that babbling is important in the normal development of social relationships. Data on development indicate vocal flexibility exists and show that calls are not always produced in adult form by juveniles. Vocal learning may or may not play a role; vocal tract maturation and developing social relationships may be responsible for such changes. Descriptions of development cannot directly test the importance of vocal learning. Considering the current lack of evidence for most primates, alternative explanations seem likely.

The potential for social modification of contact calls was studied with family groups from two different captive colonies (Elowson and Snowdon 1994). Animals were housed in family groups initially in two separate rooms during a quarantine period. Contact calls were recorded and analyzed from this initial time period. Subsequently, family groups from both captive colonies were housed in the same room in acoustic but not visual or physical contact. Contact calls recorded after the animals were introduced to each other (postquarantine) were compared with those from the initial period (Fig. 4.8B). Peak frequency and bandwidth rose in a parallel fashion in most animals from both captive colonies, duration showed some evidence of convergence within groups, and trill rate showed normal developmental changes (Elowson and Snowdon 1994). Thus, this experiment demonstrated that vocalizations were not fixed, and the changes observed appear to be in response to a changed social context. However, neither acoustic convergence nor divergence occurred, so social modification was not demonstrated. It seems likely that the animals were stressed by the presence of unfamiliar conspecifics and may have responded by increasing the frequency of calls. Vocalizations often rise in frequency when animals are stressed, and calls that are used in agonistic contexts often are of high frequency (Morton 1975, 1982). The lack of convergence in call characters is not surprising. There is actually little reason to predict convergence between animals from the two colonies because they were not social companions, had very little social interaction, and neither individuals within

family groups nor groups within colonies shared call characteristics prior to the introduction (Snowdon and Cleveland 1980). It is not clear what kind of vocal changes would demonstrate social modification in this species because the degree of similarity in calls does not appear to have functional significance. A more recent experiment investigated vocal changes in four newly formed pairs (Snowdon and Elowson 1999). No clear pattern emerged for the four variables they measured. For each variable, some pairs converged, others diverged, and others showed no change. The variable most suggestive of social modification was peak frequency because three pairs showed convergence, but in only two was it significant. Neither experiment was designed to explore call acquisition.

In 1997, Snowdon concluded that the weight of evidence does not support a role for learning in the acquisition or social modification of vocalizations in this or other species of primates. Snowdon and Elowson's latest experiment (Snowdon and Elowson 1999) is consistent with Snowdon's (1997) position. In keeping with findings for vervet monkeys and some others (Seyfarth and Cheney 1997), marmosets appear to learn the proper use of alarm calls in response to predators and may learn to recognize individually distinctive calls given by group mates (Hayes and Snowdon 1990). Learned usage is a process distinctly different from either learned acquisition or social modification, and we do not consider it vocal learning.

4. Dialects

Vocalizations often vary in structure geographically, sometimes with sharp boundaries between call types. The scale of variation can be microgeographic (variation among contiguous individuals or groups) or macrogeographic (variation among groups separated geographically) (Krebs and Kroodsma 1980). The types of geographic variation are not discrete but form a continuum (Baker and Cunningham 1985). Geographic variation has been termed dialects, although some authors prefer to reserve this term for microgeographic variation resulting from vocal learning (Conner 1985). Here, we adopt a broader definition to include geographic variation at all levels without regard to the mechanism producing such variation. We take the latter stance primarily because the causes of geographic variation are unknown for most mammalian vocalizations and bird calls, and also because dialects can be biologically important even when they arise from processes other than vocal learning. Studies of call dialects in birds and mammals have focused primarily on describing dialectical patterns. Particularly in mammals, these studies often aim at finding evidence consistent with vocal learning rather than determining the function of geographic patterns.

Dialects can emerge as a natural consequence of learning vocalizations from neighbors (Catchpole and Slater 1995). Under this scenario,

geographic variation arises due to local copying and cultural drift (or the random fixation of culturally transmitted variants). Random copying errors and innovations can be transmitted horizontally (between neighbors of similar age), obliquely (from unrelated adult to juvenile), and vertically (from parent to offspring). Thus, the closer two individuals are in space, the more they sound alike. This same pattern can arise if dialects result from genetic differences among populations, making it difficult to use pattern alone to infer vocal learning. Either learned acquisition or social modification can give rise to dialects, and the calls can function as individual or group signatures, but need not have a signature function.

The function of birdsong dialects has been debated for some time (Catchpole and Slater 1995). The simplest hypothesis is that dialects themselves have no particular function but merely reflect the underlying process of vocal learning described above (Andrew 1962; Wiens 1982). Others have argued, sometimes forcefully, that dialects have evolved to preserve local adaptation—the genetic adaptation hypothesis (e.g., Baker and Cunningham 1985), to enhance sound transmission by matching local habitat—the habitat matching hypothesis (e.g., Hansen 1979; Handford 1988), or to facilitate interactions between neighbors—the social adaptation hypothesis (e.g., Payne 1981; Rothstein and Fleischer 1987). The function of call dialects in birds is often assumed to be similar to that of song dialects even though the function of the vocalizations themselves is quite different. Dialect function has infrequently been discussed in relation to mammalian dialects.

Assuming that dialects have the same function for song and calls may not be warranted because calls and song function differently. Consequently, the underlying processes might differ. Song in oscines functions to establish and maintain territories and to attract females (e.g., Kroodsma and Byers 1991). In temperate species, males sing primarily during the breeding season. A similar function is assumed for hummingbirds. Many male hummingbirds sing in assemblages, or "leks," and couple this song with elaborate courtship displays. Temperate oscine and hummingbird females rarely sing. In contrast, contact calls appear to function in various social interactions, are given by both sexes throughout the year in birds, and are usually used by both sexes in mammals. Their primary function is not to establish and defend nesting sites, although they can be used in this way. This difference in function may be reflected in different patterns of dialect variation because selection will probably act differently. The prevalence of learned acquisition and social modification may also differ between bird song and the calls of both birds and mammals.

Calls need not be learned to vary geographically. Adaptive variation in body size can produce geographic variation that correlates with habitat, latitude, or altitude. Habitat matching itself can result from local adaptation without recourse to vocal learning. Restricted gene flow between dialect areas is required to produce the genetic divergence and local adaptation responsible for both morphological and call variation. In most cases,

data on gene flow required to test these alternative mechanisms are lacking, although the work on cetaceans, particularly humpback whales, has made great strides in this direction (Baker et al. 1990, 1993, 1998; Palumbi and Baker 1994; Larsen et al. 1996; Valsecchi et al. 1997).

Comparisons of geographic variation in genetic similarity and dialect boundaries can illuminate the extent to which dialects may result from vocal learning. In species with sharp dialect boundaries, a lack of congruence between dialect boundaries and the extent of sharing in molecular genetic markers (usually mtDNA haplotypes or microsatellite alleles) supports a strong role for vocal learning. Unfortunately, few study systems have such data available. We present case studies where vocal learning has been implicated and also briefly describe other birds (Table 4.1) and mammals (Table 4.2) for which vocal learning of dialects has been studied. Because population structure is important in testing alternative hypotheses, we describe this evidence when available, along with evidence consistent with vocal learning.

4.1. Birds

4.1.1. Parrots—Yellow-Naped Amazon Parrot Contact Call Dialects

Yellow-naped amazon parrots, *Amazona auropalliata*, are monogamous, yet gregarious birds (Wright 1997). Pair bonds are long-lasting, and pairs jointly defend nest sites against conspecifics. Pairs spend most of their days feeding and socializing with other pairs and at night congregate with others at large traditional roosts (Wright 1996) primarily for protection against predators. Dispersal patterns of juveniles are unknown. The species is resident throughout its range in semiarid woodland scrub and savannahs along the Pacific coast from southern Mexico to northern Costa Rica, Honduras, and several Bay Islands in the Caribbean (Juniper and Parr 1998).

Yellow-naped Amazons have a repertoire of calls that serve a variety of social functions (Wright 1997). The most ubiquitous call is the contact call, a multiharmonic, frequency-modulated call (Fig. 4.9). Both males and females give this call often near their nesting site and at communal roosts (Wright 1996). In other parrot species, contact calls function to maintain proximity between members of a flock or mated pairs (Farabaugh and Dooling 1996) and to recognize mates and other social companions, including siblings (Wanker et al. 1998). The function in *A. auropalliata* is not known, but is suspected to be similar to that of these other psittacines. Pairs also duet near nesting sites, and these duets are thought to function in territorial defense (Wright 1997).

Evidence for vocal learning in this species includes observational work describing dialects in the contact call (Wright 1996) and other calls (Wright 1997), and genetic analyses (Wright and Wilkinson 2001). Disjunct acoustic and geographic boundaries separate three dialect groups in Costa Rica: the southern, northern, and Nicaraguan. Dialects are characterized by different
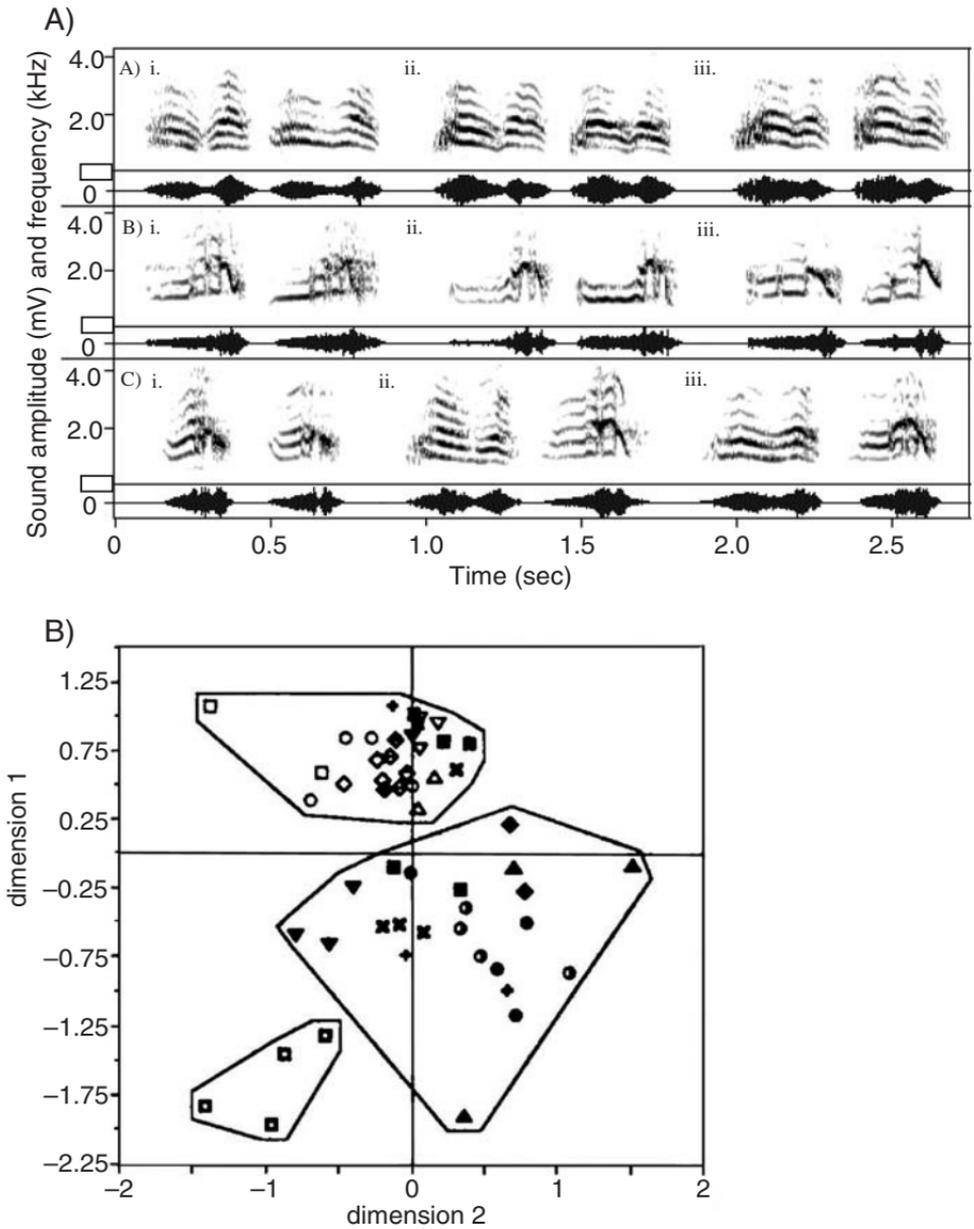
FIGURE 4.9. Yellow-naped amazon parrot contact calls from three dialects. (**A**) Sonograms and waveforms of contact calls from two birds at three roosts (i–iii) in the (a) northern, (b) southern, and (c) Nicaraguan dialects. (**B**) Multidimensional scaling of spectrogram cross correlations with calls from 16 roosts. Each point represents an individual coded by roost: northern (open symbols), southern (closed symbols), Nicaraguan (heavy-lined open squares), border roosts (cross and plus symbols). Minimum-area polygons enclose birds classified from each of the three dialects. (From Wright 1996. Reprinted with permission from The Royal Society.)

call types (Fig. 4.9). Several birds at roosts near the border between the southern and northern dialects are "bilingual"; that is, they produce some calls similar to each dialect. In addition to dialect variation, birds from roosts within a dialect differ in frequency and temporal characteristics of their shared call type. The amount of differentiation correlates with geographic distance, at least within the southern dialect (Wright 1996). Wright (1996) also reports slight differences among individuals within a roost. Several other calls in the repertoire, including short contact calls, growls, and pair duets, show dialect variation (Wright 1997). One call class, squeals and gurgles, does not show a dialect pattern but is highly variable within individuals. Pairs respond strongly to playback of roost mates' pair duets near their nest site but not to playback of calls from outside the dialect region (Wright and Dorin 2001), indicating that parrots perceive these dialect differences, that they are functionally relevant, and that local birds are attended to and thus more likely to be copied.

Genetic analyses indicate substantial gene flow across dialect boundaries (Wright and Wilkinson 2001). Thus, dialects are not a result of population genetic structure. The parsimonious interpretation is that birds copy the local dialect after dispersal, indicating strong social pressure to conform to the local dialect.

4.1.2. Trochilids—Hummingbird Song Dialects

Several studies have been conducted on dialect variation in hummingbird song using the little hermit, *Phaethornis longuemareus* (Snow 1968; Wiley 1971), Anna's hummingbird, *Calypte anna* (Baptista and Schuchmann 1990), the sparkling violet-ear, *Colibri coruscans*, and the green violet-ear, *Colibri thalassinus* (Gaunt et al. 1994). Unfortunately, no single species has been studied intensively, and the hermits are not closely related to the other hummingbirds (Bleiweiss 1998).

Hummingbirds are surprisingly long-lived birds for their size and metabolic rate, living 6–10 years in captivity (Skutch 1972). Most tropical species are rather sedentary, although species that breed in North America migrate to the tropics to overwinter. We know little of population structure in any of these species where vocal learning has been studied. Males of many tropical genera, including *Phaethornis* and *Colibri*, congregate and sing at traditional sites in dispersed leks. Several North American species perform complex aerial courtship displays and are less likely to lek, although *Calypte anna* males do sing within hearing distance of one another.

Snow (1968) first discovered dialects of little hermits, *P. longuemareus*, in Trinidad, and this discovery was further investigated by Wiley (1971). Males sing songs that are very similar to those of their nearest neighbors, yet several song groups occur on a single lek (Snow 1968; Wiley 1971). Within an individual, songs vary in the number of introductory notes and the structure of the song's terminal part (Wiley 1971). Spectral variation has not

been quantitatively studied, but inspection of published sonograms suggests that individuals may vary from one another in frequency and temporal characteristics of all song components, even when the basic structure of notes is quite similar, a possible example of by-product distinctiveness. Songs sung by different males within a song group show striking similarity in the frequency contour from the song's middle portion, and this feature differs from other song groups on a lek (Wiley 1971). Visual comparison of sonograms indicates that song at the lek studied by Snow (1968) differs from that at the lek studied by Wiley (1971). Both Snow and Wiley suggest that vocal learning leads to the song sharing they observed. To date, no experimental tests of the learning hypothesis have been conducted on little hermits.

Dialect variation has also been found in the song of Anna's hummingbird, *C. anna* (Mirsky 1976; Baptista and Schuchmann 1990). The differences between island and mainland populations include the structure of syllables and temporal phrasing of the song (Mirsky 1976). Mainland males show no response to playback of island songs, whereas they respond strongly to playback of mainland songs (Mirsky 1976), indicating that dialects are recognized as distinct by the birds. Visual comparison of sonograms from southern (Mirsky 1976) and northern California (Baptista and Schuchmann 1990) shows differences that are much less marked. The island population is only about 100 birds and was probably founded quite recently; song varies little among individuals. Mirsky (1976) speculates that the oddity of island song results from the initial founding event coupled with a subsequent bottleneck. Repeated bottlenecks may have reduced genetic and cultural variation, resulting in strong cultural drift. This hypothesis would be supported if a song resembling that found in the island song were part of the mainland repertoire.

Gaunt et al. (1994) obtained indirect evidence of vocal learning by comparing the songs of neighbors to more distant individuals in two species, the sparkling violet-ear, *Colibri coruscans*, and green violet-ear, *C. thalassinus*. They find that neighbors' songs are more highly correlated with each other than with those of nonneighbors. The degree of acoustic difference correlates with geographic distance between neighborhoods. Oddly, the within-individual correlation for *C. coruscans* is quite low (0.28), and the authors do not comment on this in their paper. They find occasional strong note similarities between distant birds in *C. thalassinus* but argue that these similarities are not as strong as those between neighbors. The lack of genetic data makes interpretation of these patterns inconclusive.

More direct evidence that song is acquired through learning comes from a single study of song development in isolated Anna hummingbirds (Fig. 4.10; Baptista and Schuchmann 1990). One male reared without exposure to conspecific song developed a song that differed significantly from that of wild adults in frequency range and syllable duration, although it retained several species-specific characteristics. Three males reared with acoustic
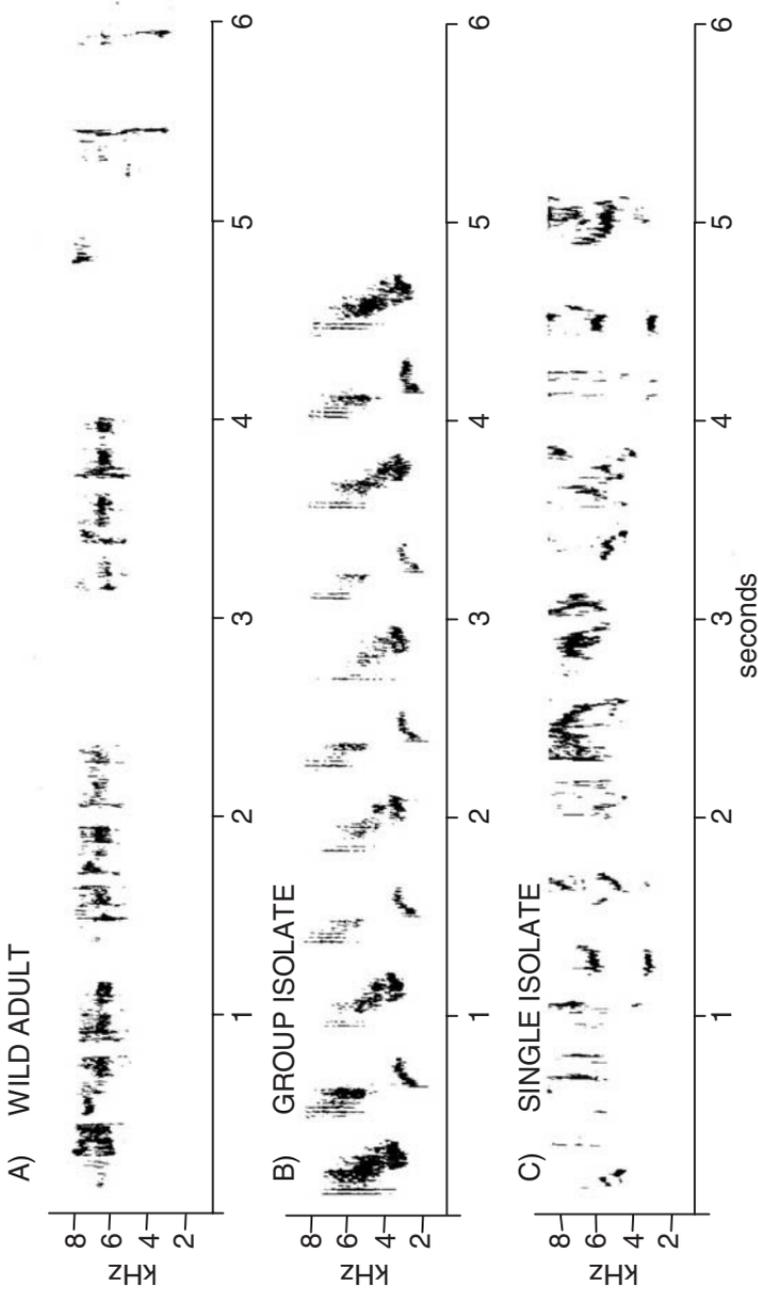
FIGURE 4.10. Anna hummingbird song phrases. (**A**) Sonograms of the song from a wild adult, (**B**) a bird acoustically isolated with two other juveniles, and (**C**) a single isolate. Note the abnormal structure of the song from the isolated birds. (From Baptista and Schuchmann 1990. Reprinted with permission from Blackwell Wissenschafts-Verlag Berlin, GmgH.)

exposure only to each other's song shared many song characteristics, including the structure of individual syllables and temporal pattern of song. The group isolates' songs differed from those of wild males in cadence and minimum frequency. One group isolate was initially raised in the nest and may have heard an adult male singing, so this group's experience differed in two ways from the single isolate, confounding tests of the relative importance of social and acoustic isolation. Both single and group isolates used a chitter that was not heard in the songs of wild males. Baptista and Schuchmann (1990) noted that the single isolate's song resembled the island songs of Mirsky's study and suggested that the initial founder of the island population may have been a young bird who had not completed song learning. Their study, although small, suggested that both learned acquisition and social modification might be involved and mirrors the patterns described in observational studies, lending credence to the vocal learning interpretation. Additional experimental tests are necessary before firm conclusions can be drawn.

4.2. Mammals

4.2.1. Cetaceans—Humpback Song

Humpback whales (*Megaptera novaeangliae*) migrate from summer feeding grounds in northern latitudes of the Pacific and Atlantic oceans to equatorial breeding grounds in each ocean basin. They are also found in the southern hemisphere, where they feed off Antarctica and winter in the South Pacific near Australia, New Zealand, and Tonga. Although highly social, they have few long-term associations except for mother–calf pairs. On the breeding grounds, mature females and their calves are often accompanied by an escort. Escorts are likely to be males, and these escorts compete for access to mature females (Tyack and Whitehead 1983), but females show no fidelity to individual males (Clapham and Palsboll 1997). In some cases, individuals feeding on locally abundant schooling fish will associate repeatedly (Perry et al. 1990), and a few recurring associations among adults are known (Weinrich 1991), but large, loosely structured aggregations are common when humpbacks feed on krill, and individuals often feed and travel alone.

Information on population structure greatly facilitates evaluation of the potential influence of cultural transmission and genetic factors on song sharing. Even though few physical barriers exist, both resighting and genetic data indicate that humpback populations are structured. Numerous genetic analyses provide detailed information on population structure, an enviable position compared with the dearth of genetic data for other species in which dialects have been described. Analyses of both mitochondrial (mtDNA) and nuclear DNA (microsatellite and intron sequence) variation indicate that ocean basins are largely isolated from one another (Valsecchi et al.

1997). Even so, the effective migration rate between ocean basins is estimated to be between 0.5 (Baker et al. 1993) and 10 (Palumbi and Baker 1994) whales per generation.

Each ocean basin contains several populations, and movement of individuals is primarily within ocean basins (Fig. 4.11). In the North Pacific Ocean, one population migrates between Alaska and Hawaii, a second between California and Mexico, and a third winters near Japan and has unknown feeding grounds. Infrequent movement of individuals between these populations occurs (Perry et al. 1990; Calambokidis et al. 1996). Isolation of California–Mexico and Alaska–Hawaii populations is indicated by differences in mtDNA haplotypes (Palumbi and Baker 1994) and nuclear DNA allele frequencies (Baker et al. 1998). However, occasional interbreeding between California and Hawaii whales must have occurred because they share some nuclear DNA alleles (Palumbi and Baker 1994). MtDNA data suggest that other California whales breed with humpbacks that feed in the South Pacific (Baker et al. 1990; Stone et al. 1990; Medrano-Gonzalez et al. 1995).

North Atlantic humpbacks may also segregate into several subpopulations (Fig. 4.11), one migrating between the West Indies and the Western North Atlantic, the other between the Cape Verde Islands and the Eastern North Atlantic (Mattila et al. 1989, 1994; Katona and Beard 1990; Palsboll et al. 1995; Larsen et al. 1996). MtDNA variation indicates that these populations form two distinct matrilineal aggregations (Palsboll et al. 1995; Larsen et al. 1996). However, some gene flow occurs because no differences were found in allele frequencies at six microsatellite loci (Larsen et al. 1996).

Genetic data support the hypothesis that males move more often between populations than females (Palumbi and Baker 1994; Baker et al. 1998). However, one study found that males were more likely to be resighted on the breeding grounds than females (Craig and Herman 1997), so whether migration is sex-biased remains unclear.

Male humpback whales sing long, complex, stereotyped songs (Payne and McVay 1971). Humpback song consists of repetitive elements ranging in frequency from 30 to 4,000 Hz combined into "themes." Themes are combinations of elements given in set patterns. A number of themes are combined in apparently fixed order to produce a single song (Payne and McVay 1971). Variation occurs in the number of repetitions of elements in a theme, the presence of themes in a song, and song duration, but not in the order of themes (Payne and McVay 1971; Payne and Payne 1985). Males sing primarily on the breeding ground, and other adult males move away from singing whales (Tyack 1981) and from song playback (Tyack 1983), suggesting that song serves to space individuals.

There are two lines of observational evidence for social modification and perhaps learned acquisition of humpback songs: shared temporal changes and dialects. Themes are shared by most of the males in a population during
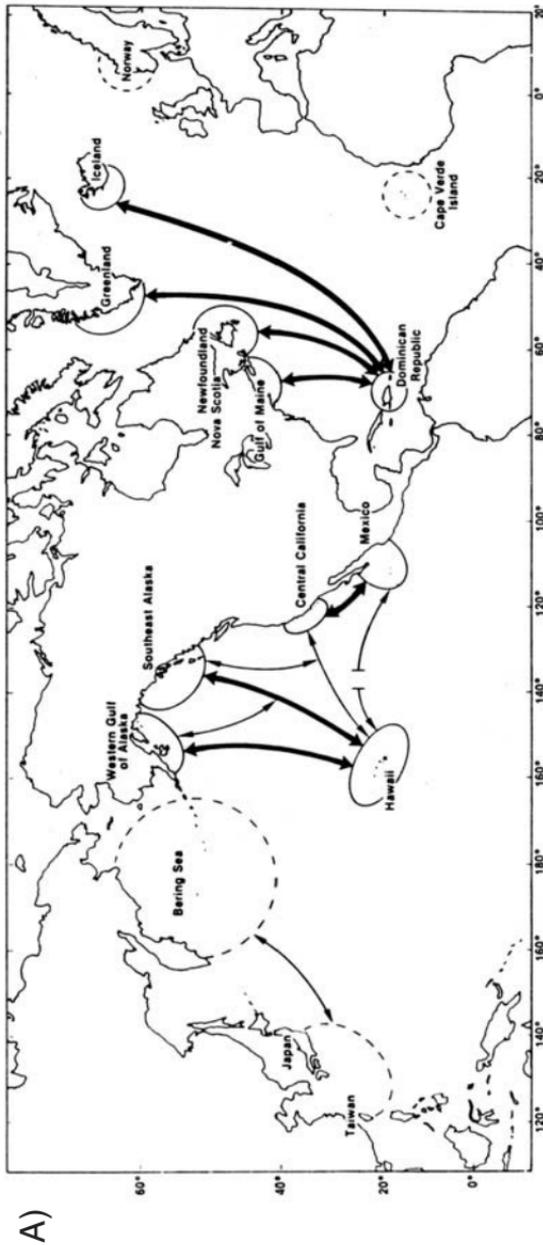
FIGURE 4.11. Humpback whale population structure and song structure. (**A**) Map showing migration patterns in the northern hemisphere based on resightings of marked individuals. Arrows connect regions with strong (heavy arrows) or weak (thin arrows) migratory exchange. (From Baker et al. 1990 Reprinted with permission from Nature. © 1990 Macmillan Magazines Ltd.) (**B**) Spectrogram tracings of humpback whale song themes. One theme is shown for two Atlantic regions in 1979 and two Pacific regions for 1978 and 1979. This theme is given repeatedly while singing. Syllables are described by phonetic terms: GRN (groan), CRY (cry), WO (wavery oo), WVPMN (wavery pulsed moan), SN (snore). (From Winn et al. 1981. Reprinted with permission from Springer-Verlag.)
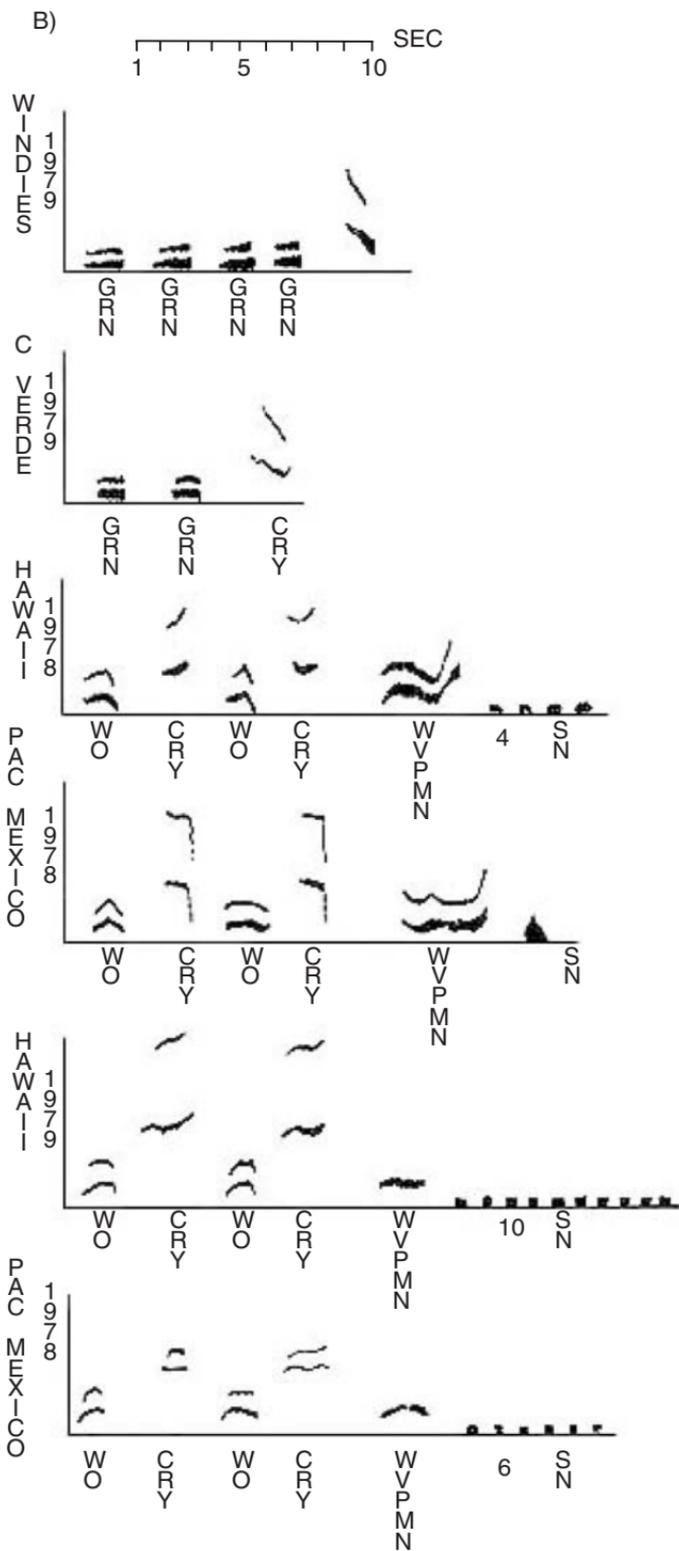
B)

FIGURE 4.11. *Continued*

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a single breeding season. However, the song is not static; progressive changes occur (Payne and Guinee 1983; Cato 1991). At the start of a breeding season, the song resembles that from the prior year. As the breeding season progresses, new themes are added and old themes deleted. Thus, the song at the end of a breeding season may bear little resemblance to that at the beginning of that year (Payne and Payne 1985). These changes can be extensive, but it is still sometimes possible to recognize songs from one year as coming from the same population as songs several years later. Observed temporal changes do not result from variation among individuals recorded because individuals recorded over two breeding seasons alter their songs in concert with others in the population (Guinee et al. 1983). The most striking finding with respect to vocal learning is that most individual males in the population make parallel changes (Payne and Payne 1985). The general consensus is that this pattern results from cultural transmission of specific song characteristics, and indeed it is difficult to imagine how such shared changes could occur without copying. The mechanism by which males copy one another and the function of copying is, however, completely unknown.

Additional data supporting the role of social modification come from studies of geographic variation in song. Three ocean basins—North Pacific, North Atlantic, and South Pacific—exhibit distinctly different songs. Recordings within those basins as far as 5,000 km apart show that songs from different populations have very similar structure and the same annual changes (Fig. 4.11; Winn et al. 1981). However, studies of several locations within the North Pacific indicated that whales in Japan, Hawaii, and Mexico share only a portion of their themes (Helweg et al. 1990). Vocal differences correspond roughly to genetic differences in the North Pacific. A similar pattern emerges for humpbacks recorded in the South Pacific in Tonga, New Caledonia, New Zealand, and Australia, although most themes were shared (Helweg et al. 1998), except between the east and west coasts of Australia (Cato 1991).

These patterns suggest a degree of acoustic isolation between populations within ocean basins with some acoustic contact or migratory exchange (Helweg et al. 1990, 1998). The extent of geographic distance, genetic differentiation, and song differentiation appear to be highly correlated. Thus, dialects could arise because of genetic differences, social modification, or both. Currently, we cannot tease apart their separate effects.

Cultural exchange of songs between populations could occur if males sing occasionally on feeding grounds, which they may share with males from other breeding populations (Payne and Guinee 1983). Winn et al. (1981) discuss the possibility that geographic variation arises because populations in one ocean basin are out of synchrony with those in another, even though they may have similar song elements in their repertoires. If this hypothesis is correct, then vocal sharing does not require learned acquisition but is more reminiscent of whistle sharing in dolphins (Smolker and Pepper 1999). This hypothesis is certainly possible; a large number of elements and

syntactical arrangements have been described, and current recordings probably do not exhaustively catalog regional repertoires. Asynchrony could result from either genetic or acoustic isolation, and thus this hypothesis does not discriminate between these two mechanisms. To our knowledge, no direct tests of any hypotheses about song sharing or song changes have been conducted. Direct tests are difficult to accomplish but would certainly be worthwhile. Comparing available long-term data sets on a larger scale than has been done in the past to determine to what extent regional repertoires of elements and themes do overlap would be an interesting first step. More direct tests of congruence between genetically defined populations and dialect groups are possible and warranted. The function of dialects and song sharing in humpbacks is completely unknown. Further playback studies to investigate responses of male and female whales to their own and foreign dialects could provide insight into why song sharing is favored and how it occurs.

4.2.2. Primates—Tamarin Long Calls

Dialects have been studied in several species of tamarins in the genus *Saguinus*. Tamarins are distributed throughout the neotropics (Kinzey 1997c) and live in small groups of multiple males and females (Garber et al. 1993; Savage et al. 1996; Kinzey 1997c) that are not close relatives. The dominant female gives birth to twins, which are cared for communally by most adult males in a group (Sussman and Kinzey 1984). Group size correlates with offspring survival (Sussman and Garber 1987) and may reduce care costs for individuals (Price 1992). Groups travel together through their large home ranges (Kinzey 1997c) and feed primarily on widely dispersed insects, fruit, nectar, and exudates from plants (Garber 1993). Home ranges of tamarin groups overlap extensively, and this overlap centers around primary food trees. Groups defend food sources aggressively against other groups to obtain priority access (Garber 1988; Payne and Payne 1997) and experience costs if such defense is unsuccessful (Pruetz and Garber 1991). Group defense involves both vocal display and physical combat (Payne and Payne 1997).

   A primary vocalization involved in group defense and group cohesion is the long call. Long calls are 1–2-sec series of frequency-modulated syllables (Fig. 4.12). Calls differ among species and have been used to clarify phylogenetic relationships among tamarin species (Hodun et al. 1981; Kinzey l997b) and the other members of the callitrichidae, including lion tamarins and marmosets (Snowdon 1993). Long calls also differ between individuals and sexes within a species (Snowdon and Hodun 1985; Maeda and Masataka 1987). Although there is no evidence of call sharing among group members, individuals do respond preferentially to long calls of their own group mates (Snowdon and Hodun 1985), suggesting that they learn to recognize each other's calls. Long calls are often given by animals separated
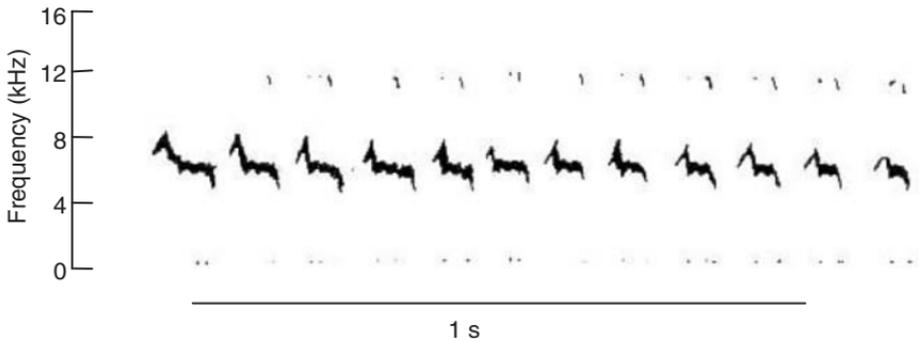
FIGURE 4.12. Sonogram of red-chested moustached tamarin long calls from Cobija region. (From Masataka 1988. Reprinted with permission from Academic Press.

from their group (Snowdon and Hodun 1985; Maeda and Masataka 1987; Masataka 1988) and are thought to facilitate cohesion within the group as it travels through the forest (Waser and Waser 1977). Long calls also function in territory defense during encounters between groups at feeding trees (Waser and Waser 1977; Garber et al. 1993). Females will respond to the calls of an intruder male unless her mate evicts him (Masataka 1988).

Studies of vocal learning in the saddle-back tamarin, *S. fuscicollis* (Cheverud et al. 1993) and the red-chested moustached tamarin, *S. labiatus*, have focused mainly on comparing calls from different populations (Hodun et al. 1981; Maeda and Masataka 1987; Masataka 1988). Contiguous populations of *S. fuscicollis* subspecies (*S. fuscicollis nigrifrons* and *S. fuscicollis illigeri*) differed in one temporal variable and three frequency variables (Hodun et al. 1981). One individual resembled *S. f. nigrifrons* morphologically, but was intermediate between *S. f. nigrifrons* and *S. f. illigeri* in long-call features. Comparison of long calls from captive hybrids between these two subspecies revealed that their long calls resembled *S. f. nigrifrons* with the exception of one frequency variable that most closely resembled the subspecies with which they were housed, *S. f. fuscicollis*. Hodun et al. (1981) suggested that learning must have taken place at least in this one variable. However, inspection of sonograms of these three subspecies' calls indicates that *S. f. fuscicollis* calls were not close matches to either subspecies but were intermediate between *S. f. nigrifrons* and *S. f. illigeri*, which is expected in hybrids if calls are heritable.

Populations of red-moustached tamarins (*S. labiatus*) only 27 km apart differ in frequency characteristics (Maeda and Masataka 1987). The proximity of these populations led the authors to suggest that they are not genetically isolated from one another but that the differences resulted from learning. Masataka (1988) subsequently determined that individuals responded differently to calls from their own and a foreign dialect, sug-

gesting that these differences were perceived by the animals and contributed to call function.

Morphological and genetic data suggest that the subspecies of *S. fuscicollis* are independent and isolated from one another (Cheverud et al. 1993), and even populations of the same species are isolated by geographic barriers (Peres et al. 1996). Combined with the data on call structure of hybrids, this suggests that vocal differences between subspecies (Hodun et al. 1981) are likely to be influenced heavily by genetic differences. It appears that some call features are more strictly under genetic control than others. This finding for *S. fuscicollis* raises the distinct possibility that dialects in *S. labiatus* (Maeda and Masataka 1987) are also influenced by genetic differences among populations. Indeed, under an additive model of genetic variation, intermediacy in acoustic structure is predicted and was found. Further study comparing genetic and acoustic variation for populations within species and between subspecies would help to reveal the extent of genetic control and whether vocal learning is possible.

5. Conclusions

5.1. Comparing Patterns

Call learning in mammals and birds is less well-understood than song learning in birds; nonetheless, progress has been made. Patterns are beginning to emerge in the preponderance of both forms of vocal learning—learned acquisition and social modification—and we have gained insight into what factors favor vocal learning. We discuss these patterns and insights here.

5.1.1. Patterns of Learned Acquisition Compared

Birds from all three families studied—oscines, psittacines, and trocholids—acquire vocalizations through learning, but the evidence for mammals is scant, inconclusive, and limited to cetaceans. Abnormal development of vocalizations in acoustically isolated or deafened birds indicates that chickadees, budgerigars, and Anna's hummingbirds acquire some aspects of calls or song through learning. Other features are apparently innate and still others socially modified. The B and C notes in chickadee calls, but not the A note, require acoustic and social input to develop normally. Tonal features of budgerigar contact calls are acquired through learning, but bandwidth, maximum and minimum frequency, and duration appear to be innate. Some features of budgerigar warble song require acoustic input for normal development. Several frequency and temporal features of Anna hummingbird song are abnormal in isolated birds, although other frequency characteristics develop normally. All members of stripe-backed wren family groups share a sex-specific repertoire. The occasional unrelated male shares its group's repertoire, implicating learned acquisition (Table 4.1). The one

phasianid studied, bobwhite quail, shows no evidence of any kind of vocal learning (Table 4.1).

The only mammalian vocalizations that seem to allow for learned acquisition are whistle signatures in bottlenose dolphins and song themes in humpback whales. Learned acquisition is implied, but not demonstrated, by the appearance of shared whistle types in dolphin repertoires and by the addition of new, shared themes to humpback songs. These instances suggest learned acquisition because complete vocalization types are shared and seem to appear relatively intact in individual repertoires after hearing them in socially relevant contexts. Current data are insufficient to rule out social modification as a mechanism for sharing of call types. Individual repertoires of dolphins appear to be large and are incompletely known; thus, whistle sharing could reflect a change in how often an individual produces a particular whistle that it already knows rather than acquisition of a novel type. Experiments should be conducted and published to test directly the importance of learned acquisition to whistle structure in dolphins. Unfortunately, experimental tests in humpbacks would be difficult.

The types of vocalizations that are acquired through learning include both song and contact calls that function as group and individual signatures and show dialect variation in birds and possibly mammals. This suggests that similarity to others is important in all types of vocalizations.

5.1.2. Patterns of Social Modification Compared

Social modification seems to be a widespread mechanism of vocal learning both in birds and in mammals. Again, birds from all three groups show social modification (Table 4.3). Convergence in frequency features of chickadee D notes depends on social modification in adults, although temporal features and note-type proportions do not seem to rely on any form of vocal learning. Juvenile budgerigars incorporate many frequency features and some temporal features of social partners' calls into their contact calls. Vocal plasticity persists into adulthood in this species also because the adult members of social groups give similar contact calls and males sing similar warble song. As with chickadees, some call and song features do not rely on learning. The structure of individual notes and the temporal pattern of song is shared by Anna hummingbird males raised together, suggesting that, in addition to learned acquisition, social modification influences song structure in this species. In addition, individual Australian magpies share songs with their group mates (Table 4.1).

The incidence of social modification in mammals, including bats and cetaceans but not nonhuman primates, is more widespread than for learned acquisition (Tables 4.2 and 4.3). Lesser spear-nosed bat infants appear to modify frequency and temporal features of their isolation calls to increase similarity to their mothers' directive calls. Greater spear-nosed bat females change the fine structure of screech calls, including frequency and

TABLE 4.3. Distribution of social modification among taxa reviewed.

Taxon	Family	Level	Function	Social modification	Species
bird	songbird	individual sig.	contact	unknown	zebra finch
bird	songbird	group sig.	contact	yes	chickadee
bird	songbird	group sig.	territory/ contact	yes	Australian magpie
bird	songbird	group sig.	territory/ contact	unknown	stripe-backed wren
bird	songbird	group sig.	contact	unknown	cacique
bird	parrot	group sig.	contact	yes	budgerigar
bird	quail	group sig.	contact	no	bobwhite
bird	parrot	warble song	song	yes	budgerigar
bird	hummingbird	dialect	song	yes	Anna's hummingbird
bird	hummingbird	dialect	song	unknown	hermit hummingbird
bird	hummingbird	dialect	song	unknown green	violet-ear hummingbird
bird	hummingbird	dialect	song	unknown sparkling	violet-ear hummingbird
bird	parrot	dialect	contact	unknown	yellow-naped amazon
mammal	bat	individual sig.	echo	yes	horseshoe bat
mammal	bat	individual sig.	contact	yes	lesser spear-nosed bat
mammal	bat	individual sig.	contact	no	evening bat
mammal	bat	individual sig.	echo	no	big brown bat
mammal	cetacean	individual sig.	contact	yes	bottlenose dolphin
mammal	primate	individual sig.	alarm	no	vervet monkey
mammal	primate	individual sig.	food	no	rhesus macaque
mammal	primate	individual sig.	play	no	rhesus macaque
mammal	primate	individual sig.	food	no	Japanese macaque
mammal	primate	individual sig.	play	no	Japanese macaque
mammal	bat	group sig.	contact	yes	greater spear-nosed bat
mammal	cetacean	group sig.	contact	unknown	orca
mammal	cetacean	group sig.	contact	unknown	sperm whale
mammal	primate	group sig.	contact	no	marmoset
mammal	primate	group sig.	contact	no	pigtail macaque
mammal	primate	group sig.	territory/ contact	no	tamarin
mammal	cetacean	song	song	yes	humpback whale
mammal	primate	dialect	territory/ contact	no	gibbon
mammal	seal	dialect	song	no	Weddell seal
mammal	seal	dialect	song	no	bearded seal
mammal	seal	dialect	song	no	N. elephant seal
mammal	rodent	dialect	alarm	no	prairie dog

temporal features, to converge on group mates' calls. Juvenile horseshoe bats alter the resting frequency of CF echolocation pulses to be more similar to their mothers' (Table 4.2). Humpback whales match the themes they sing to those that other whales are singing, although the nature of this process and how heavily it relies on learned acquisition or social modification remain to be explained. In all of these cases, social modification increases similarity and may facilitate recognition of individuals and group mates. Bottlenose dolphins may modify whistle signatures to be either more or less similar to certain other individuals, although who is copied is inconsistent. Decreased similarity may facilitate individual recognition, whereas increased similarity may facilitate social cohesion. No uncontested evidence demonstrates that primates socially modify vocalization structure, although they may learn correct usage of vocalizations through social interactions. Social modification appears to be more common in birds than in mammals, although mammals have been less well-studied so this pattern may reflect an experimental bias.

For several mammals, individual signatures are socially modified. These individually distinctive calls function as contact calls (e.g., lesser spearnosed bats), sonar signals (e.g., moustache bats; Table 4.2), or territorial advertisements (kangaroo rats; Table 4.2). Social modification occurs quite frequently in group signatures for both birds and mammals (Tables 4.1 and 4.2). In addition, dialect variation in song of two bird species (Anna's hummingbird and budgerigar) and one mammal species (humpback whale) appears to arise, at least in part, from social modification.

5.1.3. General Principles that Can Be Derived from These Patterns

Social modification may be more widespread because it is a simpler mechanism than learned acquisition with respect to required motor, perceptual, and neural substrates, or because social modification is less risky in an evolutionary sense. Normal vocal development is more certain than with learned acquisition, but enough flexibility in motor control, perceptual discrimination, and neural processing can be retained to allow vocalizations to be fine-tuned to the social circumstances. The apparent predominance of social modification may also result from our patterns of investigation. Research into call learning in birds and mammals is much less well-developed than song learning in oscine birds, and we have yet to work out the mechanism of call sharing and dialect variation in many cases. Demonstrating learned acquisition is more complex than demonstrating social modification, so we may just have more known instances of the latter. More work to elucidate mechanisms in taxa where vocal learning occurs is warranted. However, this work is not without obstacles and will require creativity in experimental design. Deafening is both unethical and likely to be unproductive in taxa such as bats and odontocetes that rely on hearing for navigation. Social isolation is less extreme but can produce abnormal

behavior in taxa that are extremely social, making interpretation of call development patterns difficult. Vocalizations may appear abnormal not because acoustic input and motor flexibility are necessary for normal development but because of pathological behavior or inappropriate social context.

The vocal flexibility required for effective echolocation in odontocetes and chiropterans may have allowed vocal learning of social signals as well, an idea also developed by Tyack (personal communication). Bats, whose echolocation behavior is well-studied, modify many aspects of their vocal output to facilitate navigation and prey capture (Griffin 1958, 1986; Schnitzler and Henson 1980). They alter the structure of sonar signals to provide appropriate information at each stage of searching for and approaching an insect prey, changing duration, extent of frequency modulation, bandwidth, and repetition rate of pulses (e.g., Kalko and Schnitzler 1993; Kalko 1995). Some species also exhibit Doppler-shift compensation, adjusting the frequency of sonar emissions to stabilize echo frequency during flight (Schnitzler 1967). This flexibility allows bats to finely tune their vocal behavior to its specific function, and this modification occurs very rapidly, often in less than a second (for reviews, see Schnitzler and Henson 1980; Griffin 1986). Such vocal flexibility in echolocation pulses is probably under fairly strong selection because of its role in foraging. Once vocal flexibility for echolocation evolved, social calls may have been readily learned, requiring little modification to vocal production or neural processing mechanisms. Indeed, it appears that processing of social calls is done by the same neurons involved in echolocation processing (Ohlemiller et al. 1996; Esser et al. 1997). Thus, adapting the similarity of individual or group signatures to social partners becomes an easy task.

Individual signatures function best when they are maximally different from others, whereas group signatures function best when group mates sound similar yet distinct from other groups. The common effect of vocal learning is to modify the extent of similarity between individuals; however, changes might be in opposite directions, depending on call function.

5.2. Are Models of Song Learning in Birds Relevant to Call Learning?

5.2.1. Sensorimotor Model

The most widely considered model for the process of song learning in oscine birds is the auditory template model (Marler 1976) that builds on the sensorimotor model developed by Konishi (1965). This idea suggests that juvenile songbirds are born with a crude neural template of their species' song. This crude template guides song memorization and attention to certain song types during the early phases of song learning. During the memorization phase, young birds memorize songs and song elements that they hear,

refining the neural template to match these memorized songs. In many species, there is a critical period during which songs are memorized. Songs heard after this critical period are not memorized and copied. During the motor phase, young males begin to sing. Song output is guided by auditory feedback, and close matching is achieved by comparing an individual's own song to the neural template. Initially, acoustic output is highly variable subsong, likened to babbling in human infants. Gradually, song comes to resemble the adult songs that young males heard during the memorization phase as they more closely match song output to the internal template. Finally, males crystallize their songs and produce adult-form songs.

5.2.2. The Process of Song Matching: Delayed Critical Period or Selective Attrition?

When exposure to normal calls as adults allows isolates whose calls are abnormal to develop normal calls, a critical period is unlikely or has an extended duration. This pattern cannot result from selective attrition because juveniles neither heard nor produced normal calls early in development. Unfortunately, studies do not regularly report repertoire size during the various stages of normal vocal development, which is essential data for testing selective attrition.

Song matching to neighbors seems to occur when a male first settles on a breeding territory. Controversy centers on whether this matching involves acquisition of those songs at that time, and hence extension of the sensitive phase (Slater 1989), or selective attrition from an overproduced repertoire of songs memorized during an early sensitive phase (Nelson and Marler 1994). While those working on song learning debate and test these two hypotheses, the controversy can ignite some very exciting work on call learning in birds and mammals. For each taxonomic group, we can begin to address several questions: Is there a sensitive phase for call learning? Does it differ depending on call function? Can it be modified or extended by social interaction? Is there a phase of overproduction followed by a loss of call types to achieve matching? Or are novel call types acquired de novo to achieve matching? Broadening our inquiry into vocal learning by including other taxa besides oscines and other vocalizations besides song may give us insight into the process in songbirds by helping to reveal which ecological and behavioral factors shape the vocal learning process. What we currently know about the process of vocal learning in taxa other than oscines is discussed below.

5.2.3. The Importance of Social Interaction

Social interaction is often claimed to override the critical period and be a powerful force shaping songs. The keen interest in how social processes affect vocal learning is highlighted in the title of a recent book on vocal learning: *Social Influences on Vocal Development* (Snowdon and

Hausberger 1997). If our premise here is correct—that call function reveals where selection operates—then social interactions should have a very strong part to play in call learning because calls often function to mediate complex social interactions. When the degree of similarity affects call function, social partners are likely to serve as call tutors, and the absence of social interaction is likely to have a profound influence on call development, especially when learned acquisition occurs.

Primates may not show vocal learning because other cues are used for identification and social facilitation, with vocalizations playing only a supportive role. Alternatively, individuals' distinctive calls are a by-product of morphological and body-size differences, which do not require vocal learning. Long lives and close association allow troop members to recognize group mates' individually distinctive calls. Under both hypotheses, vocal learning simply is not necessary.

5.2.4. Relevance to Call Learning in Birds

We would next like to apply these ideas to the few cases where data on the process of call learning are available for birds and mammals. This allows us to evaluate the extent to which auditory template or sensorimotor models describe call learning in mammals and birds. We also describe the process of call matching to evaluate the universality of critical periods and the extent of social influences on call development. Ideal studies for evaluating these hypotheses include replicated data from deafened, totally isolated, acoustically isolated, socially isolated, and normally reared individuals. Unfortunately, we have these comprehensive data for very few taxa; therefore, our conclusions are tentative. Currently, insufficient data are available for most taxa to test the selective attrition hypothesis for call learning.

5.2.4.1. Sensorimotor Model in Birds

Evidence that sensory input is essential for normal call learning comes from studies on contact calls in budgerigars (Dooling et al. 1987; Brittan-Powell et al. 1997; Heaton and Brauth 1999; Heaton et al. 1999) and chickadees (Ficken et al. 1985; Hughes et al. 1998) and for song learning in Anna's hummingbirds (Baptista and Schuchmann 1990). Early vocalizations are often structurally simple and highly variable, and they become more complex and stereotyped with age (Clemmons and Howitz 1990; Brittan-Powell et al. 1997). Deafened budgerigars developed abnormal contact calls that bore little resemblance to the species' typical call (Dooling et al. 1987; Heaton and Brauth 1999). Calls of adults without auditory feedback deteriorated (Heaton et al. 1999). Juvenile chickadees who did not hear adult calls developed abnormal variable see, gargle (Ficken et al. 1985), and chickadee calls (Hughes et al. 1998), indicating that appropriate acoustic input is essential. Isolated juvenile Anna's hummingbirds sang songs that differed from normal song in several acoustic features (Baptista and Schuchmann 1990),

again showing the importance of acoustic input. Too little work has been done to directly test the auditory template model; however, these data suggest that sensorimotor processes are important in budgerigars, chickadees, and hummingbirds. There is no evidence of a delay between memorization and production of calls in budgerigars or chickadees as has been found for song learning in many songbirds.

5.2.4.2. The Process of Call Matching for Birds: Delayed Critical Period or Selective Attrition?

Budgerigars (Farabaugh et al. 1994; Brittan-Powell et al. 1997), chickadees (Mammen and Nowicki 1981; Nowicki 1989), and Australian magpies (Table 4.1) retain the ability to match contact calls of social partners past fledging and into adulthood. This could result from a delayed closure to the critical period for call memorization, the absence of a critical period, or because of selective attrition of previously memorized calls. Taxa for which acoustic isolation experiments have been done supported extended critical periods.

When acoustically isolated budgerigars were subsequently housed with individuals who gave normal calls, they modified their calls to closely resemble species-specific calls (Brittan-Powell et al. 1997). An extended critical period is more likely to explain this result because juveniles neither heard nor produced normal calls early in development. Adult birds also changed calls to match group mates' calls (Farabaugh et al. 1994), again suggesting the absence of a critical period, although in adults this pattern could result from selective attrition. In budgerigars, group signatures clearly rely on social interaction.

Critical periods differ for each note in the chick-a-dee call. A notes develop normally in isolated birds, as do B notes, but Hughes et al. (1998) suggest that selective attrition may be involved in fine-tuning A note structure. A critical period for C notes is implied by the finding that juvenile chickadees exposed to adult chick-a-dee calls only after the age of 38 days developed C notes as abnormal as total isolates (Hughes et al. 1998). Vocal plasticity of D notes is retained into adulthood (Nowicki 1989), and selective attrition may be involved in D note convergence within flocks (Hughes et al. 1998). However, there is no direct test of the selective attrition hypothesis for group-signature development.

Hand-raised juvenile Anna's hummingbirds that were housed together from 64 days to adulthood sang remarkably similar, although abnormal, song (Baptista and Schuchmann 1990), suggesting that vocal plasticity was retained to 64 days or beyond. A single isolate showed no evidence of learning from an adult with which it was housed after one year, suggesting that this species does have a critical period that ended before this time. The data from this one study are somewhat contradictory with regard to critical period, and strong conclusions are not possible with such small sample sizes.

5.2.4.3. The Importance of Social Interaction for Birds

Social interaction strongly influences call learning in budgerigar and chickadee group signatures, and may influence Anna's hummingbird song and stripe-backed wren and cacique group signatures. Budgerigars preferentially converge on contact calls of group mates over other birds that they can hear but with which they have no social contact (Farabaugh et al. 1994). Young birds copy adults with which they have social bonds even when those adults give abnormal or heterospecific calls (Brittan-Powell et al. 1997). Social interaction is clearly important to convergence in chickadee calls. Isolated juveniles housed together shared the same abnormal song (Hughes et al. 1998), and adults converged rapidly in D note structure (Nowicki 1989). All male stripe-backed wrens in a group share a repertoire, and all females share a different repertoire (Table 4.1). Although male group mates are close relatives and could share songs because of this, female group mates are not closely related; thus, at least female repertoire sharing results from social contact. The contrasting support for a critical period in Anna's hummingbird group and single isolates could be explained by social factors. The group isolates had developed social bonds and thus were effective tutors for each other, whereas the single isolate may not have developed a social bond with the adult male, making this adult an ineffective tutor. Data to evaluate this hypothesis are not available in the original paper (Baptista and Schuchmann 1990). In many birds, social partners are copied, resulting in acoustic convergence among social groups. In the three best-studied birds, sensorimotor input and social interaction are necessary for at least some of call development, and call learning persists well past the nestling stage.

5.2.5. Relevance to Call Learning in Mammals

5.2.5.1. Sensorimotor Model in Mammals

Very few studies on the effects of deafening or acoustic isolation have been done in mammals other than primates, making it difficult to evaluate the importance of sensory input and the sensorimotor or auditory template models. The data we do have are a few observational studies of normal vocal development. Studies of sonar signal development in infant bats generally show that infants begin to produce sonar signals within a few days of birth, coinciding with the onset of hearing during the second postnatal week in many species. Infant sonar signals tend to be of lower frequency, longer duration, show less steep frequency modulation, and be more variable than adult signals for both constant frequency (CF/FM) bats (Brown et al. 1983; Habersetzer and Marimuthu 1986) and FM bats (Moss 1988; Moss et al. 1997). An increase in signal frequency corresponds with an increase in auditory responses to high-frequency sounds (Konstantinov 1973; Rübsamen et al. 1989). The auditory and vocal-production systems develop in concert.

Deafened young horseshoe bats shift the frequency of their CF sonar signals (Rübsamen 1987), indicating that auditory feedback does influence vocal output, resulting in precise matching of cochlear tuning and vocalization frequency in normal individuals. However, vocal output has no effect on cochlear tuning or responsiveness of the auditory system, so this influence is unidirectional (Rübsamen 1987) and results in fine-tuning the frequency of existing vocalizations rather than substantially reorganizing signal structure.

Several researchers hypothesize that sonar signals develop from communication signals (Moss 1988). Isolation calls in infants who had no acoustic input are normal, infants give these calls within a few hours of birth, and species that cannot hear at birth produce isolation calls. Acoustic input is clearly not essential for normal development (Ehret 1980). This appears to be true also for sonar signals (Gould 1975). In none of these instances is there direct evidence testing the role of vocal learning. Isolation calls do show age-related changes (Jones et al. 1991; Scherrer and Wilkinson 1993). Most changes are consistent with maturation of laryngeal and respiratory function and of peripheral and central nervous control, allowing greater control of vocal production (Could 1975). Functional considerations make a reliance on acoustic input for call acquisition and normal development unlikely. A bat with abnormal sonar signals would be severely handicapped in foraging. An infant unable to produce normal isolation calls risks permanent separation from its mother, on whom it is completely dependent early in life. Vocal learning, when it occurs, is probably restricted to social modification to increase individual distinctiveness (Masters et al. 1995) or increase similarity to the infant's mother (Jones and Ransome 1993; Esser 1994) and to tune vocal output to the best frequency of the auditory system (Rübsamen 1987). Thus, individual signatures and echolocation calls are more likely to be socially modified than acquired through learning.

Very young infant bottlenose dolphins give whistles, suggesting that acoustic input is unnecessary for normal call production; however, direct tests have not been done. As with infant bats, a reliance on acoustic input for normal development is risky, so social modification to adjust the degree of similarity with social partners is likely to be the predominant form of vocal learning. An interesting question is whether the preponderance of social modification over learned acquisition in bats and cetaceans is due to similar call function or because both echolocate.

5.2.5.2. The Process of Call Matching for Mammals: Delayed Critical Period or Selective Attrition?

In both bats and dolphins, the critical period seems to be either nonexistent or labile to accommodate changing group composition and social relationships. However, the mechanism of call matching is unclear. In bats,

convergence between mothers and offspring or among adult group mates results from subtle acoustic changes to a single call type (e.g., sonar signal, isolation call, or contact call). This convergence may arise through mutual imitation of acoustic characteristics or selective attrition from a more variable acoustic space. In dolphins, several studies have inferred mimicry in both juveniles and adults, suggesting open-ended learned acquisition. This is certainly possible, yet the size and turnover of juvenile repertoires suggest that individuals may choose matching whistles from a large repertoire. Experimental tests of these two mechanisms are lacking and would be fruitful.

5.2.5.3. The Importance of Social Interaction for Mammals

Experimental evidence of the relative importance of social interaction is also lacking. Much of the data on vocal learning in mammals are observations and experiments showing convergence among social partners. The apparent advantage of vocal learning is to modify the degree of acoustic similarity to enhance social function. All of this points to an important role for social factors. Individuals who serve as models for imitation are those who are the focus of other social interactions.

Recent research is just beginning to outline patterns for the importance of sensorimotor input, call matching, and social interaction in mammalian call learning. As yet, we have little data on the actual processes that underlie these patterns and cannot yet evaluate how closely call learning in mammals matches song learning in birds. Research is likely to progress most rapidly with small-bodied mammals, such as bats, because of the greater ease with which they can be housed. We hope that methods will be developed to study processes in cetaceans as well. Interest in comparing the process of call learning in both birds and mammals to song learning is high and should lead to further work on the underlying processes. This area promises rich rewards.

5.3. Future Directions

5.3.1. Studying Vocal Learning in a Phylogenetic Context

We are close to the point where we can consider comparative tests for hypotheses about the mechanisms, function, and evolution of vocal learning in a phylogenetic framework. Many fundamental questions regarding vocal learning would be possible within this framework, such as: How often has vocal learning evolved? Do learned acquisition and social modification represent distinct processes, or are they different outcomes of the same process? A comparative approach opens up the possibility to test specific hypotheses about the motor, sensory, and physiological underpinnings of learned vocalizations. Which mechanisms, if any, are common to the taxa

that learn vocalizations? A comparative approach also allows us to test hypotheses of the ecological and behavioral factors that favor vocal learning. Are certain social structures conducive to vocal learning? Are individual signatures and group signatures influenced equally by vocal learning? Is there support for the hypothesis that echolocation predisposes species to learn social calls? Although we are close to the point where we can ask these questions, we need to broaden even further the taxonomic groups we choose to study. When designing new studies, careful consideration of the phylogenetic relationship of a taxon to those for which we already have data on vocal learning is warranted.

5.3.2. Cultural Evolution and Vocal Learning

The study of learned vocalizations is an especially pertinent type of social learning that can inform both theoretical and empirical work on gene–culture evolution. Nonvocal traits that are transmitted culturally can affect the course of evolution for other traits (Feldman and Laland 1996). In the nonhuman literature, examples have focused on cultural transmission of foraging strategies, probably because foraging was thought to be under strong selection to be optimal. This focus has yielded important advances in theoretical work and some very interesting empirical results. Yet, the ability to modify the evolution of other traits might be especially true for behavioral traits that affect social organization or mating. Social interaction is nearly always involved in cultural transmission, and traits are often transmitted between the members of social groups. Consequently, cultural traits that themselves affect social organization can powerfully influence both their own transmission and other aspects of a species' biology. Culturally transmitted traits that affect the likelihood of mating almost certainly alter the fate of traits transmitted genetically. Many of the vocalizations reviewed here are integral to the smooth functioning of social groups. In at least one case, learned vocalizations actually facilitate another form of social learning—social foraging (greater spear-nosed bats—Boughman 1998; Wilkinson and Boughman 1998).

Certainly, there is a rich history of this kind of work in the birdsong literature, including applications of the "meme" concept (Payne et al. 1988; Payne and Westneat 1988; Trainer 1989; Ficken and Popp 1995). Much of this work has focused on the fate of song variants, and fewer studies have explored genetic consequences or tested gene–culture models (Gibbs 1990; Grant and Grant 1996). We urge increased focus on the processes and consequences of culturally transmitted vocalizations outside of oscine song. Both a fine-scale focus on individual species and large-scale consideration of mechanisms and patterns across species are likely to yield plentiful insights into how genes and culture coevolve. This work will require simultaneous study of vocal and genetic variation, both time-consuming occupations but likely to be well worth the effort.

6. Summary

We have reviewed data on call learning in birds and mammals for calls that function as individual or group signatures and dialects and focused on call learning rather than song learning. We distinguished two forms of vocal learning—learned acquisition and social modification. We began by predicting when vocal learning was expected and detailing the evidence necessary to demonstrate that vocalizations were learned. Studies should exclude or control factors that can produce patterns similar to those induced by learning, including maturation, body size, genetics, population structure, and local ecology. We then presented case studies for three functional levels: (1) individual signatures: lesser spear-nosed bats, bottlenose dolphins, and Japanese and rhesus macaques; (2) group signatures: chickadees, budgerigars, greater spear-nosed bats, killer whales, and pygmy marmosets; and (3) dialects: Amazon parrots, hummingbirds, humpback whales, and tamarins.

Learned acquisition of calls is rare in mammals although fairly common in birds. Social modification is more common in both mammals and birds. Social modification of group signatures is particularly prevalent. Too little data are available to carefully test the validity of song-learning theories for call learning. This area should receive further attention to evaluate the necessity of sensorimotor input, the existence and duration of critical periods, and the possibility of selective attrition. Social interaction is clearly necessary for most species. The study of call learning in mammals and birds has much promise. Not only can it provide critical insight into the neural, perceptual, and motor mechanisms that underlie vocal learning across taxa, but also into the ecological and behavioral factors that favor its evolution. These questions will benefit from putting vocal-learning studies squarely in a phylogenetic framework. Vocal learning also has potential to give us insight into cultural evolution and help us understand how the dual processes of genetic and cultural change influence biological evolution and diversity.

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