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ISBN: 978-0-12-374475-3

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Plasticity of Communication in Nonhuman Primates

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I. INTRODUCTION

Many taxa display impressive communicative abilities. From the wonderfully diverse patterns of song seen across the range of songbirds to the songs of humpback whales and other cetaceans to the highly coordinated duetting of gibbons and siamangs, nature provides us with many examples of impressive vocal complexity and vocal variability. Songbirds also provide us with an important model of vocal development that has been offered as a model for understanding the ontogeny of speech and language (e.g., Marler, 1970). Except for the songs of gibbons and siamangs, nonhuman primates, the closest relatives of humans, appear to have superficially simple vocal repertoires and none of the striking virtuosity of a tiny songbird. There does not appear to be much direct evidence of vocal learning (Hammerschmidt and Fischer, 2008; Janik and Slater, 1997, 2000) although there are many examples suggestive of learning.

Why do most nonhuman primates show so little diversity and complexity in their calls? One potential explanation is that those taxa with the greatest communicative virtuosity and ability to learn signals are species that are highly mobile. Many birds migrate and may return with a very different set of companions than from the previous year and so the ability to adjust vocal patterns to fit in with those of the neighbors may be important. Even nonmigratory birds have the ability to move across several home ranges to find mates and establish territories, Cetaceans and other sea mammals as well as bats can also cover long distances and encounter individuals from many other locations. In contrast, most terrestrial mammals including nonhuman primates do not travel far, with dispersal in nonhuman primates rarely going more than two or three home ranges from the natal group (Pusey and Packer, 1987). Thus nonhuman primates are unlikely to encounter individuals from other populations and this may militate against vocal learning as
adaptive. Another explanation for the complexity of birdsong is its role in sexual selection whereas in many nonhuman primates sexually selected traits are more often represented by morphological patterns.

A significant problem in studying the possibility of vocal learning in nonhuman primates is that few animal ethics committees today would approve the isolation rearing of nonhuman primates that has provided unequivocal evidence of vocal learning in birds. A few early studies suggest that isolate-reared squirrel monkeys (Saimiri sciureus) have a complete vocal repertoire along with appropriate usage (Herzog and Hopf, 1983, 1984; Winter et al., 1973) whereas isolate-reared rhesus macaques (Macaca mulatta) show only minor deficits in vocal signals (Newman and Symmes, 1974). Different inferential methods are needed to replace isolation rearing in order to determine if primates are capable of vocal learning.

Song is but one of many signals used by birds and relatively little is known about the ontogeny of other signals in birds. In contrast, research on nonhuman primates has focused on multiple signal types that may not meet the strict criteria of Janik and Slater in terms of vocal learning but are, nonetheless, used in complex, subtle, and innovative ways. The more interesting results from nonhuman primates may not be in vocal production, per se, but rather in how calls are used and understood by others.

In reviewing developmental studies on nonhuman primates, Seyfarth and Cheney (1997) noted that there was little evidence for plasticity in vocal production in nonhuman primates, but considerable evidence for plasticity in comprehension and in usage of calls. Subsequent research has been expanded on the notions of plasticity in all three dimensions: production, usage, and responses to calls. In this chapter, I will review some of this recent work and in addition look at the role of communication signals in facilitating social learning. Birdsong is socially learned, but do signals themselves influence social learning in primate species?

II. PLASTICITY OF PRODUCTION

Janik and Slater (2000) proposed a strict definition of production learning that requires a demonstration that vocal structure is changed as a result of social interaction with others. Many of the examples that follow cannot be explained in terms of the strong inference methods required to demonstrate that call structures are changed only through direct contact with others. Hence, I will use the term “plasticity” to indicate evidence of change that appears to be possibly due to social interactions but where strong evidence for vocal learning is not available.
A. Population Differences

Contrary to strong views that primate vocal structures are basically hard wired and consistent within a species, there are several examples of signals that show systematic variation in different populations. Green (1975) first reported that different populations of Japanese macaques (Macaca fuscata) produced different variations of food vocalizations when a caretaker approached to provision them. He, thus, hypothesized that these population-specific calls came about through conditioning by caretakers, but the same calls were heard in unprovisioned groups so the argument for learning was hypothetical. Masataka (1992) conditioned two infant Japanese macaque females to respond to their names. Each time they gave a vocal response to a human calling their name the monkeys received a food reward. Over a 4-week training period, the monkeys increased their rate of vocalization in response to hearing their names and each monkey produced a coo call variant that was idiosyncratic to each individual, suggesting conditioning of vocal production and the ability of monkeys to alter vocal structure within the parameters of a call already in their repertoire.

In other studies on Japanese macaques, Tanaka et al. (2006) described the differences in the structure of coo calls of two populations that had arisen from the same population but had been separated for more than 30 years. Coo structures differed significantly at all ages except for very young animals, suggesting that the “dialects” of the two populations were learned early in life.

Different populations of wild chimpanzees (Pan troglodytes) have different versions of pant-hoots, a long distance vocalization. The first reports illustrated differences in structure between chimpanzees at Gombe National Park and those at Mahale Mountains National Park, both in Tanzania (Mitani and Brandt, 1994; Mitani et al., 1992), although the Gombe calls were not recorded contemporaneously with those at Mahale, so differences may represent historic drift. Mitani et al. (1999) compared contemporaneous recordings made at Mahale and Kibale National Park in Uganda and found quantitative differences in structure between the two populations. They suggested that these were due to genetic drift, differences in habitat acoustics, or ambient noise spectra, but did not do simultaneous measurements of habitat acoustics or ambient noise spectra.

Marshall et al. (1999) found significant differences in pant-hoot structure between two captive populations of chimpanzees in the United States and argued that since the males within each group had come from different origins, the common theme to each group must have been due to learning after the males joined each group to allow the development of group-specific variants.
Crockford et al. (2004) reported differences in pant-hoot structure in males from three contiguous populations of chimpanzees in Tai Forest, Ivory Coast using discriminant function analysis. They found no differences between these contiguous populations and a fourth distant population, suggesting that vocal divergence may be important to distinguish local populations from each other. They also reported no correlation between acoustic differences and genetic differences in pairs of animals. They suggested that there should be little variation in habitat among the areas of the three populations, but they did not directly evaluate habitat acoustics. Based on the lack of relationship of acoustic variation and genetic variation and the assumption of no differences in habitat acoustics, they suggested that the differences in pant-hoot structure must be due to social learning.

Fischer et al. (1998) recorded shrill bark vocalizations of two populations of captive Barbary macaques (*Macaca sylvanus*) to the presence of a dog and reported distinct population differences in the structure of shrill barks on the basis of discriminant function analysis. They also played back calls of the same population and calls of the other population to both and found a slight (ca. 1 s), but significant, increase in looking time to calls from the other population. Both groups had been from the same founder population and the study was done approximately 20 years after each group had been established, making it unlikely that the differences were genetic.

De la Torre and Snowdon (2009) studied five populations of the pygmy marmoset (*Callithrix (Cebuella) pygmaea*) in Ecuador. Pygmy marmosets have two types of vocalizations exchanged between group members at close distances, the Trill and the J-call. The five populations spanned an east–west transect of about 300 km and a north–south transect of about 100 km. De la Torre and Snowdon (2009) studied the adult male and female from two to three separate groups and found that within each population there were significant individual differences. However, after controlling for individual variation, there were clear differences in both the trill and the J-call across populations using both discriminant function analyses and testing individual call variables. For trills, rate of frequency modulation, minimum frequency, and call duration were the main contributors to the discriminant analysis and calls were classified correctly 71.4 % of the cases compared with an expected value of 20%. For J-calls, maximum frequency and duration were the main variables with 78.6% of cases being correctly classified. Based on the analyses of individual variables, each population differed from each other population on at least one acoustic variable.

De la Torre and Snowdon (in preparation) also measured the spectrum of ambient noise and the degree of reverberation in each habitat and found significant differences between habitats. Whereas some of the acoustic differences in call structure could be interpreted as adaptations to local
acoustic environment, other differences could not be explained on the basis of habitat differences. Because rivers serve as barriers to dispersal in the Amazon, it is possible that the differences are due to genetic drift leading to population differences, but as captive pygmy marmosets quickly change vocal structure in response to social changes (Elowson and Snowdon, 1994; Snowdon and Elowson, 1999), we cannot rule out the possibility of some form of vocal learning.

Interestingly, we found parallel differences in the same five populations in the tree species used for exudates feeding. Each population had a preferred tree species, but the preferences were not based on the relative abundance of the preferred tree species in that habitat (Yepez et al., 2005), suggesting that the five different populations vary not only in vocal structure but in foraging choices as well.

In summary, there are some examples of population differences in vocal structure across a broad taxonomic range of primates. However, only in Japanese macaques there is clear experimental evidence of vocal change at an individual level. All other claims for vocal learning are at present inferential and in the absence of genetic analyses and careful measurements of habitat acoustics, current field data do not support that vocal learning occurs using the criteria of Janik and Slater (2000).

B. ENVIRONMENTAL INFLUENCES

Ey et al. (2009) studied grunt vocalizations of wild olive baboons in a forest and in an open habitat and found that grunts given in the forest population were longer and had a lower fundamental frequency and/or lower emphasized harmonic than the baboons in the open habitat as expected if vocal structure was adapted to habitat acoustics. As predicted, forest-living baboons also produced contact calls at a higher rate than those in an open habitat.

The Lombard effect is the increase in amplitude of speech that occurs when background ambient noise is increased. Two Old World monkeys, a male long-tailed macaque (Macaca fascicularis) and a female pig-tailed macaque (Macaca nemestrina) increased the amplitude of their vocalizations when presented with increased levels of ambient noise in the range of their own vocalizations (masking). They showed no change in amplitude to increases in high-frequency ambient noise (nonmasking). Amplitude of vocalizations tended to increase with increased amplitude of masking noise (Sinnott et al., 1975). Common marmosets (Callithrix jacchus) also increased the amplitude of their twitter calls with increasing amplitude of ambient noise and they also increased the duration of individual units within their twitter calls (Brumm et al., 2004). Using a different
methodology involving a burst of white noise in the middle of an on-going long call in cotton-top tamarins (*Saguinus oedipus*), Miller et al. (2003) found that this noise would interrupt the production of long calls with the call terminating after completion of the syllable that was interrupted. Egnor et al. (2006) expanded on this paradigm and found that white noise bursts during long call production lead to shorter notes and calls with higher amplitude and longer interpulse intervals consistent with the idea that tamarins can adjust calling facultatively to environmental noise. Both the Lombard effect and the truncation of a call in response to a burst of white noise imply that these nonhuman primates must have some degree of control over the structure of their vocalizations. Vocalizations are not simply due to fixed motor control systems.

C. **Social Influences**

Another approach to understanding variation in primate communication involves natural or experimental changes in social status or social housing of animals. Fischer et al. (2004) studied the “wahoo” calls of wild baboons (*Papio cynocephalus ursinus*) in Botswana. Among other contexts, wahoons are given in aggressive interactions between males. High ranking males produce wahoons at higher rates and for longer duration bouts than subordinate males, and call structure changes with rank as well. Both fundamental frequency and call duration are positively correlated with male rank. The finding of higher fundamental frequency with increased rank is different from the expectation of studies in other species that low-frequency calls are markers of dominance. More energy may be required to sustain a higher pitched call over the longer bouts of dominant males and this may be an honest indicator of male quality. In support of this, Fischer et al. (2004) found that fundamental frequency of wahoons decreased as males aged and lost dominance status. However, neither dominance nor higher pitched wahoons are age-determined since subordinate males of the same age as dominants did not have increased fundamental frequencies. This study suggests that male baboons can manipulate the fundamental frequency of wahoons to reflect their dominance status.

In cotton-top tamarins, Roush and Snowdon (1999) noted that food-associated calls of young monkeys were not as consistent and well-formed as those of breeding adults and that young monkeys also inserted many other call types into feeding bouts. Curiously, there appeared to be no maturation of call structure over a broad age range with even postpubertal monkeys still producing immature forms of food calls. Since tamarins are cooperative breeders with older individuals often caring for infants rather than breeding themselves, one hypothesis is that older individuals use
infant versions of food vocalizations to communicate a subordinate status to reproductively dominant animals. If this hypothesis is true, then when the social status of tamarins is changed, call structure should change as well. Postpubertal, sexually mature animals were recorded in feeding contexts in their natal groups and then they were paired and housed in a different colony room. Within 3 weeks of pairing, tamarins no longer produced other forms of calls when feeding and within 6 weeks they were producing adult-typical forms of food calls. Different animals were paired at different ages so the results are not due to age, but must be related to change in social status.

Changing the social group of animals and evaluating vocal behavior before and after the social change has been an effective experimental method for showing vocal plasticity (e.g., Boughman, 1998 in greater spear-nosed bats). A few studies on marmosets have demonstrated vocal plasticity. Elowson and Snowdon (1994) used the opportunity of bringing two different colonies of pygmy marmosets together in one colony room to examine the structures of trill vocalization before and after the change. Groups within each colony remained in the same social groups as before; the only difference was that two previously unfamiliar groups were housed in the same space. Animals from both populations increased the bandwidth and peak frequency over the first 10 weeks after the animals were housed in the same room. Subsequently, Snowdon and Elowson (1999) measured parameters of trills in individual marmosets before pairing with a new mate, during the first 6 weeks after pairing, and 3 years later. In the pairs with individuals that differed significantly prior to pairing, there were significant changes in call structure in at least one of the animals leading to a convergence in call structure between pair members. Although many of the acoustic parameters had changed over the course of 3 years, the pairs still maintained very similar call structure.

In a similar study on Wied’s black tufted-ear marmosets (Callithrix kuhlii), Ruckstalis et al. (2003) found stability in phee call structure over several weeks of baseline, but when some monkeys were moved and housed adjacent to novel conspecifics, the discriminant function that had successfully identified each individual was no longer accurate, suggesting that the monkeys that had been moved had significantly altered the structure of their phees. In contrast, for monkeys that remained in a stable social environment, the discriminant functions that had successfully assigned calls to individuals in the baseline condition were still successful in assigning calls recorded after the baseline to appropriate individuals.

Mitani and Gros-Louis (1998) found convergence in the structure of chimpanzee pant-hoot vocalizations when they were given in choruses and by examining the structures of calls given alone and in choruses, they
concluded that chimpanzees actively altered the structure of their calls to accommodate the calls of the individual(s) with which they were currently chorusing.

Lemasson and colleagues (Lemasson and Hausberger, 2004; Lemasson et al., 2005) have described similarities in calls of individual captive Campbell’s monkeys (*Cercopithecus campbelli*) that were closely affiliated. Call structure changed over time and was especially labile when social disruptions occurred. Different captive groups had different call variants suggesting group-specific call variants. Japanese macaques also appeared to match the acoustic features of the coo vocalizations of familiar group members when these were played back, suggesting that Japanese macaques could adjust the fine structure of their calls to match those of the specific caller they heard (Sugiura, 1998). Koda (2004) reported that Japanese monkeys altered the structure of coo calls depending on whether the first call in a sequence elicits a response from others. When a call fails to elicit a response, the second call is higher in pitch and has a longer duration. In playback studies, monkeys responded more often to the playback of the second call than to the first suggesting that monkeys adjust their call structure to increase the likelihood of response by others.

In summary, with the precision of digital analysis methods that can detect subtle changes in vocal structure, it is clear that vocalizations can change within individual monkeys as a function of changes in social status or social companions in both wild and captive populations. Furthermore, the changes can take place very quickly (within a period of a few minutes in short-term vocal accommodation or over a few weeks in terms of developing longer term social relationships) and vocalizations also show drift over time. Primate vocalizations are not as precise and stereotyped as once thought and manipulation of social status or social partners is a valuable experimental method for studying vocal plasticity.

D. DEVELOPMENTAL INFLUENCES

Early isolation-rearing studies of squirrel monkeys found no impairments in vocal production (Winter et al., 1973) and even though Newman and Symmes (1974) noted pathologies in the vocalizations of isolate-reared rhesus macaques, these were found in only one type of vocalization, the coo. Hybridization between two species of squirrel monkeys with two very different forms of isolation calls led to offspring displaying the form of isolation peep appropriate for their mothers (Newman and Symmes, 1982). Studies of hybrid gibbons (Geissmann, 1984) found that hybrid songs had elements of calls of each parent. Since mothers are the only
caretakers of squirrel monkeys and both parents stay together during the
development of gibbons, the apparent genetic results from hybridization
may be due to the experience an infant gains from hearing its parent(s).

One way of avoiding this confounding variable is to cross-foster animals
between species. Thus, an infant of one species will be exposed only to the
signals of its foster parent. When Japanese macaques were cross-fostered to
rhesus macaques and vice versa, there was no evidence that the fostered
infants showed any ability to acquire the calls of their foster parents indi-
cating no social influence on vocal production (Owren et al., 1993). These
results do not conflict with those of Sugiura (1998) previously described.
Although many species of nonhuman primates appear capable of making
minor changes in call structure in response to social companions, they do
not appear to have the capacity to learn to produce calls of another species.

Several studies have recorded calls from monkeys across early develop-
ment. Lieblich et al. (1980) followed the development of isolation peeps in
infant squirrel monkeys and found that the species-typical structure was
present in the earliest recordings with the only changes being an increase in
call duration which could be related to physical maturation. Similarly, Ham-
merschmidt et al. (2000) recorded coo vocalizations from rhesus macaque
infants over the first 5 months and found that adult-like structure was present
at the first week with the only changes being reduced fundamental frequency
and decreased variability in calls. In contrast to the earlier results of Newman
and Symmes (1974), Hammerschmidt et al. (2000) found no differences
in structure between mother-reared and peer-reared monkeys.

Vervet monkeys (Chlorocebus pygerythrops formerly Cercopithecus
aethiops) have a suite of alarm calls specific to different types of predators
and young monkeys produce alarm calls that are very similar to those
produced by adults, but for grunts, a series of calls involved in social
interactions, young vervet monkeys did not display adult structure until
adolescence (Seyfarth and Cheney, 1986).

Stephan and Zuberbühler (2008) compared a population of Diana
monkeys exposed to leopard predation with a population that did not
have leopards as predators. Both populations produced similar calls to
playback of leopard growls and leopard alarm calls of other Diana monkeys
responding to leopards, suggesting an innate response to cues associated
with leopards. However, alarms from the leopard-free population were
acoustically more complex and also were used in response to general
disturbance compared with the population that had leopards present. This
suggests some ontogenetic modification of alarm call structure.

Marmosets and tamarins appear to develop their call repertoires more
slowly. Cotton-top tamarins have eight chirp-like vocalizations that are
each specific to a different context (mobbing, alarm, food, territorial
defense, cohesion; Cleveland and Snowdon, 1982). Castro and Snowdon (2000) experimentally induced several of these chirp types in adult animals. They subsequently did the same manipulations on groups with infants present over the first 5 months of infant development. Although infants produced sounds that could be identified as chirps, they typically produced them in series of two or three calls with descending pitch. In contrast, adult chirps were not produced in series and the call structure was precise and appropriate for the experimental manipulation. It is possible that infants do not have the vocal control to allow them to produce calls with the same precision as adults, but there may also be an interaction with maturation of physical control and learning to know which specific structures to use in specific contexts. In a detailed study of the ontogeny two of the chirp types (C and D chirps) used in feeding contexts, Roush and Snowdon (1994) found that calls of immature animals were consistently less “well-formed” than adult chirps.

The pygmy marmoset is unusual among nonhuman primates in that infants engage in long repetitive bouts of vocalization that can go for minutes (Elowson et al., 1998). These bouts contain many of the vocalizations that are part of the adult repertoire, but the same call types are repeated frequently and different call types are temporally associated that in adults would be seen in specific and different contexts. Thus, an infant might produce two or three contact calls followed immediately by some threat vocalizations followed by some alarm calls and so on. This “babbling” is highly energetic with infants producing up to three calls per second and continuing for as long as 6 min. Most of the call structures were similar to those seen in the adult repertoire with only 2 of 16 call types being unique to infants. This vocal activity is superficially similar to the subsong and plastic song of birds which has been labeled as analogous to human babbling. But pygmy marmosets show three important exceptions. Unlike birds, pygmy marmosets begin their vocal activity as infants and it is not a function of puberty. Both male and female marmosets engage in this behavior whereas in many songbirds only the male sings. Finally, song is but one part of the vocal repertoire of birds whereas marmosets produce 70% of adult call types in their “babbling” vocalizations. For these reasons, this complex vocal behavior of pygmy marmosets may be more relevant than birdsong as a model of human vocal development. However, it is unclear why this complex vocal behavior is seen only in pygmy marmosets. The author has observed similar behavior in wild infant common marmosets (unpublished observations).

What are the possible functions of this complex infant vocal behavior? It is not an artifact of captivity since we have observed it in the field (De la Torre and Snowdon, unpublished observations) where infant vocalizations
can help us to locate a group. The behavior is energetically costly to infants and by making their location easily identified can also increase vulnerability to predators. The vocal behavior does draw the attention of adults and “babbling” infants are more likely to be subsequently involved in social interactions than a quiet infant (Elowson et al., 1998). Thus, this complex vocal behavior may lead to parental contact much as crying does for human infants and the vigor of calling may communicate to parents about the health of offspring and guide parental investment (Snowdon and Elowson, 2001).

But is there any effect of this babbling behavior on vocal development? Since subsong and plastic song seem to be critical to a bird developing a normal adult song, and babbling appears important in human vocal development, could the complex vocal behavior of young pygmy marmosets also be involved in developing adult vocal skills? As infant pygmy marmosets mature, they showed a decrease in bout length, but continued to show babbling behavior through puberty. There was a reduced frequency of infant vocal types and adult-variant calls with a corresponding increase in calls that matched adult acoustic parameters. Peripubertal monkeys acquired the long call which had not been observed in any of the infant babbling bouts (Snowdon and Elowson, 2001). We selected the call type most commonly found in babbling and most commonly used by adult marmosets, the trill, and examined changes in structure with age and as a function of variation in infant babbling. Infants that exhibited greatest diversity of calls in infancy had better formed trills in the fifth month than infants with less call diversity in their bouts \( R_s = 0.714 \) and infants that produced a greater number of calls when babbling displayed a greater change in trill structure \( R_s = 0.857 \). Thus, the diversity and amount of vocal activity in infancy predicted the quality and amount of change in trill structure in 5-month-old marmosets.

Trill structure did not reach final form until adulthood. Infant trills were shorter, more asymmetric in structure and rarely displayed a constant frequency range within the call. Prepubertal juveniles produced calls that were of normal duration and had a constant center frequency, but they continued to produce asymmetric calls (Fig. 1, Snowdon and Elowson, 2001). These results suggest that different components of adult call structure appear at different developmental ages and thus could be due to maturation of motor control systems. At the same time, there is also an apparent effect of vocal practice on the rate at which marmosets develop adult features of trills.

In summary, the preponderance of evidence supports the notion that vocal learning is not involved in vocal production of nonhuman primates. At the same time, it is also clear that infant primates are not born with the ability to produce the complete adult vocal repertoire. In many species,
physical maturation leading to lower fundamental frequency and to improved breath control to produce longer vocalizations and greater motor control could account for the variation in structure that is seen developmentally. Vocal practice may be important in developing motor skills. At the same time, some calls such as the long call of pygmy marmosets, used mainly in territorial interactions do not appear until relatively late in development meaning either that the appropriate contexts for the calls are not experienced by young monkeys or that these calls are acquired late in development.

E. Summary

The structural plasticity of primate vocalizations is much less than that found in bird song. Nonetheless, primates do not show completely stereotyped vocalizations, but are able to adjust subtle aspects of call structure to different social and environmental circumstances and group-typical and pair-typical call structures do emerge. In some cases, conditioning can change the structure of calls. Developmental studies suggest that call structure undergoes modification with practice and physical maturation being the most likely mechanisms. The overall result is that despite little direct

![Diagram showing the proportion of well-formed, partial, sloped, and asymmetric trills in pygmy marmosets across infant, prepubertal, and adult stages. The percentage of well-formed trills increased significantly over age (Friedman Anova, $P = 0.005$), partial trills decreased from infant to prepubertal (Friedman Anova, $P = 0.005$) and the percentage of asymmetric trills decreased significantly between infant and prepubertal levels to adult levels (Friedman Anova, $P < 0.01$). (Adapted from Snowdon and Elowson, 2001.)](image-url)
evidence of vocal learning, nonhuman primates do exhibit some ability to control vocal production and that practice and maturation may both be critical in vocal ontogeny.

III. PLASTICITY IN USAGE

A. DEVELOPMENTAL INFLUENCES

We next look at plasticity in how calls are used by primates, where there is much more evidence of flexibility in communication. Many primates are able to use their signals in a variety of contexts, suggesting that there is not a one-to-one mapping between a call and how it is used. However, early results on development suggested that call usage might be innate. Herzog and Hopf (1984) reported that isolate-reared squirrel monkeys produced alarm vocalizations when first presented with a naturally threatening stimulus. Miller (1967) also reported that isolate-reared rhesus macaques in a fear conditioning paradigm produced facial expressions to a stimulus predicting a shock that allowed a typically reared monkey to respond to avoid the shock to both animals. Seyfarth and Cheney (1986) reported that young vervet monkeys produced appropriate type of predator alarm calls in generally appropriate contexts (i.e., an “eagle” alarm was restricted to some aerial stimulus such as a bird of any type or a leaf falling from a tree and a “snake” alarm to objects on the ground). Young vervet monkeys eventually became very precise in their use of specific predator alarms to specific predators, but even in infancy they appeared to have a general concept of what calls should be used in what contexts.

In contrast to these results, Koda et al. (2008) studied two different populations of Japanese macaques that lived in habitats differing in visibility. Call rates during feeding and moving were greater in adults in the visually restricted habitat compared to adults in the more open habitat and this difference in call rate emerged developmentally, suggesting the authors that some learning process is involved in call usage.

Young captive cotton-top tamarins do not appear to distinguish between contexts in call usage. As noted earlier, Castro and Snowdon (2000) developed experimental manipulations to elicit specific chirp variants from adults. When the same manipulations were presented to families over the first 5 months of infant life, the most common reaction from infants was to produce a sequence of chirps that was not related in structure to the forms adults used. Some, but not all, infants did produce an appropriate form of chirp on at least one trial over the 5 months, but no one chirp type was produced in the appropriate context by all infants, and no single infant
produced each of the five chirp types that could be elicited in adults. Furthermore, if an infant did produce an appropriate chirp in an appropriate context, it was unlikely to produce that chirp again in the same context. The one exception was a chirp type used in feeding and, as we will see later, adults provide infants with considerable experience with these call types during food transfers. Interestingly, however, the infants inhibited calling in contexts eliciting alarm and mobbing. Possibly alarm, mobbing, and territorial calls are dangerous for infants to practice in contrast to food and affiliative calls. Thus, captive infant tamarins do not appear to be able to use calls in appropriate contexts.

As noted earlier in the description of babbling in pygmy marmosets, a characteristic of this vocal behavior was the juxtaposition of calls used by adults in a wide variety of contexts, suggesting that the connection between context and call type is something that both tamarins and marmosets need to acquire through some development process. In addition, we noted in both captivity (Snowdon and Elowson, 2001) and in the wild (de la Torre, unpublished observations) that adult marmosets occasionally showed babbling behavior, typically in the context of a subordinate reacting to aggressive behavior from another. Thus, babbling behavior is not restricted to infants but can be used by adults in response to conspecific aggression.

B. AUDIENCE EFFECTS AND CALL INHIBITION

If primates modify their vocalizations as a function of whether or not other individuals or which specific individuals are present, then the audience is influencing call usage. The ability of animals to inhibit call production is another index of vocal control. Several examples show that primates are sensitive to the audience they have.

Wich and de Vries (2006) found that Thomas langur males only gave alarm calls when other group members were present, and that a male initiating alarm calling continued to call until all other group members in his group had given at least one alarm call, suggesting that the initiating male was keeping track of each individual in the group. Papworth et al. (2008) found that blue monkeys produced significantly more eagle alarm calls (hacks) in response to playbacks when other group members were close to the playback location, than when they were further away, suggesting sensitivity to the danger experienced by other group members.

Slocombe and Zuberbühler (2007) found that the structure of chimpanzee agonistic screams varied as a function of the severity of aggression received by the caller, but victims produced scream structures that
exaggerated the degree of aggression they had experienced when there was at least one group member present that was of higher rank than the aggressor.

Zuberbühler et al. (1999) have shown that Diana monkeys (Cercopithecus diana) have specific alarm calls for aerial predators and for leopards, but they do not vocalize when they hear chimpanzees. Leopard alarm calls deter leopards from attacking, but a group of chimpanzees will use the calls of Diana monkeys to localize them and attack. Thus, inhibition of calling to predators is adaptive with certain predators.

Food-associated vocalizations have been a curious category of communication. What does it benefit an animal to communicate when it has found food, when that signal can recruit others to compete over food? Hauser and Wrangham (1987) studied food calls in chimpanzees in response to varying amounts of food and found that chimpanzees did not respond to small amounts of food, but only vocalized when large amounts of food were available. Subsequently, Hauser et al. (1993) presented chimpanzees with a watermelon cut into several pieces versus a single, intact watermelon and found food-related vocalizations only to the multiple pieces of melon. These results suggest that chimpanzees can control the production of food vocalizations according to whether the resource can be shared or not.

Rhesus macaques also produce food-related vocalizations and here there is evidence of punishment of group members that fail to give food calls when discovering food (Hauser, 1992). Interestingly, punishment is reserved for group members that fail to call and not for solitary animals that do not belong to a group.

Pollick et al. (2005) found that brown capuchin monkeys were more likely to give food vocalizations when other group members were present. Subordinate monkeys were more likely to call than dominants, but as audience size increased, even dominant monkeys gave food calls.

Female chimpanzees in Budongo Forest in Uganda often give copulation calls while mating, but the production of calls is not correlated with female reproductive cycle but rather with having a high ranking male as a partner. Interestingly, females inhibited copulation calls if higher ranking females were nearby, indicating an ability to control calling as a function of social environment (Townsend et al., 2008).

In contrast to these studies, Roush and Snowdon (2000) failed to find any audience effects in food calling in cotton-top tamarins. Pairs of tamarins were separated from their mates and were either in visual contact or visually isolated. Rates of food calling did not differ as a function of whether the mate was visible or not.
C. Captivity as Novel Ecological Niche

Captivity can be conceptualized as a novel ecological niche and can be used to ask questions about flexibility of usage. Studies that we have done on cotton-top tamarins have indicated that they show little initial alarm response to the presentation of a large boa constructor, which is a natural predator (Campbell and Snowdon, 2009; Hayes and Snowdon, 1990). Captive tamarins never display mobbing responses to a live snake in their cage (although wild tamarins have been observed to mob snakes), and we have been unable to condition a fear response to snakes using playbacks of mobbing vocalizations (Campbell and Snowdon, 2009). Captive-reared tamarins react no differently to a live snake than they do to a laboratory rat, reacting to both with curiosity and mild arousal. In contrast, captive tamarins do react with mobbing behavior to caretakers dressed in garb to capture monkeys and, curiously, to a bright blue duster used in cage cleaning (Campbell and Snowdon, 2007) and to caretakers wearing unfamiliar shoes (Neuburg and Snowdon, unpublished data). For captive tamarins, mobbing vocalizations and mobbing behavior was elicited not by natural predators but by unfamiliar and unusual objects in their captive environment. These objects may represent danger in the context of captivity and hence ecologically appropriate for mobbing calls. In another study, we adulterated a familiar, highly preferred food with white pepper and animals that tasted this adulterated food for the first time produced alarm calls, a totally novel context from even their prior captive experience (Snowdon and Boe, 2003).

D. Call Variation Related to Distance

Captivity is not the only place where one can see flexibility in usage. Pygmy marmosets have four different call types that appear to be used in contexts involving maintaining vocal contact with group members (quiet trill, trill, J-call, and long call from Pola and Snowdon, 1975). Two separate studies in the Western Amazon have shown that monkeys use different forms of these vocalizations as a function of how far apart they are from other conspecifics. In the first study, done in Peru, Snowdon and Hodun (1981) argued on the basis of acoustic cues for sound localization that quiet trills would be most difficult to localize, and J-calls had many more cues for sound localization. If marmosets could systematically vary call structure according to distance from others, then they would be expected to use more cryptic calls when close to other animals and more easily detected calls when they were farther apart. Snowdon and Hodun found that most quiet trills were given when animals were within 5 m of each other, other trills at distances up to 15 m and J-calls were exclusively used beyond 15 m.
In a follow-up and extension, de la Torre and Snowdon (2002) studied marmosets in Ecuador and compared trills, J-calls, and long calls. They studied call degradation as a function of habitat and found that trills degraded rapidly (due to both reverberation that made distinction of temporal features difficult as well as decrease of high-frequency components due to excess attenuation) whereas the long call was less affected over the same distances. They also recorded the distance between animals when each call type was given and found that most trills were given within 10 m of another animal, J-calls within the range of 10–20 m, and long calls given at distance of 15 m or more from the caller (Fig. 2). Both studies also measured the ambient noise spectrum and found that most of the acoustic energy was at frequencies above most of the ambient noise. Thus, marmosets in the wild appear to use different call types flexibly adjusting call type to the distance between themselves and their neighbors.

E. Food-Related Vocalizations

Food-related calls are not automatically produced in response to food. In cotton-top tamarins, the rate of food calling was proportional to the preference that an individual had for a particular food type (Elowson et al., 1991). Tamarins produced more food calls to foods that the individuals
preferred most. Clay and Zuberbühler (2009) found that bonobos produce five different call types during interactions with food and these call types are produced in long sequences. The authors established individual food preferences for 10 individuals and, like Elowson et al. (1991), found that call types conveyed information about each individual’s food preferences.

Slocombe and Zuberbühler (2005, 2006) showed that chimpanzees produce “rough grunts” in feeding contexts. Variants of these grunts reliably corresponded to differences in food quality and in playback experiments, chimpanzees responded readily to a location with high-quality food after playbacks of grunts given to it than to grunts indicating a low-quality food. These results from captive chimpanzees were not replicated in analyses of calls from wild chimpanzees, suggesting that the differentiation of food calls to different quality foods may be an adaption to the ecology of captivity.

Chapman and Lefebvre (1990) studied wild spider monkeys (Ateles sp.) and also found that food-related calls were given only at food patches with high-quality fruit. The production of food calls appears to be paradoxical in the context of primates feeding on live prey that might be able to hear the calls and avoid predation. We found that pygmy marmosets, like tamarins chimpanzees, bonobos, and spider monkeys, tended to produce more food calls with more preferred foods. However, when live prey was presented the animals were silent (Snowdon, unpublished observations). Gros-Louis (2004) reported a similar result for wild white-faced capuchin monkeys (Cebus capucinus) where calls were produced to fruits but not to animate prey. These examples of food calling indicate contextual influences on call usage. Food calls are not given at all times when food is available but rather calling is related to both food quality and to whether it is animate or not.

Addington (1998) studied vocalizations in the context of feeding in captive pygmy marmosets and identified a call that occurred regularly in feeding contexts. However, some individuals combined the food call with the long call used in long distance communication. In almost every case when the two vocalizations occurred together as a single call, the caller was an unmated animal. The function of the combined call might be to communicate to a potential mate that the caller had sharable food. For the current purposes, the example serves to illustrate the ability of monkeys to create novel call combinations.

F. SUMMARY

Many nonhuman primates display plasticity in how they use vocalizations. Although there is some evidence that isolate-reared animals or very young wild animals appear to use calls in generally appropriate contexts. Other species appear to acquire appropriate usage of calls over a relatively
long developmental period and call usage may be related to social status. Captive animals provide an interesting example of how communication is affected in a novel ecological niche and many animals respond to the features of captive environments in ecologically appropriate ways that are unrelated to natural conditions. Monkeys can adjust call structure to the distance from other conspecifics, adding features to make calls more detectable as distance between caller and other conspecifics increases. Many species produce calls in feeding contexts but call rate is adjusted to food quality and quantity and also whether foods are animate or inanimate. All of these examples support the notion of signal usage as highly variable and plastic in many species of nonhuman primates.

IV. PLASTICITY IN COMPREHENSION

It is in how nonhuman primates comprehend or respond to signals when the clearest evidence of plasticity in communication occurs with examples of cross-species comprehension of signals and signals having differential effects as a result of differing social status or life history.

A. DEVELOPMENT

As with each of the previous sections, early studies suggest that isolation rearing has a major influence on how monkeys interpret responses. The data are conflicting. Herzog and Hopf (1983, 1984) argued that isolate-reared squirrel monkeys responded appropriately to playbacks of species-typical calls including alarm calls and more affiliative vocalizations. In contrast, Miller (1967) used a fear conditioning paradigm where one rhesus monkey could see the stimulus predicting shock, but the monkey that controlled the response to avoid the shock could only see the face of the first monkey. Isolate-reared monkeys were quite good in producing the signals, but when they were in the role of responding to fear cues in another monkey, they were unable to respond to its signals of fear. As noted earlier, captive-born cotton-top tamarins did not respond to live snakes in their cage nor to playback of predator cues (Campbell and Snowdon, 2009; Friant et al., 2008; Hayes and Snowdon, 1990) although they produce alarm calls and mobbing calls in other contexts.

B. CROSS-SPECIES COMPREHENSION

The strongest evidence for primate flexibility in comprehension of communication signals comes from studies of cross-species communication. Vervet monkeys in Kenya learn to respond to the alarm calls of an avian
species, the superb starling (Cheney and Seyfarth, 1985; Hauser, 1988) and in habituation–dishabituation studies that involved habituation to alarm calls of one species with transfer tests to calls of the other species, vervet monkeys appear to categorize starling aerial alarms in similar fashion to their own aerial alarm calls. Starlings were less specific in the targets to which they gave terrestrial alarm calls and vervet monkeys were less specific in their reactions to these calls (Seyfarth and Cheney, 1990).

Oda and Masataka (1996) showed that ring-tailed lemurs would respond appropriately to playback of alarm calls of Verraux’s sifakas, Diana monkeys in areas where they are sympatric with Campbell’s monkeys respond to the eagle and leopard alarm calls of Campbell’s monkeys as strongly as to the playbacks of calls of the actual predators (Zuberbühler, 2000a). However, Diana monkeys responded to the leopard alarm calls of chimpanzees but only if they share a home range with chimpanzees (Zuberbühler, 2000b). In a reversal of the study with vervet monkeys responding to alarms of superb starlings Rainey, Zuberbühler and Slater (2004) found that yellow-casqued hornbills responded to playbacks of Diana monkey aerial alarm calls though not to Diana monkey leopard alarm calls, as would be expected since leopards could not prey upon hornbills.

As mentioned earlier, the cross fostering of Japanese macaques with rhesus macaques did not show any evidence of changes in vocal structure in the cross-fostered infants (Owren et al., 1993). However, the foster mothers of these infants responded more readily to food calls and play calls typical of their foster infant than they did to playbacks of calls of infants of their own species, clearly indicating that foster mothers have learned the vocal characteristics of their foster infants and respond appropriately to them (Seyfarth and Cheney, 1997). If mothers have the capacity to be flexible in response to infant vocalizations, then there may be no selective pressure for offspring to be flexible in their vocal production.

C. PARENTAL STATUS AFFECTS RESPONSES

Although the primary focus of this chapter has been on vocal communication to this point, I would like to make a brief digression to olfactory signals as a way to illustrate how parental status can affect responses to signals. Olfactory cues can have important influences on reproduction. We have shown using functional magnetic resonance imaging methods that presenting a male common marmoset with the odor of a novel, ovulating female produced increased neural activation in the anterior hypothalamus and medial preoptic areas, parts of the brain known to be involved in male sexual arousal (Ferris et al., 2001). Activation of these areas also activates the pituitary gland to secrete gonadotrophins that in turn activate the
gonads. We, subsequently, were interested in behavioral and hormonal responses to odors of novel, ovulating females and predicted that marmoset males would increase several behaviors relating to scent exploration and reproduction. We also predicted that testosterone levels would be increased after exposure to the odor of a novel female. Indeed, many males had significant increases in erections and in sniffing and licking at the stimulus. The same males also displayed a significant increase in testosterone levels within 30 min of exposure to the odor (Ziegler et al., 2005). However, there was a class of males that did not respond to odors of novel ovulating females—those who were fathers currently active in infant care. Fathers were not interested in exploring the scent stimulus and they showed no change in testosterone levels after exposure to odors from novel females.

In a subsequent study, in marmoset, we presented fathers and nonfathers with either a live infant in an adjacent cage or the vocalizations of an infant. All fathers responded rapidly to both a live infant and the playback of a live infant, and they responded equally to both their own infants and unrelated, unfamiliar infants. Nonfathers did not respond to live infants or their vocalizations (Zahed et al., 2008). Do fathers have different hormonal responses than nonfathers? Adult males were presented with odors of an infant versus the vehicle control and fathers, but not nonfathers, displayed a significant reduction in testosterone levels to infant odors compared to the vehicle (Prudom et al., 2008). This, the identical olfactory stimulus, elicits different behavioral and hormonal responses in male marmosets dependent on whether or not they were fathers.

In cotton-top tamarins, we have seen a sequence of changes in hormones in males during the last half of their mate’s pregnancy with increases in testosterone, estrogens, and prolactin. But these changes are seen only in experienced fathers and not in first-time fathers (Ziegler et al., 2004). The proximate cause appears to be the increased secretion of glucocorticoids by mothers at the midpoint of pregnancy, likely due to the maturation of the fetal adrenal gland. Within a week of this increase in excretion, experienced father began the sequence of hormonal changes, but first-time fathers do not. Since all females exhibit the midpregnancy change in glucocorticoid excretion, the most likely explanation for the differences between first-time and experienced fathers is experience. Thus, parental status is an important social variable that can influence response to communication.

D. SUMMARY

Nonhuman primates are quite flexible in their responses to signals from both their own species and those of other species. Of course, many birds are able to respond to alarm and mobbing calls of other species but this could
be due to the convergence in vocal structure typical for each type of call (Marler, 1955). However, Magrath et al. (2009) showed that birds responding to heterospecific alarm calls did not have similar call structure and they responded to another species alarm call only when the species were sympatric implying that the birds learn each other’s alarm calls and there is no convergence of call structure. Some primate species born and reared in captivity do not respond to visual or auditory cues from nature but do respond to cues appropriate to captivity. Cross-species reactions to alarm calls cannot simply be explained by convergence in signal structure, since the alarm calls of, say superb starlings and hornbills are quite different from those of the primates responding to them. This flexibility of response in captive-reared or cross-fostered animals and the responses to calls of other species in wild populations suggest some form of learning about signals is important to nonhuman primates. Finally, there is flexibility in how animals respond to signals, both behaviorally and hormonally as a function of parental status.

V. COMMUNICATION SIGNALS AND SOCIAL LEARNING AND TEACHING

There has been much interest in recent years in understanding the potential of nonhuman primates for social learning with considerable debate about whether nonhuman primates have a capacity for imitation and emulation. There have been some impressive demonstrations especially in great apes with considerably less success seen with monkeys (Visalberghi and Fragaszy, 1990). Nonetheless, results with cooperatively breeding primates have been more impressive with evidence of imitation (e.g., Völkl and Huber, 2000) and other forms of social learning. One hypothesis for the abilities of cooperatively breeding primates to learn from others is that this breeding system leads to greater tolerance and closer coordination between individuals than other types of breeding systems (Cousi Korbel and Fragaszy, 1995). An additional hypothesis may be due to frequent communication between animals to manage coordination or greater sensitivity by recipients to signals from others. Here, we look at some examples of how communication may affect social learning in both positive and negative ways and examine the possibility of teaching in cooperatively breeding animals.

A. AVOIDING NOXIOUS FOOD

Galef and Giraldeau (2001) reviewed the studies of social influences on foraging behavior in a wide array of species and noted the lack of evidence in nonhuman primates for socially learning to avoid toxic or unpalatable
foods. In one study, Visalberghi and Addessi (2000) presented capuchin monkeys with mozzarella cheese adulterated with ground white pepper and found no evidence that capuchin monkeys learned socially to avoid the distasteful food. Rather each individual learned when the food was distasteful and when it was palatable again. In a study of similar design, Snowdon and Boe (2003) presented groups of cotton-top tamarins with tuna fish, a highly preferred food that all animals ate readily, that was adulterated with white pepper. In contrast to the capuchin monkeys, cotton-top tamarins readily learned from others to avoid the adulterated food. Only one-third of animals ever sampled the foods and when nonadulterated food was returned, a minority of monkeys continued to avoid eating tuna fish, some for months and even years later even though they had not been the individuals who had sampled the food (Fig. 3). What could account for the species differences in learning to avoid a noxious food? One major difference was the presence of communicative signals in the tamarins. Tamarins that sampled the adulterated tuna gave fewer than normal food-related vocalizations and instead produced alarm calls (Fig. 4). They also gave facial expressions of disgust—chin wiping, retching, etc. No such signals were reported in the study on capuchin monkeys.

**B. FOOD TRANSFERS AND TEACHING**

Caro and Hauser (1992) set three criteria for determining whether nonhuman animals exhibited teaching behavior: the demonstrator had to engage the learner; there was a cost to the demonstrator; and the learner’s

![Fig. 3](image-url)
subsequent behavior was affected by the interactions. Although teaching is often thought to require a theory of mind, the operational definition of Caro and Hauser (1992) allows examination of possible cases of teaching without requiring demonstration of a theory of mind.

Rapaport and Brown (2008) noted that in great apes and most monkeys, there was little evidence of teaching foraging skills to the young. Rather, young primates acquired skills by closely watching a demonstrator. Rapaport and Brown noted, however, that food transfers commonly seen in cooperatively breeding primates appeared to be an exception where adult transfers of food to infants appeared to be a good nonhuman primate example of teaching behavior. Food transfers from adults, often animals other than the mother, are seen in many species of marmosets and tamarins and are usually characterized by specific vocalizations given in feeding contexts. In cotton-top tamarins, these vocalizations are similar in structure to individual calls given by adults when encountering food. However, in the context of food transfers to infants, the calls are given in a rapid sequence and higher amplitude not observed in feeding contexts among adults (Joyce and Snowdon, 2007). Infants frequently beg for food but only when adults produce the intensified form of food vocalizations will the infants be successful in obtaining food (Fig. 5, Joyce and Snowdon, 2007; Roush and Snowdon, 2001). Furthermore, infants that are involved at an earlier age with food transfers eat independently and produce food vocalizations sooner than those for whom food transfers began at a later age. This is most striking in comparing twin infants with singletons (Fig. 6). Family members engaged in food transfers and associated vocalizations with twin

![Figure 4](image-url)
infants significantly earlier than with singletons and twins eat independently significantly sooner as well (Joyce and Snowdon, 2007). Adults also phased out food transfers and vocalizing to infants as the infants began to forage on their own (Fig. 7).
Food transfers in marmosets and tamarins appear to meet the criteria of teaching. Adults share a preferred resource and have special forms of vocalizations used only with infants. The infants are attracted to the vocalizing adult and are able to receive solid food and this, in turn, leads to development of independent foraging behavior and production of food vocalizations in the young.

Whether information about food quality or novelty is also transmitted has led to conflicting results. Working with captive lion tamarins (*Leontocebus* spp.), Rapaport (1999) found that adults were more likely to transfer food that was unfamiliar to the infant (but not to the adult) as well as food that was difficult to process suggesting that the lion tamarins understood something about the knowledge base of the infants. In contrast, Brown et al. (2005) did not find evidence that common marmosets were more willing to transfer novel food or food that was difficult to obtain.

In field studies of golden lion tamarins in Brazil, Rapaport noted that animate prey were extremely difficult for juvenile monkeys to obtain and that adults frequently vocalized in the presence of animal prey and transferred them to juveniles but did not otherwise transfer food (Rapaport, 2006; Rapaport and Ruiz-Miranda, 2006). In addition, she noted that tamarins often showed “scaffolding” behavior. That is, an adult would give food transfer vocalizations and the juvenile would approach and
located near the vocalizing adult was a prey item that the juvenile captured and ingested (Rapaport and Ruiz-Miranda (2002)). As juveniles gained more skill in foraging on their own, adults gave fewer food transfer calls and transferred food less often (Figs. 8 and 9).

![Graph showing decline of adult food vocalizations to young golden lion tamarins at different ages](image1)

**Fig. 8.** Decline of adult food vocalizations to young golden lion tamarins at different ages ($F(1,18) = 8.462$, $P = 0.009$). (Adapted from Rapaport and Ruiz-Miranda, 2006.)

![Graph showing changes in approach and begs by and successful food transfers to young golden lion tamarins decline as a function of age](image2)

**Fig. 9.** Changes in approach and begs by and successful food transfers to young golden lion tamarins decline as a function of age (approaches $F(2,10) = 17.56$, $P < 0.0001$), begs $F(2,16) = 83.30$, $P < 0.001$, transfers $F(2,16) = 122.89$, $P < 0.00001$). (Adapted from Rapaport and Ruiz-Miranda, 2006.)
We developed a laboratory analogue of foraging using an apparatus with two possible solutions and we trained one parent on each solution (Humle and Snowdon, 2008). Highly preferred food was hidden in Styrofoam dishes suspended by a string in two opaque cylinders and one parent was trained to obtain food by reaching from a perch underneath to obtain food and the other parent was trained to pull the string up hand over hand from the ceiling. Following training, one parent was tested with each twin juvenile. Testing was not started until all of the juveniles were routinely foraging on their own with no evidence of food transfers from parents. In control trials, we did not observe food transfers between parents and juveniles, but in the test trials, juveniles frequently emitted food begging vocalizations to adults who had food from the foraging apparatus, and adults would give food transfer calls and often transfer food. Paradoxically, the adults that transferred food to begging juveniles most frequently had the least successful offspring. A possible reason for this is that adults frequently took the food to another part of the cage and so food transfers were done at a distance from the apparatus, possibly not allowing the recipient of food transfers to make the connection between the apparatus and the food. In this case, vocalizations and food transfers inhibited learning in juveniles in contrast to the data from the field on lion tamarins (Rapaport, 2006). One other intriguing result was that as soon as a juvenile successfully solved the task, the parents no longer vocalized with food or allowed those young to beg successfully (Fig. 10, Humle and Snowdon, 2008). Thus, these parents rapidly adjusted their vocal and food transfer behavior when a juvenile successfully solved the foraging task. Furthermore, in this context, greater parental response to juvenile vocal begging led to less success in learning the novel task.

In contrast to the helpfulness of tamarin parents to offspring in learning about food and foraging techniques is the absence of such support in chimpanzees. The chimpanzees at Bossou in Guinea engage in ant-dipping behavior, placing sticks into the nests or in columns of driver ants and then as the ants bite on to the stick the chimpanzees pick up the sticks and ingest the ants. The ants produce severe bites and one might expect that adults would provide some sort of guidance to infants in this context where foraging could be quite painful. However, in a longitudinal study of infant and juvenile chimpanzees there was no evidence of maternal assistance in helping young offspring to find the right size stick or develop the proper skills to minimize the likelihood of being bitten by ants. Instead, each individual learned in its own by observing its mother and other adults, but there was none of the vocal or visual communication seen in tamarin parents (Humle et al., in press).
C. COOPERATION AND DONATION BEHAVIOR

One more example illustrates the negative role of vocal signals in a social task. Several recent studies on chimpanzees (e.g., Silk et al., 2005; Vonk et al., 2008) find that when chimpanzees have the opportunity to provide food for a companion at no cost to themselves (by choosing a tray that has food rewards for both versus a food reward for themselves alone), they do not pull the two reward trays more often when a partner is present to receive the food. In contrast, cotton-top tamarins rapidly learn to cooperate with each other when both must act simultaneously to obtain a food reward (Cronin et al., 2005) and tamarins will continue to cooperate even when only one individual at a time is rewarded showing reciprocity over a period of days (Cronin and Snowdon, 2008). It seemed logical to expect that tamarins would succeed at the food donation task where chimpanzees had failed. Burkart et al. (2007) found that common marmosets were successful at an even more stringent task of pulling a tray that provided food only to the partner and not to itself. This donation behavior occurred between unrelated as well as related animals. We completed an almost identical test using pairs of tamarins that had lived together for long periods of time. To our surprise, the tamarins failed to donate food to their partners and more strikingly, there was a decrease in donating to the mate on trials where the mate was observed to give food vocalizations and/or to reach for the food (Fig. 11, Cronin et al., 2009), indicating that tamarins are attending to...
the signals of their mates and adjusting behavior even if it is not in the expected direction. Lakshminarayanan and Santos (2008) reported that capuchin monkeys would provide food for a companion. The positive results with capuchin monkeys and common marmosets contrasting with the negative results with chimpanzees and cotton-top tamarins suggest that neither phylogeny nor cooperative breeding are adequate explanations for prosocial behavior.

D. Summary

The role of communication signals in social learning and teaching is not consistent and varies between tasks. Aversive signals such as alarm calls and visual disgust responses appear to help tamarins learn to avoid adulterated food and may explain why such social learning has not been seen in other species where such communication is not present. Specialized versions of food vocalizations are given by adult tamarins that are willing to transfer food to infants and in wild tamarins these signals continue to be used with juveniles in the context of feeding on animal prey, the food most difficult for young tamarins to acquire on their own. Similar food transfers are seen in captive tamarins when their juveniles are faced with a novel foraging task. In both cases, adults appear to reduce their vocalizations and food transfers as the young acquire more skills. Offspring of parents that do not withdraw support are less likely to learn foraging skills. Finally, in studies where...
tamarins can donate food to a long time mate, the donors are less likely to provide food if the recipient mate has shown any interest by food calling or reaching toward the food.

VI. LONG-TERM MEMORY

Relatively little work has been done to explore the limits of memory in nonhuman primates. However, long-term memory would appear to be valuable in foraging in the wild where fruit resources may be available only at certain time of the year. Long-term memory for communication signals may also be useful to prevent inbreeding after animals have dispersed. We have examples of long-term memory for vocalizations in captive tamarins and Campbell’s monkeys.

In one study, we collected long call vocalizations from many colony members and then played back the calls of (1) the subject’s current mate, (2) a former family member from which the subject had been separated in a different colony room for periods ranging from 6 months to 5.5 years, and (3) the call of an unfamiliar animal, which had always been in a different colony room. Monkeys reacted with a high level of arousal to the call of the unfamiliar animals and showed very little reaction to the calls of their mates. When the calls of a formerly familiar animal (parent, offspring, or sibling) were played back, the subjects responded with few alerting and orienting behaviors similar to the response to calls of their mates, indicating a memory for the calls of familiar animals. This result held no matter how long had been the separation (Matthews and Snowdon, unpublished data).

Lemasson et al. (2005) found that adult female Campbell’s monkeys will alter the structure of calls that they use in vocal exchanges over time. Playbacks of current variants elicited significant responses in other monkeys within a minute of playback. Playbacks of formerly used variants (from 4 years earlier) as well as calls of strange females did not elicit any vocal responses from others. However, playback of former variants of current group members did lead to a significant reduction in call rate over 10 min whereas neither the current variant nor the call of a stranger affected call rate over 10 min. Long-term memory for calls of former relatives would be adaptive to avoid inbreeding after animals have dispersed from their natal groups.

VII. OVERALL SUMMARY AND CONCLUSIONS

I have tried to provide evidence in this chapter that communication behavior in nonhuman primates is more complex and flexible than the earlier views that have been presented. Since the review by Seyfarth and
Cheney (1997) which concluded there was evidence of limited plasticity in vocal production, but increased plasticity in signal usage and responses to signals, many new studies have shown that primates can control vocal output in response to environmental and social changes and there is increasing evidence of local and population variation in call structure. Developmentally, young tamarins do not produce context-appropriate adult calls and pygmy marmosets engage in long bouts of vocal behavior with calls structurally similar to adult calls but not given in appropriate contexts. Production of the full adult repertoire develops slowly and may involve practice, physical maturation and, possibly, imitation, for full development. None of these new results suggest that primates will soon challenge songbirds for vocal virtuosity, but nonetheless the accumulation of results suggests a much greater degree of vocal control and flexibility of production than previously thought. However, direct evidence in controlled studies for vocal learning is still rare.

In both the usage of calls and how primates respond to calls, more recent findings support the conclusions of Seyfarth and Cheney (1997). Considering captivity as an ecological niche allows examination of how primates can use and respond to signals in novel ways that would not be possible in field studies. Thus, captive primates respond to people in veterinary garb and to cleaning apparatus with mobbing calls and apply alarm calls to novel situations such as discovering familiar food that has been made unpalatable.

Changes in social status also provide tools for examining plasticity in communication. As male baboons attain dominance status they change the structure of their calls and as tamarins move from being alloparents to breeding adults, they also change the structure of some calls. These changes cannot simply be due to age or physical maturation. Social status also affects response to signals with some of the strongest evidence emerging in how fatherhood in marmosets alters not only behavioral but neuroendocrine response to some signals as well.

Social learning may be facilitated by use of communication signals in avoiding noxious food or learning how to forage in a novel task, but communication does not always facilitate social learning and can even reduce food provisioning behavior in the case of cotton-top tamarins. The role of plasticity in communication becomes clearest in the teaching behavior of tamarins. In both wild lion tamarins and captive cotton-top tamarins, adults adjust their communication signals according to the skill levels of their infants and juveniles, with withdrawal of signals as young animals acquire skills or using signals in different contexts to help older offspring succeed. Finally, there is evidence in tamarins of long-term memory for calls of socially important individuals as well as memory for foraging tasks.
I have focused here on the structure, usage, and response to signals and have not dealt with any of the cognitive components of primate communication. The chapter by Zuberbühler provides clear evidence of cognitive abilities. Taken together, these chapters provide an impressive documentation of the plasticity and cognitive skills of nonhuman primates. Although few primates can sing like birds or humpback whales, they still show impressive sophistication in their production, use, and interpretation of communication signals.

References


