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Food calls in a captive population of rhesus macaques (Macaca mulatta)

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FOOD CALLS IN A CAPTIVE POPULATION
OF RHESUS MACAQUES
(Macaca mulatta)

by

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Food Calls in a Captive Population of Rhesus Macaques *(Macaca mulatta)*

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Research on wild populations of rhesus macaques (*Macaca* mulatta) suggests that food calls are a frequent component of rhesus behavior. The existing research does not, however, fully answer the question of whether food calls are involuntary or voluntary in this species. The present study seeks to further test whether these food calls are involuntary or voluntary in nature. The University of Montana, houses a colony of nine rhesus macaques (*Macaca mulatta*) which were used for this study. Laboratory experiments for this study were carried out between November 1998 and January 1999, to examine three contexts that may result in food call elicitation. No food associated calls were elicited from the colony during 110 trials. If the food associated calls of this colony were involuntary, some of the monkeys would have produced food calls during some of the trials. Since this was not the case it may be concluded that the use of this call type is voluntary for these monkeys.

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Sir Isaac Newton has been quoted as stating "If I have seen farther than other men, it is because I have stood on the shoulders of giants." I am not sure that this thesis has afforded me the opportunity to see half as far as the members of my thesis committee. However, there were many giants that aided me in seeing as far as I did.

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CHAPTER 1

INTRODUCTION

Much work has been published concerning the vocalizations of New World monkeys, Old World monkeys, and Prosimians. This work has revealed two major findings. First, the call repertoires of monkeys are more extensive and complex than once believed (for examples see Hohmann & Herzog, 1985; Zimmermann, 1985). Second, all species of monkeys appear to have the same basic calls in their repertoires: submission calls, contact calls, threat calls, alarm calls, play calls, and food calls, among others. In most of these cases the species in question has more than one call that falls into any one of the above categories.

Food calls are used by monkeys to communicate the discovery of a food source to the rest of the individual's population during foraging activities. Often these activities place the population outside visual communication range of one another, necessitating vocal communication (Baldwin & Baldwin, 1976; Moody & Menzel, 1976; Benz, 1993; Caine, et al, 1995). This is the case for arboreal primates such as tamarins, marmosets, and squirrel monkeys.

Non-arboreal monkeys, such as baboons and macaques generally maintain visual contact with the other members of the troop when foraging, due to a large extent to the terrestrial environment in which they live. However, research conducted by Hauser (1997) on the macaques of Cayo Santiago, Puerto Rico, indicates that these monkeys produce at least five distinct food associated vocalizations even when in visual contact with their troop. This would suggest that the food call is an involuntary behavior in the rhesus macaque. Evidence collected by Hauser (1997), however, indicates the food calls of the rhesus macaque are, to some extent, voluntary. Hauser and Marler (Hauser 1992, Hauser and Marler, 1993a, 1993b) report that when food is discovered by a rhesus macaque the monkey will not immediately give a food call. Following the discovery of a food source, the monkey may take a moment to look around, possibly noting which other individuals are in call range. Hauser and Marler have found that when a favored individual is in close range of the caller and no other members of the population are within call range the caller will produce a very low decibel food call. Thus, only the favored individual will hear it. This suggests that this call type is voluntary in this species.

Recently, I initiated research to study the food calls of a colony of rhesus macaques housed at the University of Montana. The present study focuses specifically on the food calls of a captive colony of rhesus macaques (*Macaca mulatta*) housed at the University of Montana, Department of Psychology, Laboratory Animal Resources (LAR). This study was chosen to test the hypothesis that the food calls of this colony contain affective and representational information (i.e.,affective information being the emotional state of the individual, and representational information being the external environment of the individual). During the early stages of this research it became evident that during regular daily feeding activities no food calls were produced by the colony. This was obviously surprising to me and I began to search for an explaination. Sutton, et al (1973) have reported that the rhesus macaque can be conditioned to make a specific call in an inappropriate situation. For example, the macaque can be conditioned to produce a contact call when food is presented. Additionally, Sutton et al found that a call can be withheld during a situation that would otherwise result in the macaque producing the call. It is possible, therefore, that the LAR macaques have become conditioned to withhold a food call when food is presented in a normal, daily, manner. However, the work of Sutton et al does not rule out the hypothesis that food calls are voluntary and the colony has never learned to elicit food associated calls in the appropriate contexts.

This study will accomplish two things. First it will record the calls produced by this colony of rhesus monkeys during controlled presentations of food. Those calls will be spectrographically analyzed and compared to previously published (Hauser, 1997) spectrographs of rhesus monkey food associated calls to determine if any of this colony's vocalizations are food associated calls. Second, these data will be used to test wheter the food associated calls of the University of Montana Laboratory Animal Resources (LAR) rhesus macaques are voluntary or involuntary behavior.

Classification and Background

The rhesus macaque (*Macaca mulatta*) is a species of Old World primate of the Genus *Macaca*, Subfamily *Cercopithecinae*, Family *Cercopithecidae*, Suborder *Cercopithecoidea*, Infraorder *Catarrhini,* and Suborder *Haplorhini*, (Napier, 1985; Smuts, et al, 1987). Macaques are divided into four species groups: the *M. Sylvanus* group, the *M. Sinica* group, the *M. Arctoides* group, and the *M. fascicularis* group, of which the rhesus macaque is a member. These species groups are defined by the anatomy of the male and female genitalia of the monkey (Fooden, 1976).

Rhesus monkeys are one of the hardiest species in the macaque family (Napier, 1985). This is evident in the fact that they inhabit a variety of environments; from the harsh cold of the Himalayan foothills in Nepal to the humid tropics of India and Vietnam (Macdonald, 1984). Generally, rhesus macaques are not finicky eaters. Field researchers have observed this primate eating everything from insects and young leaves to the sap of pine trees. On occasion, rhesus monkeys will hunt small game and have been observed doing so and eating the meat gained from the hunt (Macdonald, 1984; Smuts, et al, 1987).

The rhesus monkey is one of the largest species in the macaque family. Average weight for a wild adult female is twelve pounds; males seventeen pounds. Body length of the adult ranges from eighteen to twenty-five inches, with a tail length of seven to twelve inches (Macdonald, 1984).

Gestation for this species is from five to six months. Research indicates that first conception generally occurs at the age of three and one half years and first birth at four years. Additionally, these births generally occur between the months of March and May. Variation within this time period will occur due to environmental conditions, most notably climate (Smuts, et al, 1987). Longevity averages twenty to thirty years in the wild (Macdonald, 1984), and up to thirty years in captivity (Strobel, 1999).

The multi-male social organization of the rhesus monkey is common for most species of macaques. In such an organization there is generally a ratio of one male to two females (Smuts, et al, 1987). The foundation of the troop's social structure is maintained by the female group, as they do not emigrate from the troop. The males however, upon reaching sexual maturity, are forced out of the troop to search for a new population to attach themselves to. This generally occurs at the age of seven years (Macdonald, 1984; Smuts, et al, 1987).

Hierarchy for females in a wild population is based on the mother's rank in the troop. The offspring of a given mother will take on a rank commensurate with her mother. However, the offspring cannot surpass the mother's rank. Males in the wild must earn their rank through conflict and affiliations. Whereas female's rank does not change significantly throughout her lifetime, the rank of a male is in constant flux (Smuts, et al, 1987). Strobel (1999) has found that in the laboratory rhesus females change their rank with male concorts and when having offspring.

Home range size for this species varies from one environment to another. Rhesus monkeys in Asarori-Siwaliks, India, have home ranges that vary from 350-2,820 meters. Researchers have discovered that the major factor that effects the size of a home range is the size of the troop. In this area, troop sizes vary from nine to eighty individuals (Macdonald, 1984; Smuts, et al, 1987).

Because the rhesus monkey is such a hardy animal, it is one of the most popular species of primates for use in medical and psychological research today (Smuts, et al, 1987). The macaques housed at the University of Montana provide a good example of how rhesus monkeys can adapt to a wide range of conditions. The environment that these animals inhabit in the wild is widely divergent from that in a research laboratory.

The monkeys used by the University of Montana were not taken from the wild. Due to the constraints of medical and psychological research, the health of the subjects must be well known to the researchers and this includes any viruses the subject may have. Therefore, the LAR monkeys were captive born and bred. This means that these monkeys have never been in a wild environment. In fact, some of the macaques at the University of Montana have never seen the outside of their colony room.

Additionally, research designs often call for the isolation or separation of a few macaques from the colony proper. This is the case for the LAR monkeys. Recent research requirements have separated most of the males from the main colony. Thus, the multi-male social group that wild macaques are accustomed to has been temporarily replaced by an all female social group.

CHAPTER II

BACKGROUND TO VOCALIZATION RESEARCH

Early studies into the vocalizations of nonhuman primates focused on the basics of vocal communication. Researchers attempted to understand the variety of calls made by some species and the variations in the acoustic structures of those calls. In the 1990's research efforts are being directed at more difficult questions about nonhuman primate vocal communication. Some of this work is directed at understanding what information is communicated in the nonhuman primates' vocalizations. Are they communicating affective in formation? That is information about the emotional status of the signaler. Or are they communicating representational information? That is information about the signaler's surroundings. Additionally, work is being conducted to understand the congnition of nonhuman primates as understood through their vocalizations.

Regardless of what is going on now in nonhuman primate vocalization research, the progress made in the past, whether it was in cataloging the calls of a species or trying to understand those calls, paved the way for the ground breaking work conducted in the last ten years.

New World Monkeys

The category of non-human primates, known as the New World primates, consists of at least 47 known species. This is increasing as scientists discover new species in the rain forests of Central and South America (Smuts, et al., 1987). Vocalization research has been conducted on a large number of these species. A variety of species including golden lion tamarins (*Leontopithicus rosalia*), pygmy marmosets (*Cebuella pygmaea*), and squirrel monkeys (*Saimiri sciureus*) have been studied. This research has been primarily directed toward studying long-calls, play-calls, food-calls, isolation peeps, and contact calls.

Moody and Menzel (1976) recorded and spectrographically analyzed the calls that are characteristic to the saddle-back tamarin (*Saguinas fuscicollis)*. This study employed a tamarin population consisting of one adult female, one adult male, one sub-adult male, one juvenile female, four infant males, and one infant female. The population was housed in a 10x4x4 meter green house with a soil floor and adequate foliage for travel throughout the enclosure (Moody and Menzel, 1976).

Results of the study indicate that the saddle-back tamarin population had no less than thirty distinct types of vocalizations (Moody and Menzel, 1976). Five functional categories of these vocalizations were developed: spatial cohesion, alerting, aggression, infant calls, and adult vocalizations during infant calls (Moody and Menzel, 1976). Within these five functional categories were two complexes of sounds: twitter-hook and squawk. In addition, the study revealed that each individual in the population above sixteen months old had a distinct repertoire of calls that reflected its group status and the nature of the individual's interactions (Moody and Menzel, 1976).

Moody and Menzel's work with the saddle-back tamarins is useful in two respects. First, it illustrates the complexity that researchers can expect to find in vocalization repetoirs of primate species. Second, it suggests that some calls may have significantly different meanings depending on the individual sending the message and on the individual(s) receiving it. This is what Snowdon, et al (1983) have concluded from research with cotton-top tamarins *(Saguinus oedipus)* long calls.

The subjects used by Snowdon, et al, were five mated pairs of captive born and bred cotton-top tamarins. All five pairs were housed in large home-cages and fed their normal diet of Zu Preem Marmoset Diet, and fresh eggs. Vocalizations were recorded from freely behaving monkeys and monkeys placed in situations designed to stimulate long-calls. The calls were all recorded on reel to reel tape and analyzed on a spectrograph (Snowdon, et al., 1983).

Results of this work reveal that there are distinct variants of long-calls used by cotton-top tamarins. Two long calls were defined. First, the normal long call, used in response to the long call of a different population than the tamarin receiving the call. Second, a quiet long call, used in response to calls made by members within the population of the vocalizing animal. As with Moody and Menzel's (1976) work with the saddle-back tamarins, Snowden, et al (1983) discovered there are individual differences in the long calls. These differences are in the first syllable and second syllable start frequencies of the calls. The results of play-back experiments indicate that tamarins within a given population know the individual difference in the long-calls of other tamarins in their group. Therefore, a distinction is made by the tamarin between long calls made by members of its population and those of an outsider. This was supported by differences in the behavior associated with a member's long-call as opposed to a non-member's long call. When a non-member's long-call was played back to the subject, the subject appeared agitated and vocalized at a higher frequency than it did to play backs of member's long calls. This suggests that the long-call is used somewhat as a group identifier, maintaining group cohesion through vocal cues (Snowdon, et.al., 1983).

Play vocalizations are the calls elicited by some primates during play sessions. Biben and Symmes (1986) studied these calls in young male squirrel monkeys to test the hypothesis that play vocalizations have a wider range of variation than previously believed. This experiment focused on two pairs of young male squirrel monkeys. One pair was thirty months old and the other was twelve months old. Squirrel monkeys were used because they have a definite play vocalization, one of only a few species of primates that do (Biben and Symmes, 1986). Free-response play calls were recorded and the accompanying behavior was videotaped for several hours each day of the two month study. Results indicate that the young squirrel monkeys' vocalizations can be grouped into five categories of play calls and four categories of tonal-calls (Biben and Symmes,1986). Contrarily, Winter's (Winter et al,1966; Winter,1969) study with the same species of primate revealed only two categories of tonal calls.

The frequency of play vocalizations was also studied by Biben and Symmes (1986). Results of this study suggest that the play vocalizations may carry the message, 'my actions are playful' and that the recipient of the call is the intended play partner. Biben and Symmes (1986) caution that although this is the best conclusion drawn from the observed behavior of the monkeys in this study, the hypothesis still remains untested.

The isolation peeps of two subspecies of squirrel monkeys, the Gothic and the Roman varieties, have also been studied. Isolation peeps are vocalizations made by some primates when visually separated from other troop members. Liebich, et al (1980) tested the hypothesis that each individual produces a characteristic sound in its isolation peep. Vocalizations were recorded during spontaneous behavior of six male and six female adult Gothic variety squirrel monkeys and six male and eight female adults of the Roman variety (Liebich et.al., 1980).

Results indicate that a basic isolation peep is made by squirrel monkeys. Additionally, the basic parameters of the call are different for the Gothic and Roman subspecies. Evidence also indicates that the isolation peeps of each individual vary within their parameters. However, they always contain a limited number of variations from the wide variety of variations possible from the overall acoustic parameters (Liebich et al, 1980). That is, if 250 possible tones exist in the acoustic parameter of the isolation peeps of a given population, only 30-40, were used by any one individual. Thus, the isolation peep of these two species of squirrel monkey serves to communicate to the rest of the troop that one of its members is out of visual range. Additionally, it tells the population which individual is eliciting the peep (Liebich, et al, 1980).

Symmes, et al (1979) also studied the development of the isolation peep in squirrel monkeys. Seven captive reared squirrel monkeys ranging in age from one day to two years old were used. The subjects were separated from adults and housed in peer groups at six months of age. This ensured that all subjects were in vocal contact with conspecifics, but were unable to possibly learn isolation peeps from adults. Vocalizations were recorded at regular intervals: 1, 2, 4, 8, 12, and 24 weeks of age, and 1 year old.

Results of this study indicate that squirrel monkeys make individually characteristic isolation peeps starting at one week of age. This vocalization remains stable into adulthood, changing only in response to what is expected for differences in physiology.

Isolation peeps have also been studied for another reason. Snowdon et al (1985) hypothesized that isolation peeps in squirrel monkeys could be used to make a sub-species differentiation between the Guyanese and Bolivian/Peruvian populations. Infant isolation peeps of two groups of squirrel monkeys were recorded from thirteen subjects (5 wild-caught Guyanese, 4 wild-caught Peruvian, and 4 wild-caught Bolivian). These calls were randomly played back to adult conspecifics (4 male and 10 female Bolivian, 6 male and 10 female Peruvian, and 4 male and 20 female Guyanese). Sound spectrographs of the peeps indicate variance in the calls from one group to another. Peruvian and Bolivian were found to be most similar, with Guyanese most divergent. The adults shared population specific responses to the infant calls. They were significantly more active during playbacks of peeps from same population infants than those from a different population. This supports the hypothesis that Guyanese and Bolivian/Peruvian squirrel monkeys are different sub-species (Snowdon et al, 1985).

Over the last ten years, food calls have been closely studied to determine their functions. Many New World primates, from spider monkeys (*Saimiri sciureus*) to golden-lion tamarins (*Leontopithicus rosalia*), have been studied. Attempts have been made to understand the nature of the food calls in feeding group control, meanings behind the food calls, symbolism, and food preference as indicated by the calls.

Benz et al (1992) studied the food calls of seven male and three female golden-lion tamarins (GLT's) (*Leontopithicus rosalia*) housed at the Callitrichid Research Center, University of Nebraska, Omaha. Two experiments were run. The first studied the food preferences of the ten subjects. The procedure involved presenting in pairs, six food types to the tamarins and recording which food type was chosen from the pair of foods. Results indicate the GLT's preferred meal worms and raisins significantly more than the apple, egg, carrot, or Marmoset Diet. These data were applied to the second experiment that tested the relationship between food preference and the vocalizations elicited by the tamarins.

The same six food types (meal worms, raisins, apple, egg, carrots, and marmoset diet) used in the first experiment were presented to one female and four male GLT's. The vocalizations made by the tamarins were recorded and spectrographicaly analyzed. To generate the vocalizations in the experiment, the food types were placed within sight of the subjects but just out of reach. The vocalizations were recorded for twenty seconds after which the food was given to the tamarins. Results of this experiment were expected to reveal a difference in call rate between favored and less favored foods. Data indicate the change in call frequency was only observed with one type of food, meal worms. The presentation of the other food types resulted in the same general frequency of vocalizations. This suggests food-calls in GLT's do not have a representational factor to their vocalizations as had been hypothesized by Benz, et al (1992).

Benz (1993) continued research into golden-lion tamarin food calls to uncover what information they contained. The subjects were three males and four females, again housed at the Callatrichid Research Center (Benz, 1993). Two types of information were sought by Benz. One of these was the affective type: the emotional information about events external to the sender. The second type was the representational type: information which constitutes the meaning of the call (Benz, 1993). To test the hypothesis that food calls contain affective and representational information, twelve food types were presented to the tamarins. One type of food was presented at a time and each subject was given food individually. This was done to determine the food preferences of the subjects. This study was performed according to the same research design as Benz et al's 1992 experiment with the same species. The vocalizations made by the tamarins at each food presentation were recorded and played back to the subjects in the absence of food. The results of these trials support the findings of the 1992 experiment; the tamarins prefer meal worms to any of the other food types. Preferences to all twelve food types were recorded, counted, and compared to spectrographic records of the subjects' vocalizations.

Results indicate that the tamarins tend to vocalize more often when presented with food types they prefer and the frequency of the vocalization differs between preferred and non-preferred food types. These data indicate that there is a more pronounced response to preferred food types, but no correlation is made between most preferred food type and highest rate of vocalizations. Rather, the top three preferred food types all elicited high and equal rates of vocalizations, more so than the other food types. This provides support for the affective hypothesis. The difference in vocalization rates between more preferred and less preferred food types was small for the study population as a whole, and not correlated when each individual was compared to each other. No support for the representational hypothesis was found (Benz et.aL, 1992).

Elowson et al (1991) ran a similar experiment with adult cotton-top tamarins (*Seguinus oedipus*). The same procedure employed by Benz (Benz et al,1992; Benz,1993) was used and the same results were observed. Data from the research show that cotton-top tamarins produce two vocalizations upon food presentation. Both calls are used to communicate food preference effectively, but do not communicate any representational information (Elowson et.aL, 1991).

The representational and affective information is not the only area of study done with this type of vocalization. Chapman and Lefebvre (1990) studied the use of food calls as a device to control the size of the feeding group. Chapman and Lefebvre studied free ranging spider monkeys (*Ateles geoffroyi*) in Costa Rica's Santa Rosa National Park. Vocalizations elicited by the monkeys when they came upon food were audio recorded and the number of individuals that responded to the calls by going to the food was charted. Data collected indicate the monkeys produce a "winnie" call when they find a food source. The frequency of the call varies depending on the size of the food source and the dominance rank of the monkey. Additionally, data reveal that this vocalization functions to call together a feeding group. Interestingly, this group is often above the optimal size for the environment (Chapman and Lefebvre, 1990). That is, if a feeding group becomes too small, its members will attach to another group, thus responding to the new group's winnies. This new attachment may push the size of the group above the optimal number of individuals that can be sustained by the environment. To maintain a viable feeding group, the individual that discovers the food source may manipulate or forego the food call, thus limiting the number of individuals that respond to the vocalization (Chapman and Lefebvre, 1990). This raises the question; whether this is deceptive behavior, and if so, does it indicate a knowledge of self as independent from other members of the group? Further, is it simply an innate adaptive behavior that ensures reproductive success?

Contact calls are another type of vocalization that have been the emphasis of much New World monkey research over the last twenty years. Snowdon and Pola (1978), of the University of Wisconsin, studied the interspecific and intraspecific responses to synthesized pygmy marmoset (*Cebuella pygmaea*) vocalizations. This study tested the hypothesis that pygmy marmoset contact calls vary somewhat due to individual idiosyncrasies and environmental noise. The basic form of the vocalization is, however, constant. Thus, no matter how a call varies due to the individual or environment, it is still understood by the receiving marmoset (Snowdon and Pola, 1978).

To test the hypothesis Snowdon and Pola synthesized the four contact calls, or trills, made by pygmy marmosets. Each trill was played back to individual marmosets through hidden speakers in the research enclosure. Some of the trills were modified from their original acoustic structure to determine whether the marmosets would behave in the same way to both the modified and unmodified trills. Results of this experiment indicate that marmosets react to the modified trills in the same manner as the unmodified trills. The data suggest that marmosets are tolerant of variation in their contact calls in much the same way as humans are tolerant of variations in speech due to individual accents or environmental noise (Snowdon and Pola, 1978).

In 1980 Snowdon and Cleveland continued this work testing the hypothesis that individual recognition occurs with two of the contact calls made by the pygmy marmoset. The study involved playing back individual calls to a colony of seven pygmy marmosets housed in three large wire-mesh chambers within one room. The two contact calls studied were the closed-mouth trill and the J-call. The closed-mouth trill occurs in situations of low disturbance when animals move freely throughout the environment and sometimes when they are able to see one another. The J-call is given only by adults under conditions where animals are dispersed or visually isolated from each other. Results of this experiment support Snowdon and Cleveland's hypothesis, except when the vocalization comes from an expected source location. For example, when play backs were made from a location that the receiver didn't expect the call to originate from, the receiving marmoset did not respond in the same manner as when the call came from an expected location (Snowdon and Cleveland, 1980). This suggests that an element of expected location interplays with the contact call to create an individualized affect to the call.

Snowdon and Hodun (1981) studied three of the four distinct variations of the trill call elicited by pygmy marmosets. Previous research (Liebich et.al., 1980) show that pygmy marmosets make four distinct trill calls. This previous work revealed that one of the calls has a different meaning than the other three. The purpose of this study was to discover the meaning of the other three trill calls. The research was conducted with a troop of free-ranging pygmy marmosets in the Amazon River Basin in northern Peru. The observations and recordings continued for a period of seven weeks. After ten days of recording habituation vocalizations, the data were compiled and analyzed spectrographically (Snowdon and Hodun, 1981).

Results show that the three trill calls are types of location calls. The differences between them lie in the location of the marmoset when the call is made. When in close proximity to the receiving marmoset the caller uses the "quiet trill". When the space between the two marmosets is increased the "closed-mouth trill" is used. At distances that preclude visual contact the "J-call" is elicited. Thus, the calls due to their acoustic construction, provide cues to spatial separation between the calling marmoset and the receiving marmoset (Snowdon and Hodun, 1981).

Old World Monkeys and Prosimians

As with New World monkeys, Old World monkeys and Prosimian (here grouped together with Old World monkeys for simplicity) vocalizations have been extensively studied. Much of this work, as with New World monkeys, has been directed at understanding one or a few of the call types of a given species. Very little work has been done in the area of cataloguing the call repertoires of Old World monkeys. There is, however, more interest in this area now than ever.

Research on the repertoire of the only strictly arboreal macaque species, the lion-tailed macaque (*Macaca silenus*) was conducted in captivity (Hohmann and Herzog, 1985). This study entailed audio and video recording of no less than 17 basic call patterns and their behavioral contexts. Acoustic analysis has revealed that some of these calls are discreetly structured. Other calls, however, are more graded. When these calls were compared to calls from other species of macaques the lion-tailed calls were more structurally varied that those of the other more terrestrial macaques (Hohmann and Herzog, 1985).

Hohmann (1989) carried out the same type of study with two species of langur: the Nilgiri langur (*Presbytis johnii*) and the Common langur (*Presbytis entellus*). The vocal repertoires of the two species were acoustically and behaviorally recorded and compared. Analysis indicates that the repertoires of both species contain discrete and graded variants of calls. Additionally, some of the calls of both species' display pronounced sex-differences in acoustic structure and behavioral contexts. Hohmann (1989) also discovered that some of the calls are used only by the males or the females of the population.

The common slow loris (*Nycticebus coucang*) was studied by Zimmermann (1985) in order to catalogue the species vocal repertoire. Data from this free-range study indicate that this species produces eight calls in either one of two functionally defined categories. The first is contact calls and contact finding calls. These are used by the animal to maintain or establish vocal contact with its troop. The second category is aggressive and defensive calls. These are elicited during threatening events (Zimmermann, 1985). Of the eight calls defined into the study, three fall into the contact/contact finding category; and the other five in the aggressive/defensive category. This repertoire is simple when compared to that of the lion-tailed macaque, but this is not anomalous for a member of the family *Lorisidae* (Zimmermann, 1985).

A major portion of the published work on Old World monkey calls deals with alarm calls, specifically, those calls used by vervet monkeys (*Cercopithecus aethiops*). Owren (1990a, 1990b) employed a two-choice operant procedure to test the categorization abilities of vervets to alarm calls from unfamiliar sources. Results indicate that the monkeys express the same level of ability as human subjects to categorize an alarm call from an unfamiliar vervet monkey. Statistical analysis of vervet monkey responses to unfamiliar source alarm calls indicates the subjects categorize the calls correctly 80% of the time. This suggests the subjects (both monkey and human) use acoustic cues to categorize the threat referred to by an alarm call.

Research (Cheney and Seyfarth, 1990; Seyfarth, Cheney, and Marler, 1980a, 1980b; Owren, Hopp, and Seyfarth, 1990; Owren and Bernacki, 1988) has revealed that the alarm calls of vervet monkeys may contain referential as well as affective information. Research conducted at the Amboseli National Park, Kenya, indicates that vervet monkeys have three acoustically distinct alarms calls in their repertoire. The information in each of these calls appears to represent each of the categories of predator that threaten the monkeys: leopards, large birds, and snakes. This information was discovered during playback experiments with a troop of Amboseli vervet monkeys.

To run the experiments Cheney and Seyfarth (1990a) hid a loudspeaker near a group of vervets. They proceeded to playback recordings of the alarm calls elicited by the monkeys when no threat was present to the subjects. The behavior of the troop immediately following the playbacks was documented and analyzed. The data gathered reveal that the behavior of the troop varies discreetly depending on the alarm call received by the troop. Specifically, when the call for 'leopard' is played back to the monkeys the troop runs for the trees. When the researches played back the alarm call for 'large bird' the troop would run to the bushes where they would be safe from an attack from above. Additionally, the adults of the troop would stand erect and scan the ground when the "snake" alarm call was played. Later research (Seyfarth, Cheney and Marler, 1980a, 1980b) revealed that in a situation where the snake is found by the troop, the adult monkeys will mob it until it leaves the area. These data provide compelling evidence supporting the referential hypothesis in vervet monkey alarm calls.

Cheney and Seyfarth (1990a) have also found evidence supporting the affective information hypothesis. Further analysis of the behavior of the vervets following alarm call playbacks has revealed additional data about the information contained in the calls. Analysis of video tapes made of the vervets during actual predator events indicates that the monkeys' immediate behavior following an alarm call is contingent on the level of stress in the call. For example, during one incident a female elicited an alarm call for 'large bird' which was barely audible to the researchers. However, two vervets accompanying the signaling individual responded to the call. The two monkeys scanned the sky for the bird rather than run for cover. The researchers did the same thing and located the bird approximately 2000 feet overhead, which is too high to be an immediate threat to the monkeys. The three monkeys continued to scan the sky for the bird, which after a short time, flew out of sight. This event suggests that vervet monkeys can change the acoustics of their alarm calls to communicate the urgency or immediacy of the threat that is present.

Additional work (Seyfarth and Cheney, 1990) with vervets has revealed that the monkeys use the alarm calls of other species to give them cues about their environment. This work was also conducted with the Amboseli vervets. Data collected during field observations indicate that when a superb starling (*Spreo superbus*) elicits a 'snake' alarm call, vervet monkeys will respond in the same manner as if the call were made by another vervet. This occurs although the superb starling's alarm call is acoustically very different from the vervet's.

Additionally, this research (Seyfarth and Cheney, 1990) indicates that when the alarm call of the superb starling incorrectly references the perceived threat over several calls, the monkeys will cease to respond to the call. This behavior was recorded by the authors when the alarm calls of young vervet monkeys failed to accurately identify the perceived threat. As with the previous research, these data provide compelling evidence for the presence of referential information in the alarm calls of vervet monkeys.

One of the first studies of vocal communication in non-human primates was conducted with rhesus macaques (*Macaca mulatta*) (Rowell and Hinde, 1962). This research helped to prove that captive rhesus monkeys produce both tonal and atonal vocalizations. Rowell and Hinde audio recorded and spectrographically analyzed a variety of calls produced by the rhesus monkey. They discovered that although not all calls contain the same tonal or atonal sounds, all of the rhesus monkey calls do contain at least one of each these types of sounds. This would seem obvious, however, before this study it was believed the calls of all monkeys contained only the simple atonal sounds.

Early in rhesus monkey vocalization research, a study conducted by Lieberman et al (1969) concluded that rhesus monkeys cannot produce vocal sounds as complex as those produced by humans. At most, they were able to produce a few consonant sounds and some graded vowel sounds, but nothing near the complexity of a human voice. It was found that this was the result of the morphology of the monkey's vocal track.

Recent advances in computer analysis software, as well as the development of more reliable and accurate vocalization acquisition techniques, has provided additional information about the findings of Lieberman et al (1969) and (Hauser, 1997). Field research conducted with the macaques on the island of Cayo Santiago, Puerto Rico, provide a case in point. Two projects run on this population reveal a repertoire consisting of 25 to 30 distinct call types (Gouzoules et al, 1984; Hauser and Marler, 1993a). The social contexts of the calls include finding and eating food, intergroup encounters, and dominance interactions.

Further research conducted by Hauser and Fowler (1991) has helped to explain the complexity found in the call bouts of rhesus monkeys. Data indicate that the call bouts incorporate a significant change in the fundamental frequency of the call. This change occurs at the end of the call bout, possibly acting as an indicator to the receiver that the call bout is ending.

Functional analysis of the rhesus monkey call repertoire has focused on calls produced in the context of food discovery (Hauser, 1997). Hauser and Marler (Hauser 1992; Hauser and Marler, 1993a, 1993b) have discovered that when rhesus monkeys locate food, they produce a food call. Five acoustically different variants of the food call have been defined, specifically, warbles, harmonic arches, chirps, coos, and grunts. Additionally, the type of call given will depend on the quality of food discovered as well as the availability of the food source.

Hauser and Marler's (Hauser 1992; Hauser and Marler, 1993a, 1993b) research has also revealed significant behavioral facts about the contexts of the food calls. Findings indicate that females vocalize more often than males do. Further, females with a long matriline will vocalize more often than females with short or no matrilines. This suggests that kin selection may exert extensive pressure on this calling system (Hauser, 1997).

Observational research has further indicated that a rhesus monkey that vocalizes when food is discovered will receive more food when the food is eaten by the troop than a monkey that does not vocalize. Additionally, those monkeys that do not vocalize pay a price. The troop will exact punishment on the monkey in the way of a severe beating for not vocalizing at the discovery of food. In most cases, the males do the punishing, although some females have occasionally been observed to participate in the castigation.

The food calls of the rhesus macaque not only indicate the discovery of a food source, they also indicate the hunger level of the caller. Hauser and Marler (1993a, 1993b) have learned that when a rhesus monkey has been deprived of food for an extended time it will call at a higher rate than just after being fed. This suggests the food calls communicate the level of hunger the caller is experiencing.

In the last thirty years, there has been a wide range of research conducted on the vocal communication of monkeys and a great deal has been learned from this work. Scientists now know that the call repertoires of monkeys are much more complex than once believed. They are also gaining an understanding of what types of information the calls are communicating and to whom this information is being communicated. Possibly, the most interesting thing scientists have learned about vocal communication is that the calls of one species can be understood and used by different species. The results of all the research conducted to date in this light reveal one major fact: there is still an abundance of knowledge to be gained from studying how our primate relatives vocally communicate.

CHAPTER III

METHODS

Subjects

The subjects for all of the experiments in this study belong to a colony of captive rhesus macaques (*Macaca mulatta*) housed at The University of Montana, Department of Psychology, Laboratory Animal Resources (LAR), Missoula. The colony is composed of eight females and one male. Ages of the subjects range from infant to adult. The colony is housed in a 23'L x 7'W x 7'3"H enclosure which is located in a 37'6"L x 9'2'W x 8'H room (colony room) located in the basement of the Psychology/Pharmacology building. This colony has been captive for thirty years and has been located in the present facility for the last ten years. All subjects are captive born and raised. The subjects were fed by the LAR animal care personnel between 8:00 a.m. and 9:30 a.m. Monday thru Friday, and between 1:00 p.m. and 1:30 p.m. on Saturdays and Sundays. During these regular feeding times the subjects were provided monkey chow and oranges.

Materials and Equipment

Five different food types were used as the food sources for this research: Monkey Chow, unshelled sunflower seeds, oranges, bananas, and cantaloupe. The food types used in each experiment are listed in the corresponding PROCEDURE section.

Vocalizations for all experiments were recorded on a Marantz PMD-222 cassette recorder, modified for bird recordings, using a Sennheiser ME66 short shotgun microphone on a Sennheiser K6 power supply. Monitoring of the recordings was accomplished with Sony MDR-CD550 headphones. Timing of all trials was accomplished with the use of a Timex electronic chronograph stop watch. Spectral analysis of the calls elicited during the trials were conducted using the Sound Technology Spectra Plus Audio Analysis Program for Windows 95. The spectrographs were then compared to spectrographs of food associated calls published by Hauser (1997) to determine whether they were or were not food calls (see fig. 1).

A call was defined as a food associated vocalization only if its spectrograph matched one of the five food call spectrographs published by Hauser (1997).

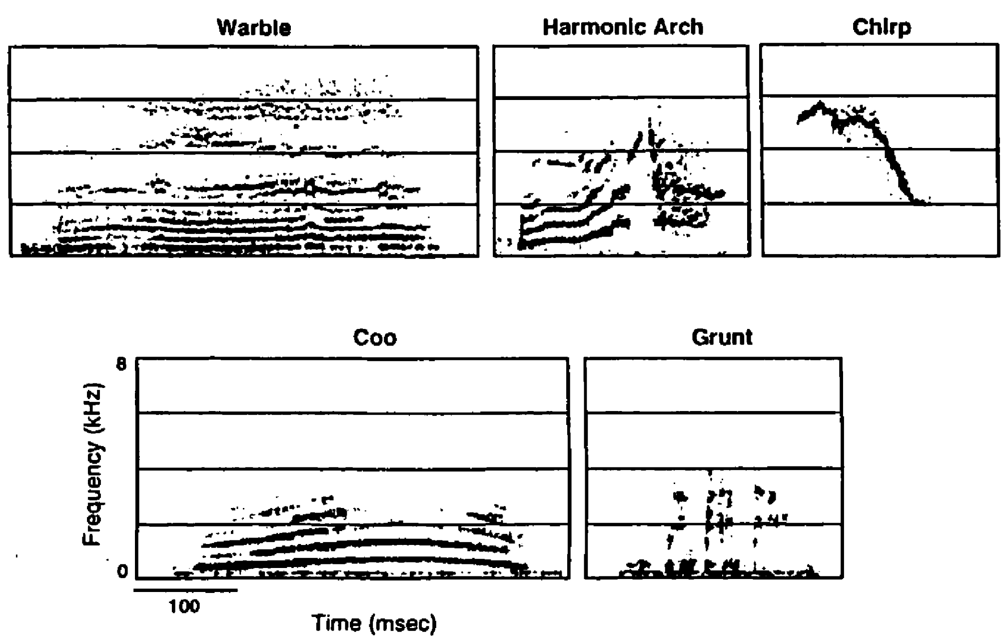


Fig. 1 The five main call types used by rhesus monkeys during the discovery or consumption of food. From: The Evolution of Communication, by Marc D. Hauser, 1997. If a call matched one of these patterns it was considered a food call.

The recording equipment was set up in the hallway adjacent to the colony room with the microphone set up on a tripod in the colony room three feet from the subjects' enclosure. During all trials the person monitoring the recorder remained out of sight of the subjects. This was done to eliminate the possibility of distraction to the colony during the trials. The recording was monitored with headphones, thus ensuring that the sound would not distract the colony.

Procedures

Experiment #1

This experiment tested the hypothesis that the colony will produce food associated calls when food is presented to them in a container rather then in the normal feeding bin. It is possible that the colony has become conditioned to not calling upon the presentation of food in a normal daily context. That is, when food is routinely placed in the feeding bin attached to the enclosure. This experiment tested this by presenting food in a manner that the colony is not routinely accustomed to. There are occasions when the keepers present food to the colony in the container used for this experiment. However, this does not occur on a daily basis or at the same time every day. Presenting food to the subjects in this particular container, on a random schedule, should result in the production of food associated calls if the use of this call type is involuntary.

For this experiment the presenter entered the colony room with the container held in front of them. No members of the colony could see into the container until it was held up to the enclosure. The presenter stated into the microphone the type of food in the container (Monkey Chow, cantaloupe, oranges, or sun-flower seeds). The presenter then approached the enclosure, placed the container with food against the enclosure, and stood there for one minute allowing the monkeys to freely take food out of the container.

After the one minute time limit on randomly determined trials the presenter gave the remaining food in the container to the colony and then left the room. Food was not given to the subjects after every trial to reduce the possibility that they would become conditioned to receiving food after each trial, and therefore producing a food call. Whether or not the subjects were given food was determined by the flip of a coin. A trial consisted of one presentation of a container of food. A total of fifty-two trials was run over thirteen days. No more than four trials were run per day.

Experiment #2

Hauser and Marler (Hauser 1997; Hauser and Marler 1993a, 1993b) have found that wild rhesus monkeys give food associated calls when they unexpectedly discover food. Thus, the macaque's food calls may be communicating 'I have discovered food'. Working from this assumption, this experiment tested the hypothesis that the LAR colony of rhesus monkeys will produce food associated vocalizations when they unexpectedly discover a food source. If food associated calls are elicited under the conditions of this experiment it may be concluded that the calls communicate the discovery and location of a food source by the caller. Additionally, this result may also support the hypothesis that the use of food associated calls by rhesus macaques may be involuntary bahavior.

The colony was presented food in a container with which they were unfamiliar. Their unfamiliarity ensures they do not associate the container with food. Therefore, the discovery of food in the container should be a surprise. The container is an apparatus designed to present two types of food, simultaneously, to a primate. The apparatus is a feeding station similar to that used by Elowson et al (1991) with her research into the food associated calls of cotton-top tamarins (*Saguinus oedipus*).

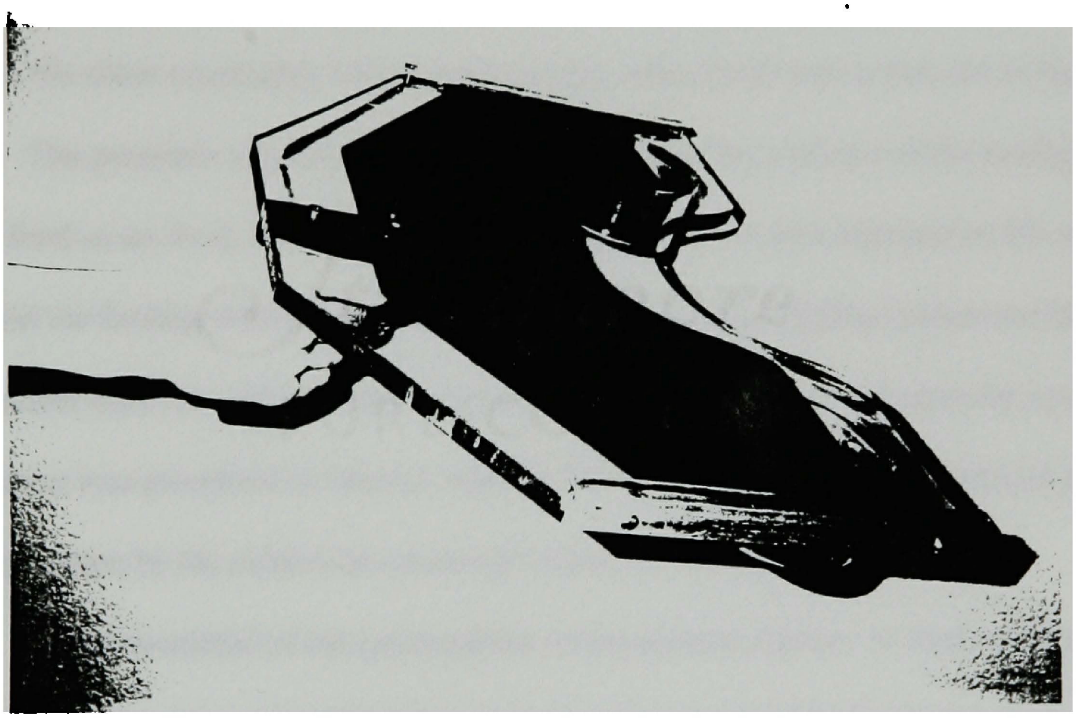


Figure 2: The feeding station used in experiment #2 of this study.

The feeding station operates as follows: food is placed into each of the two bins located at either end of the front of the station. The cover is then closed, hiding the food from the subject's view. When the feeding station is within reach of the subject the cover is slid back revealing the food.

For this experiment the same type of food (bananas) was placed in each of the bins, for all trials. The same procedure as described above was used to present the food to the subjects. On a random basis, the feeding station was presented to the colony without food in the bin. This was done to ensure that the colony did not become conditioned to the presence of food in the feeding station. This was also done to provide a way to ensure that the colony would vocalize to the food and not to the feeding station, if perhaps they would elicit a food call. Whether or not food was placed in the bins was determined by the flip of a coin. No other constraints were placed on how often food was or was not in the bin.

The presenter entered the room and stated what the contents of the feeding station were: food or no food, into the microphone. The presenter then approached the enclosure and held the feeding station within reach of the colony. The feeding station was held in this manner until one subject tried to open it. The presenter then slid open the cover and the subject was permitted to interact with the food. After the food was removed from the feeding station by the subject the presenter exited the colony room.

A trial consisted of one presentation of the feeding station. A total of thirty trials was run over five days. Vocalizations were recorded and analyzed with the equipment and procedures described earlier.

Experiment #3

This experiment tested the hypothesis that the LAR rhesus monkeys will produce food associated calls when food is within their view but just out of reach. If this hypothesis is supported by the following experiment, then the hypothesis that the food associated calls of this population communicate the information 'Give me that food' may also be supported.

Benz et al (1992) conducted research into the food associated calls of golden-lion tamarins. In this research they enticed the subjects to produce calls by presenting food to the subjects, but just out of their reach. This third experiment attempted to get the LAR rhesus monkeys to produce food calls by using this strategy.

Food was presented to the colony of rhesus monkeys in a clear container. The monkeys had seen this container before in the context of food. The food presenter entered the colony room and approached the enclosure. At this time the presenter stated the trial number and "start" into the microphone The presenter then placed the container on the floor one foot away from the enclosure. This permitted the subjects to see into the container without being able to reach into it. The presenter then left the room for one minute. After one minute had elapsed the presenter returned to the room and stated into the microphone the trial number and "stop".

Food was presented to the colony during every trial. However, the food was only given to the subjects following random trials. This was done for two reasons. First, it was difficult to know definitely that a given call was a food call without spectrographically analyzing it. This analysis could not be performed until after a call was recorded. Thus, any call elicited from the subjects during the experiment was treated as if it were of an of unknown type until after the experiment was completed. If food was given to the colony every time they produce a vocalization during the trials, they may have become conditioned to produce the wrong call to receive the food that is out of reach. Second, this experiment was not intended to condition the subjects to make any calls, it was meant to ascertain under what conditions the subjects will produce food associated calls. If food was given to the subjects every time they vocalized during the trials, whether the call was of the food call type or not, they may have become conditioned to produce a call under conditions that they normally would not. Additionally, if food was not given to them at all during the trials the subjects may have become conditioned to not produce a food call. Thus, by not giving them food, at least on a random basis, they may have ceased to produce a food call under conditions that they normally would. To maintain the integrity of this experiment the colony was given food on a random basis whether they vocalize or not. This random basis was determined by the flip of a coin.

The food was presented to the colony as a group. All calls elicited during the trials were audio recorded and spectrographically analyzed. A total of thirty trials was run over five days. No more than five trials were run per day.

CHAPTER IV

RESULTS

Experiment #1

No food associated calls were elicited from any member of the colony during any of these trials. Some vocalizations were elicited by the subjects upon the researcher entering the colony room. However, spectral analysis (see fig. 3) of these calls indicated they were most similar to alarm calls described by Hauser (1997).

Experiment #2

No food associated vocalizations were elicited from the colony during any of the trials. Spectral analysis (see fig. 4) indicates the colony did elicit alarm calls during entry into the colony room the first few times the presenter entered the room. However, these ceased to occur after the passage of time.

An interesting event did occur during the trials. The male macaque became very interested in the feeding station and its sliding cover. After becoming habituated to the station, he began to experiment with opening the cover himself. On the sixth trial of the second day the macaque opened the cover himself.

Experiment #3

After thirty trials over five days, no food associated calls were elicited in this context. Some call types were produced by the colony. Spectral analysis indicates that the infant gave what may have been isolation peeps(see fig.5)on each of the five trials run on day three and the same type call following trial five of the fourth day.

The male produced aggressive vocalizations and behavior on trials five, six, and seven on day two of the experiment, as well as during trials three and four of day four. This was confirmed by comparing of the subject's spectrograph with aggressive call spectrographs published by Hauser (1997). As they have consistently done over all of these experiments, the colony produced alarm calls when the researcher entered the colony room to set up the microphone before the trials and upon entering the colony room to begin the first trial of each day.

CHAPTER V

DISCUSSION

Experiment #1

Research conducted by Hauser (1998) with wild rhesus monkeys indicates that no less than five food associated calls are elicited by this species of primate in the wild when food is provisioned by the researchers. Contrary to these findings, the colony of captive macaques at the University of Montana produced no food associated calls during these trials. This suggests that the use of food associated calls in this context has not been learned by these subjects.

Experiment #2

The results of this experiment, coupled with the results of the first experiment, suggest that the food associated calls of this colony of rhesus macaques do not communicate the information 'I have found food'.

This suggests that the food associated calls of this colony may communicate the information 'Give me that food'. If this is the information that is being communicated, it is a possible explaination why they have not used the call in either their normal daily activities or in experiments #1 and #2. The colony has not been presented with a situation that would require them to 'request' food. This colony is provisioned on a daily basis with enough food to feed the entire group. There is so much food provided to the colony that at feeding times there is still ample remains of food from the previous day's provisioning.

Additionally, that food source is within reach of the entire population. It is possible that when the food source is known to the colony but outside their reach, they may elicit food associated calls to get the food presenter to give them the food.

Experiment #3

After 30 presentations of food to the LAR colony with no food associated calls elicited, this research is at an end. Enough data have been collected to validly conclude that this colony either does not use a food associated call or does not use it in this context. The results of Experiment #3 provide convincing evidence that in the least, this colony does not ever produce food associated calls when food is withheld from them for short periods of time. Further study may reveal that the duration of withholding food needs to be longer to cause the production of food calls. Permission to withhold food from these monkeys could not be obtained from the LAR veterinarian.

CHAPTER VI

CONCLUSION AND IMPLICATIONS

This study was designed to provide information about the meaning of the calls that rhesus macaques use in the context of food. However, because of the unique situation with this colony, no food associated calls have been available to conduct such a study. Therfore, this study has focused on a question that has not been adequately addressed in the published works on primate communication. Is the proper use of the calls of non-human primates voluntary or involuntary? This study has provided evidence in support of considering at least one call type of the rhesus macaque to be voluntary. This finding advances many more questions about the vocal communication behavior of this species of non-human primate and possible other species as well.

A total of 110 trials were run in three different contexts in an effort to produce an appropriate situation that would cause the LAR rhesus moneys to produce food associated calls. Although some call types were elicited during the trials, none of the analyses have suggested that any of them is a food associated call. Therefore, it may be concluded that the use of food associated calls by this species is a form of voluntary behavior.

This conclusion does not negate the possibility that the calls are a part of the macaques' genetic blueprint. Research conducted with birds has suggested that the songs of birds are genetically predisposed, however the use of the song is not. Experiments (Brown and Farabauch, 1998; Hausberger, 1998; Owings and Morton, 1998) have indicated that if some bird species are not taught to produce their particular song by a certain age they will never produce it. The call itself must be either a part of the bird's genetic makeup or it is learned from the mother. No research to date has demonstrated that the individual calls of birds are taught to the offspring by the mother. In fact, research has shown that when the offspring of one species of bird is paired with a mother of another species, the offspring will not learn to produce the mother's song even though the mother has attempted to teach it to the offspring. This suggests that the acoustics of the song is hard-wired into the bird, but not the use of the song. This appears to be the case for the rhesus macaque. This also suggests that if the rhesus macaque infant is not taught to use its food associated calls by a certain age it will never use them. Additionally, if the macaque is taught to use food associated calls in an incorrect context initially, it will always use the calls in that context unless it has been taught to do otherwise.

Future work in this area should investigate whether the nature of learning to use food calls by macaques is similar to that of some bird species. This work should also investigate whether a macaque can be taught to elicit a food call in an incorrect context. This work should test this possibility both before the monkey has been taught to use the calls in the correct contexts, and after they have been taught, by conspecifics.

Scientists have discovered through research that when a rhesus macaque is not producing a food call when a food source is discovered, other members of the population will exact punishment on the individual. This serves to socialize the proper use of food associated calls by the population (Hauser, 1997). This behavior was never observed in the subjects of this study. Rather than attack an individual that did not produce a food call, the colony would sit quietly and wait until it was their turn at the food bin.

This behavior suggests that the colony has never learned the proper context in which to produce food associated calls. Further, it suggests they never learned to use the food calls in their environment. This can be tested by recording all of the calls and the associated behaviors of the colony over a period of one or two weeks. These calls can then be spectrographically analyzed and compared with Hauser's (1997) spectrographs to ascertain the possible use of food associated calls in contexts other than food. If this is discovered it may provide evidence that the use of this call type is a socialized behavior in this species. If this call type is instinctual, then it will not be elicited in a non-food context, because the forces of natural selection would have ensured that no genes would perpetuate from an individual that did not elicit food associated calls in the proper context. This study has proved that this is most likely not the case.

One of the hallmarks of a good scientific study is the generation of new questions. This has been accomplished by the present work. This study must be verified to be more certain that the data are correct and that the procedures are not flawed. These experiments should be run on the colony used in the present study and other captive and free ranging populations. Further research needs to be done to determine the level and role that socialization and genetics play in the food calls of this species and other non-human primates. Lastly, further research should be conducted to test the abilities of the rhesus macaque to learn the proper context that they use food associated calls in different stages of psychological development.

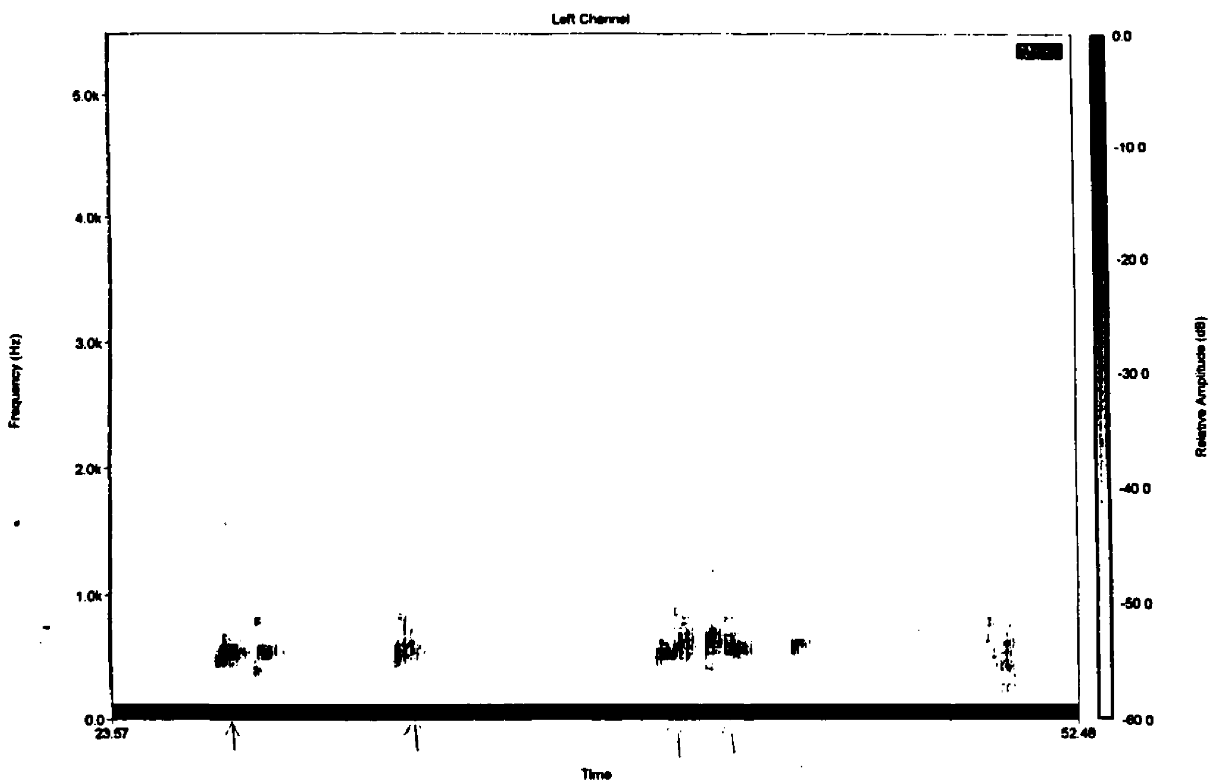
CHAPTER VII

APPENDIX

Alarm Call

Throughout the course of these experiments one call was produced by the rhesus macaques each time the colony room was initially entered by the researchers in this study. After the initial entrance the call was not elicited again during any of the trials for that day. It is highly probable that call was an alarm call. Alarm calls are used by the monkeys to alert the other members of the colony to the presence of a real or perceived danger. Comparisons of the spectrograph of this call (see below) to those published by Hauser (1998) indicate they are alarm calls.

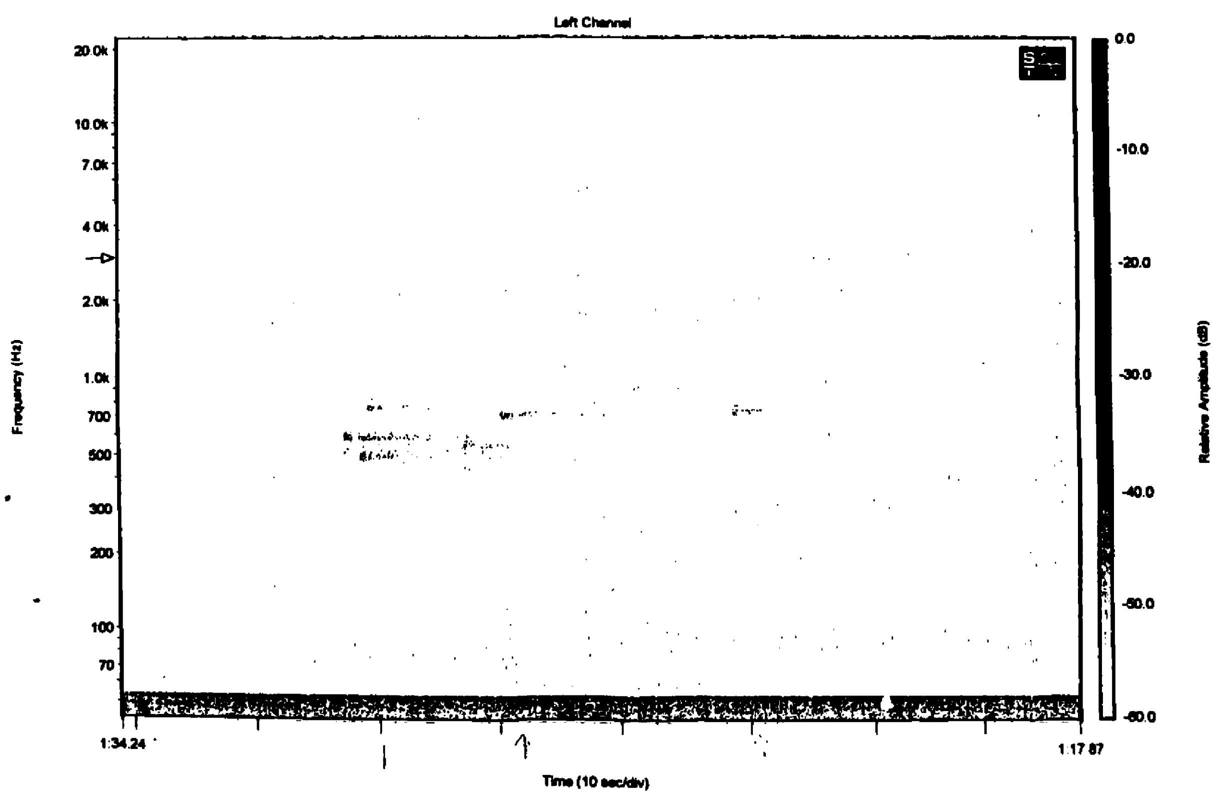
Figure 3. Spectrograph of alarm call produced by the subjects during this research.



Infant Isolation Peep

During some of the trials run for experiment 3 the infant was observed and audio recorded producing the call shown below in the spectrograph. It is believed this call was an infant isolation peep. Isolation peeps are produced by infants when they are separated from their population (Lieblich et al, 1980). During the trials that the infant produced this call the entire colony was spatially separated from the infant because they were in the process of investigating what the researcher was doing at the front of their enclosure. The infant was located alone at the back of the enclosure. It is highly probable that the infant produced this call in an effort to communicate its location to either its mother or the colony or both.

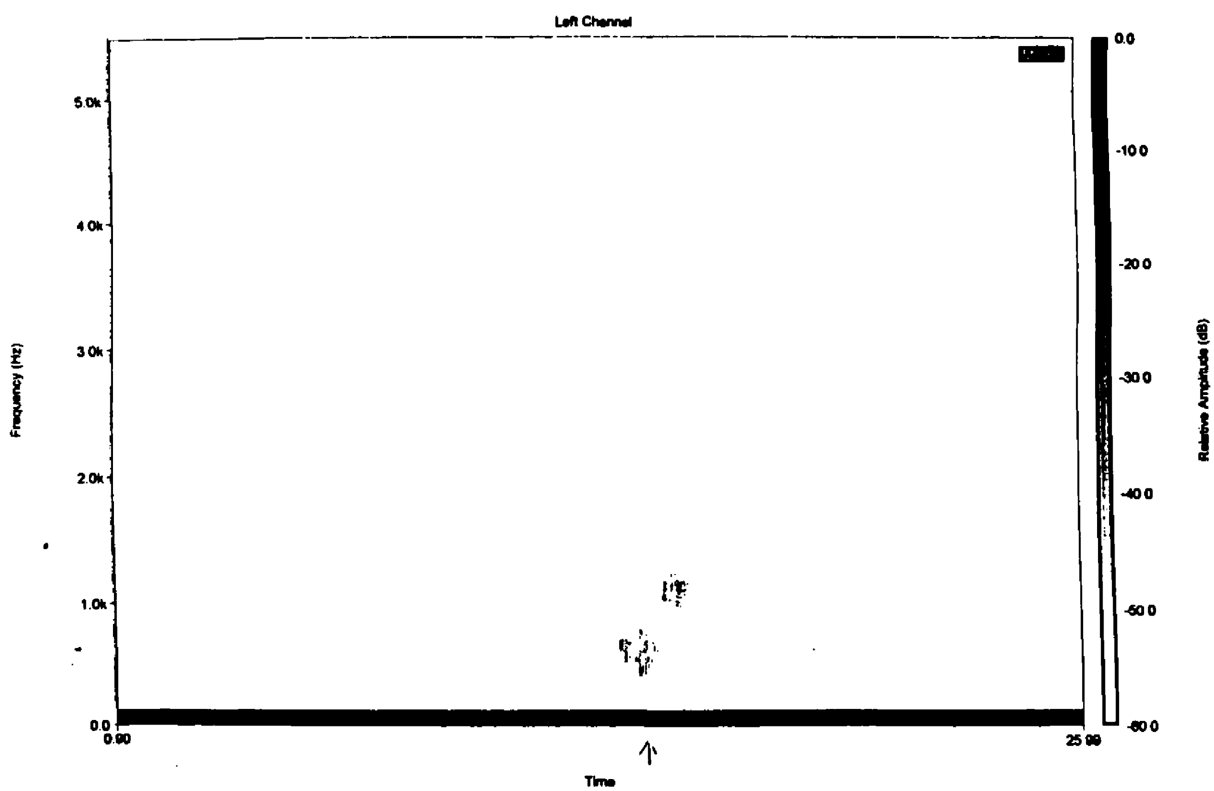
Figure 4. Spectrograph of what the isolation peep produced by the infant rhesus macaque during the course of this research.



Threat Call

During experiment 3 the colony was shown food but not afforded access to it. This was done to entice a food call from them. During some trials the colony did elicit vocalizations. They were, however, not food calls but threat calls. No comparison could be made between the spectrograph of the threat call elicited by this colony, (see below) and those elicited by other populations of rhesus macaques because none have been published. However, the behavior of the monkeys prior to, during, and after they elicited this call provides conclusive evidence that it was a threat call.

Figure 5. Spectrograph of a threat call produced by the colony during this research.



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