

RECOGNITION OF MATE AND SPECIATION IN MARMOSET GENUS *CALLITHRIX* (PRIMATES, CEBIDAE, CALLITHRIQUINAE)

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RESUMO

Reconhecimento do parceiro sexual e especiação em saguis do gênero *Callithrix* (Primates, Cebidae, Callithriquinae) O reconhecimento de potenciais parceiros sexuais como membros da mesma espécie em *Callithrix*, está baseado na informação transmitida por sinais visuais recebidos pelo casal residente (= avaliador) provenientes do intruso (= portador do sinal). Os diferentes padrões de cor da cabeça observados em saguis são interpretados como responsáveis por mecanismos de isolamento reprodutivo. Nós comparamos a resposta (componente de ação) de casais residentes perante intrusos em 4 espécies, *Callithrix kuhli*, *C. penicillata*, *C. jacchus*, e *C. geoffroyi*. As freqüências de abanar os tufos ("tuft-flicking") e apresentar genitália ("genital display") (= componentes de ação) foram registradas durante confrontações e foram interpretadas como níveis de reconhecimento de animais conspecíficos. Intrusos da mesma espécie que o casal residente, sendo potenciais competidores sexuais, estimularam mais respostas que os intrusos de espécie diferente e com padrões de coloração facial diferentes. A freqüência de resposta registrada foi dependente do par de espécies confrontado.

Palavras chave: *Callithrix*, padrão de cor da cabeça, mecanismos de isolamento reprodutivo, especiação.

ABSTRACT

Recognition of mate and speciation in marmoset genus *Callithrix* (Primates, Cebidae, Callithriquinae). Recognition of potential mates as member of the same species in *Callithrix*, is based on the information transmitted by visual signals received by members of the resident couple (evaluator) from the intruder (cue-bearer). The different head color patterns observed in marmosets are here interpreted as responsible for reproductive isolation mechanisms. We compared the answer (action component) of members of resident couples before intruders in 4 species, *Callithrix kuhli*, *C. penicillata*, *C. jacchus*, and *C. geoffroyi*. The frequency of tuft-flicking and genital display behaviors as action components was recorded during confrontations

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and interpreted as levels of recognition of co-specific animals. Intruders of the same species of resident animals (evaluators), potentially sexual competitors, stimulated more responses (action) than did intruders of different species bearing different facial color patterns. The frequency of responses depended of the pair of species considered.

Key Words: *Callithrix*, head color pattern, reproductive isolation mechanisms, speciation.

INTRODUCTION

In mammals, recognition of potential mates, co-specific or not as member of the same species or not, is based on the information transmitted by visual, acoustic, olfactory, and other signals received by the evaluator from the other animal, the cue-bearer (Starks 2004). Lutz *et al.* (1998), stated that in primates, the face is the area of the body of greatest importance for communication and recognition among individuals and species. A good example is the array of colors around the face in many *Cercopithecus* species which serves to enhance the message (Zeller 1996).

Recognition of animals of the same species during mating through species specific cues (Reed 2004) is very important to avoid waste of gametes and energy due to a behavior that will not lead to reproduction, or alternatively to potential loss in fitness to females if hybrid infants are less viable. Divergent or mismatched signals, and preferences reduce the probability of mating between populations, the greater the divergence in male signals and female preferences, the greater sexual isolation will be (Boughman 2002).

The subject of reproductive isolating mechanisms and their importance in maintaining species individuality, addressed experimentally in this paper, has been deeply treated by Mayr (1963). We refer to the chapter of this book on isolating mechanisms in general and therein, to the sections on ethological barriers, visual stimuli, hybrid inferiority and the role of isolating mechanism in particular.

Different patterns of facial color and auricular hairs have diagnostic value for each species in *Callithrix* taxonomy. The genus *Callithrix*, family Callitrichidae includes the following species: *Callithrix jacchus*, *Callithrix penicillata*, *Callithrix geoffroyi*, *Callithrix kuhli*, *Callithrix aurita* and *Callithrix flaviceps* (Rylands *et al.* 2000). The last two will not be included in this study.

The more conspicuous morphologic character that distinguish these four species from each other is the coloration pattern of face and ear tufts (Fig. 1). *Callithrix jacchus* presents white fan shaped ear tufts and the face is of dark pink gray color with a white patch in the forehead. *Callithrix penicillata* possesses long and narrow ear tufts, of the same color of the face which is black or dark brown; it has also the white patch in the forehead similar to the previous species. *Callithrix kuhli* has a light gray pelage around the face and in the cheeks, long narrow and dark ear tufts, and as in the other species, it

shows a white patch in the forehead. *Callithrix geoffroyi* shows a totally white face, black ear tufts and no patch in the forehead. Hershkovitz (1977), Vivo (1991) and Rylands *et al.* (1993) described the geographical distribution of these species over Northeastern and Southeastern Brazil.



Figure 1 - The species studied. From top left clockwise *C. jacchus*, *C. geoffroyi*, *C. penicillata* and *C. kuhli*. Observe color pattern and form of ear tufts.

Callithrix species are considered in the literature some times as full species (Vivo 1991, Coimbra-Filho *et al.* 1993) and other times as subspecies (Hershkovitz 1977). In spite of the species concept adopted, there is now a consensus about their specific status (Rylands *et al.* 1993, 2000).

It is important to note that several hybrids among these species obtained in captivity have been reported by Coimbra-Filho (1970, 1971, 1978) and Coimbra-Filho *et al.* (1993). Natural hybrids have been also reported in the wild (Hershkovitz 1977, Alonso *et al.* 1987, Coimbra-Filho *et al.* 1993). Specimens with intermediary characters between *C. jacchus* and *C. penicillata*, specially in color and distribution of hair in the ear tufts, were collected by Alonso *et al.* (1987) in the zone of secondary contact between these species,

located in some municipal districts of the Recôncavo, near Salvador, Bahia state. Alonso *et al.* (1987) believe in the existence of a reproductive isolation mechanism among these species, since little penetration of characters (genes) of *C. jacchus* was verified in the population of *C. penicillata* and vice-versa. Individuals with parental phenotypes were absent in the hybrid groups found.

Our hypothesis is that behavioral reproductive isolation mechanism (Mayr 1963) are related, in *Callithrix*, to the recognition of the different facial color patterns, typical of each species. Therefore, we looked, in these marmosets, for some behavior linked to individual or to species recognition.

Behaviors related to facial communication have been reported in *Callithrix*. Lipp (1978) described the tuft flicking (TF) in *C. jacchus* as: "The monkey stares with protruded head at another monkey. The ear tufts are retracted for about half a second and subsequently flick back. With retracted tufts, the eyes appear as slits, and the mouth-corners are turned downwards. After the ear-tufts have flicked back, the monkey frowns and the ear-tufts tend forward".

Tuft flicking was also observed in *C. jacchus* by Stevenson & Poole (1976), during intra- and inter-group communication and considered as a medium level of aggression. It was only performed by dominant resident animals facing strange individuals introduced in a stable group. The response of the intruder was a "bared-teeth gecker".

Lipp (1978) also recorded this behavior toward humans when an individual of the group was disturbed. He also observed alpha individuals directing TF to members of lower social status. The inverse situation, however, was never observed.

When introducing strange individuals (intruders), Lipp (1978) noticed another associated agonistic behavior, the genital display (GD) described as: "The animal directs its genital region towards another monkey or an observer and raises the tail, the most distal part of it bent downwards. The hind legs are extended, the back show a dorsal flexion, and the forelegs are flexed. The tail is ruffled, mainly at its base, other body hairs may be erected in a variable degree. The monkey remains in this position for 1-2 sec".

The external anatomy of the genital region has been described by Hershkovitz (1977). We observed no anatomical differences in this region between the studied species.

Lipp (1978) recorded that GD was done by both sexes, predominantly by dominant individuals, and it was evoked by the simple presence of a non-familiar animal. A subordinate individual never directed GD to a dominant one, although it was frequently done against other strange animals and humans.

Lipp (1978) also noticed that TF and GD, generally preceded the violent attacks and fights regularly showed during confrontations of adult animals of different cages.

FRENCH & SNOWDON (1981) observing the response to intruders in *S. oedipus*, considered that there was discrimination between its own and the other species (*S. fuscicollis*), because the aggressive responses were more frequent toward animals of the same species than toward animals of different species. When introducing strange individuals (intruders) of the same species to an adult male-female pair of *C. jacchus*, Araújo & Yamamoto (1993), and Evans (1983), noticed both TF and GD. As seen above, the animals response with the same behavior, TF or GD, to different stimuli such as presence of man, of conspecific and potential sexual competitor or presence of heterospecific animals. The response, however, differ in frequency according to the different stimuli. As in humans, agonistic behavior toward the potential mate competitor is used to keep the pair bond.

We can use, therefore, the frequency of TF and GD as an indicator of kinship recognition of an intruder (cue-bearer) by a resident animal. One might expect that if an individual of any of the four *Callithrix* species here studied is placed before another of different species, the response should have a lower frequency than the response observed when placing it before an individual of its own species.

We believe that if the intruder is not recognized as a potential reproductive partner of the residents mate, (low frequency of TF and GD) then the formation of hybrids (matting) among the tested species will be more difficult and a reproductive isolation mechanism may be already installed. Recognition behaviors related to facial color pattern may be significant as reproductive isolation mechanisms. In this paper, we also address two questions that are important to understand speciation mechanisms in *Callithrix*:

1) is the color pattern of the ear tufts related to the TF behavior? Would species with more contrasting tuft color prefer TF rather than GD ?

2) is the frequency of both TF and GD displayed by evaluators before cue-bearer intruders of different *Callithrix* species the same or different than the frequency observed before conspecific intruders ? Different patterns of action by evaluators would mean recognition of con/hetero -specific animals?

MATERIAL AND METHODS

The present study was carried out at the Laboratório Tropical de Primatologia (LTP), Departamento de Sistemática e Ecologia (DSE) of the Universidade Federal da Paraíba. Each group of resident marmosets was maintained in outdoor enclosures at TLP, placed within an Atlantic Forest remnant in the University Campus of João Pessoa. They were exposed to the climatic variations of this habitat. Three enclosures measured 1,6m x 1,6m x 2,0m and the fourth enclosure measured 1,6m x 3,2 x 2,0m. Sides and roof of cages were of wire mesh and the ground was covered with forest litter. The cages were provided with tree branches as roosting sites and a wood case

as shelter. The diet was composed by fruit salad (banana, papaya, grape, melon and other), bread with milk, bovine meat or hard eggs. Food was supplied twice a day.

Resident (target) animals of each studied species were kept in groups varying from two to six individuals. In each group only the reproductive pair was observed. The initial four months were used to train the researcher to observe the rapid facial behavior of the animals, as well as to habituate the marmosets to the observer's presence.

Only the behaviors of tuft flicking (TF) and genital display (GD) (Lipp 1978) were observed, see description in the introduction.

Observations of both members of the reproductive pair were done by the method of "all occurrences" (Lehner 1996). Each occurrence or record started with the beginning of the behavior by the animal observed and finished with the change of posture of its body. The observations were made from February to October 1999, between 8:00 and 15:00 hours.

Each pair of evaluators was stimulated to display TF and GD, by presenting an strange individual (cue-bearer), inside a small cage of wire mesh of 50 cm x 25 cm x 40 cm. This cage was placed at approximately 20 cm from the enclosure where the resident pair was kept, in order to avoid physical aggression from both parts through the wire mesh as well as scent marking.

The animal used as cue-bearer (in half of the observation sessions a male and in the other half a female) was a conspecific, or belonged to one of the other studied species. Resident (evaluator) and stimulus (cue-bearer) animals were not in visual contact except during experiments. Stimulus animals were neither relative of resident animals nor have shared the same enclosure before.

Four resident pairs were observed, each belonging to one of the 4 studied species. Forty observation sessions of one hour were done for each resident pair, corresponding to 10 sessions for each of the four species used as stimulus. The total number of sessions and of observation hours was 160.

After several trials it was found that one hour provides enough data without habituating the pair to the stimulus, because with longer periods the frequency drops significantly. After the first session, we waited at least 48 h before conducting the next set of observations, in order to avoid habituation of the animals to the stimulus. A different stimulus species from that presented in the previous session was always used.

Frequencies were computed for each behavior displayed by the pair of each resident species. The results were compared between species. The non-parametric Friedman (ANOVA) was used when comparing the frequencies of TF or GD in the same individual under four different stimuli. The Wilcoxon test (Siegel 1975) was used to verify if significant differences existed between the observed frequencies of TF or GD stimulated by

conspecific animal and by animals of different species.

To verify the existence of preference by each resident species in displaying TF or GD, the absolute frequencies of each behavior were computed after the four different stimuli were presented. With Wilcoxon's test it was verified, in each case, if frequency differences in TF or GD were significant. Results were considered significant with $p < 0,05$.

RESULTS

The figures 2 to 5 show the frequencies of tuft flicking (TF) and genital display (GD), performed by the resident species in the presence of the four stimulus species. Tests of differences between frequencies were performed and results are summarized in tables 1 to 3.

Preference for doing the behaviors TF or GD

We compared TF with GD responses to know which species prefers TF and to determine if preferences, independent of stimulus, were correlated with anatomical characters that enhance the signaling of TF. If this is the case, the pelage color pattern of face and ears and the behavior of TF are related, adapting the marmoset to this behavior and to threaten intruders. Results are summarized in Table 1

Table 1 - Preference for displaying the behaviors TF or GD. **Bold** indicates a behavior significantly more frequent than the other, probability is given at right. = indicates that TF and GD frequencies are not significantly different. * indicates that the absolute value suggests a preference for this behavior, although frequencies of TF and GD are not significantly different.

Resident \ Intruder	<i>jacchus</i>	<i>kuhlii</i>	<i>geoffroyi</i>	<i>penicillata</i>
<i>jacchus</i>	TF ($p=0,007$)	TF ($p=0,008$)	TF ($p=0,005$)	TF ($p=0,005$)
<i>kuhlii</i>	*TF	=	=	*TF
<i>geoffroyi</i>	TF ($p=0,03$)	TF ($p=0,005$)	*TF	TF ($p=0,01$)
<i>penicillata</i>	TF ($p=0,01$)	*GD	*GD	GD ($p=0,007$)

Reaction of residents to intruders of the same and of different species

The response to the cue-bearer of the own species should be more frequent, since it means the recognition of a potential sexual competitor, and this would not be the case with the remaining species. To test this, the TF and GD frequency toward conspecifics was compared with the frequency of TF and GD toward other species. The results are summarized in table 2, and figures 2 to 5.

Table 2. - Reaction of residents to intruders, tuft-flicking and genital display. Probability is given in parenthesis when frequency of response before another species is significantly different from frequency of response before the own species. In this case response before the own species was always higher. =: indicates that frequency of response is not significantly different from response before the own species. The lowest frequency values for TF in *C. penicillata* occurred in front of the own species.

TUFT-FLICKING				
Resident \ Intruder	<i>jacchus</i>	<i>kuhlii</i>	<i>geoffroyi</i>	<i>penicillata</i>
<i>jacchus</i>	-----	($p < 0.03$)	=	=
<i>kuhlii</i>	=	-----	=	=
<i>geoffroyi</i>	($p = 0,03$)	=	-----	($p = 0,01$)
<i>penicillata</i>	=	=	=	-----

GENITAL DISPLAY				
Resident \ Intruder	<i>jacchus</i>	<i>kuhlii</i>	<i>geoffroyi</i>	<i>penicillata</i>
<i>jacchus</i>	-----	=	=	=
<i>kuhlii</i>	=	-----	=	=
<i>geoffroyi</i>	=	=	-----	($p = 0,01$)
<i>penicillata</i>	($p = 0,006$)	=	=	----

DISCUSSION

Preference for doing the behaviors TF or GD

In general, a preference for TF in relation to GD was shown by species such as *C. jacchus* and *C. geoffroyi* that have a high color contrast between face and tufts. Preference was not observed in species such as *C. kuhli* and *C. penicillata*, with less contrast. These displayed GD and TF with similar frequency.

Callithrix kuhli, has no contrasting tufts coloration, and showed no significant difference between GD and TF, independently of the cue-bearer species employed in the experiment.

In *C. penicillata*, the frequency of GD was not significantly different from TF toward *C. geoffroyi* and *C. kuhli*, but toward *C. jacchus* the responses with GD were significantly smaller than with TF. This was due to a low frequency of GD and not to high TF. The frequency of GD in *C. penicillata* was significantly higher than TF when the response was stimulated with the own species. The preference in doing GD by *C. penicillata* toward the other cue-bearer species although not significant is also shown by the absolute values (Fig. 2). Given

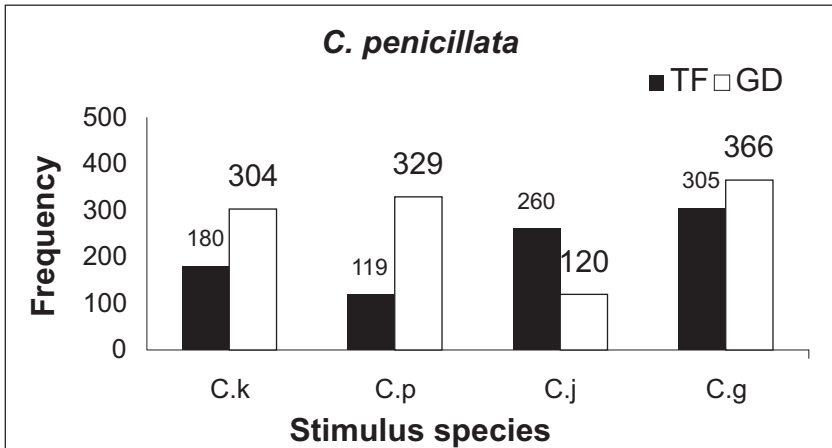


Figure 2 - Absolute frequencies of tuft flicking (TF) and genital display (GD) in *C. penicillata* stimulated by the presence of *C. kuhli* (C. k.) *C. penicillata* (C. p.), *C. jacchus* (C. j.) and *C. geoffroyi* (C. g.).

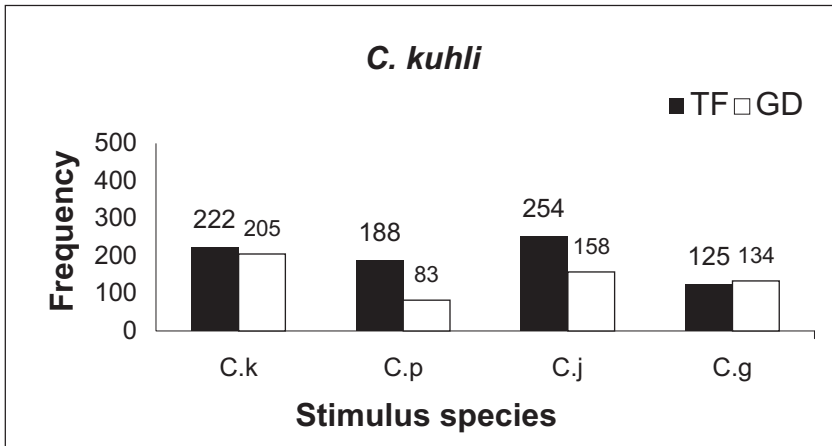


Figure 3 - Absolute frequencies of tuft flicking (TF) and genital display (GD) in *C. kuhli* stimulated by the presence of *C. kuhli* (C. k.) *C. penicillata* (C. p.), *C. jacchus* (C. j.) and *C. geoffroyi* (C. g.).

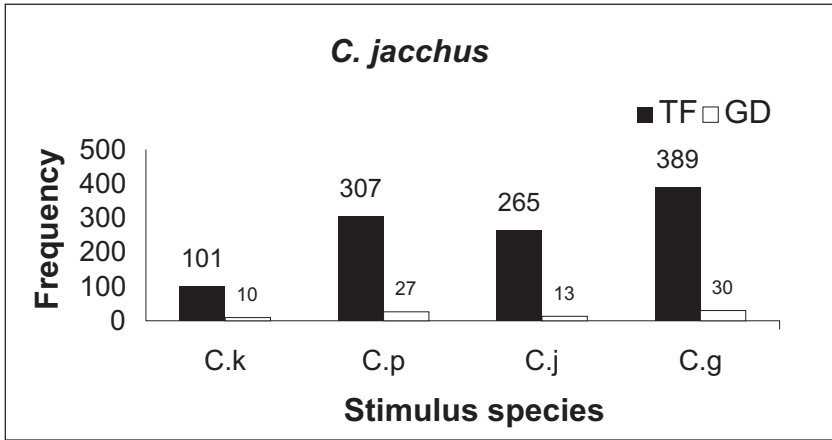


Figure 4 - Absolute frequencies of tuft flicking (TF) and genital display (GD) in *C. jacchus* stimulated by the presence of *C. kuhli* (C. k.) *C. penicillata* (C. p.), *C. jacchus* (C. j.) and *C. geoffroyi* (C. g.).

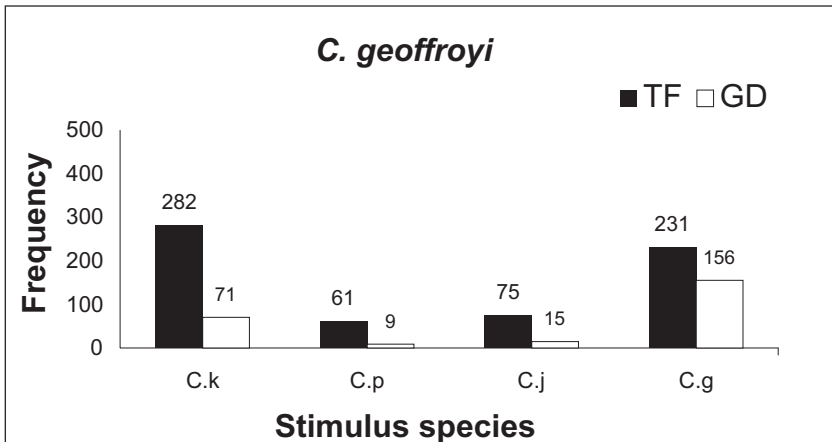


Figure 5 - absolute frequencies of tuft flicking (TF) and genital display (GD) in *C. geoffroyi* stimulated by the presence of *C. kuhli* (C. k.) *C. penicillata* (C. p.), *C. jacchus* (C. j.) and *C. geoffroyi* (C. g.).

that *C. penicillata* does not present the color of the tufts contrasting in relation to the face, this was expected by our predictions.

In *C. jacchus* and *C. geoffroyi*, the frequencies of TF were always significantly higher than GD before all intruder species. When *C. geoffroyi* was presented to conspecific, it did not show significant differences between the frequencies of TF and GD.

C. jacchus has white ear tufts in form of a fan that contrast on the darker color of the head. Thus, color and form of the tuft favor the perception of the fast movements of the ears by the intruder.

In the case of *C. geoffroyi* the tufts and ears are black not contrasting with the color of the rest of the head and body that are dark. The movement of the ears may contrast against the white face, although the white face seems more an adaptation to highlight the movements of eyelids and eyes, which are also a component of TF. Besides those functions, certainly the white face has the function of guiding the intruder's attention to the area of the animal where important signals are being emitted, more conspicuously in *C. geoffroyi* than in any other *Callithrix* species.

Thus, *C. jacchus* and *C. geoffroyi* show a correlation between a head color pattern that enhances visual communication and high frequencies of TF. This hypothesis could be tested by changing tuft color from light to dark in a cue-bearer species such as *C. jacchus* or bleach the tufts of *C. geoffroyi* and compare the frequency of the resident evaluator toward normal and toward modified patterns.

Response to intruders of the same or different species

The existence of significantly higher frequencies of aggressive responses to conspecifics, than to different species, can be an indication of species level recognition (French & Snowdon 1981). The animal probably recognizes only two categories: conspecific and not conspecific.

It was expected, therefore, that each species would react more frequently in the presence of conspecific cue-bearers than before individuals of different species, as observed by French & Snowdon (1981). However, this did not always happen. It was observed only in *C. jacchus* in the presence of *C. kuhli*; and in *C. geoffroyi* in the presence of *C. jacchus* and *C. penicillata* for TF behavior. For GD behavior this was observed in *C. geoffroyi* in the presence of *C. penicillata* as well as in *C. penicillata* in the presence of *C. jacchus* (Table 3).

Such results suggest that in spite of the conspicuous differences in the pattern of facial coloration, the evaluator species recognize some of the other cue-bearer species as potential sexual competitors, responding with high frequencies of aggressions.

It must be considered, that if a member of certain pair of species does not recognize the other member -even if the reciprocal is not true- the communication would be hindered, thus the potential mate recognition would

be diffculted and hybridization reduced. A possible obstacle to hybridization, may occur when the frequency of response to cue-bearer of a different species is significantly smaller than the response to the conspecific. This behavioral shift is favored by natural selection because it reduces the number of hybrids. Once established in one of the two species the response reduction to heterospecifics is no longer under selection pressure in the other species because communication (and hybridization) is already hindered (Mayr, 1963).

In the table 3 we summarized the results of pair of species confrontations. The response may be TF or GD according to species preferences. Bi-directional recognition as potential mates exists between the species *C. penicillata* and *C. kuhli* because the frequency of responses to the cue-bearer of the other species is not significantly different from the responses to cue-bearer of the own species. This was expected because they are very similar in the head color pattern and Vivo (1991) and Hershkovitz (1977) questioned their identification as different species.

Table 3. Responses to mutual confrontation in pairs of species. TF or GD was used according to the species preference. Plain *italics* indicates the species of the pair that stimulates a response significantly lower than before a conspecific. **Boldface** indicates the species that stimulates a response not significantly different from that observed before a conspecific. Low frequency responses were not observed in both members of a pair. Data from table 2.

One member of the pair of species is not recognized as a potential mate	Both members of a pair of species are recognized as a potential mate
<i>C. penicillata</i> ↔ <i>C. geoffroyi</i>	<i>C. penicillata</i> ↔ <i>C. kuhli</i>
<i>C. penicillata</i> ↔ <i>C. jacchus</i>	<i>C. kuhli</i> ↔ <i>C. geoffroyi</i> .
<i>C. jacchus</i> ↔ <i>C. geoffroyi</i>	
<i>C. jacchus</i> ↔ <i>C. kuhli</i>	

Bi-directional recognition as potential mates seems to exist also between *C. kuhli* and *C. geoffroyi*. Here, the differences in head color pattern are remarkable. The area of geographic distribution of *C. kuhli* contacts with the area of *C. geoffroyi* In Southern Bahia. Natural hybrids between them are not known. Species with adjacent distribution should have more efficient recognition mechanisms of potential mates than those separated by large geographic areas. This is apparently not the case here. The reproductive isolation mechanism between this pair of species would be of a different sort

(see Mayr 1963).

Among the other four pairs of species (*C. jacchus* vs. *C. penicillata*, *C. jacchus* vs. *C. kuhli*, *C. jacchus* vs. *C. geoffroyi*, and *C. penicillata* vs. *C. geoffroyi*, Table 3), isolation mechanism based on head color pattern possibly exist, since one of the species of the pair responded to the other with significantly less frequency than toward its own species.

If the aggressive response addressed to a different species has the same frequency of that demonstrated to a conspecific, then the differences in head color pattern, as visual signals, are not enough for the resident animal to distinguish as potential mates, between marmosets of the own species from marmosets of the other species tested.

During speciation events in *Callithrix*, the reproductive isolation mechanism not necessarily appeared simultaneously in all presently recognized species. Populations of each species have a different history. Therefore, the same frequencies of TF or GD are not expected in all the tested pairs of species. The speciation process in the four species here studied is not in the same evolutionary stage. Molecular phylogeny studies have been conducted by Meireles *et al.* (1998). They place *C. jacchus* and *C. penicillata* as sister groups at the end of the phylogenetic tree and as sister group of this clade they place *C. geoffroyi*. Therefore, the speciation event that lead to *C. jacchus* and *C. penicillata* is more recent than the event that originated *C. geoffroyi*. *Callithrix kuhli* is placed close to *C. penicillata*.

Genital display is probably a more primitive behavior because it is present in other unrelated primates as *Macaca* sp. (Maestripiéri 1996, Maestripiéri & Wallen 1997) and it is not related to the face. TF, however, seems to be a specialization proper of *Callithrix*. It is an adaptation to reinforce the differentiation of the facial color patterns.

Concluding, species that show a higher contrast between color of tufts and color of face such as *C. geoffroyi* and *C. jacchus* used more frequently the aggressive behavior related to tufts (tuft flicking) than did species that show less conspicuous contrast between color of tufts and color of face. The last used genital display more frequently or show both behaviors with the same frequency.

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