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PLAYFUL BEHAVIORS OF SUBORDINATE ADULT MALE HOWLER MONKEYS (*GENUS ALOUATTA*) IN COMPETITIVE CONTEXTS: CASES OF TACTICAL DECEPTIONS?

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Abstract: Individuals can have conflicting interests, which become more conspicuous when involving disputes over resources. In these situations, subordinates can tacitly deceive others, eventually using affiliative behaviors to buffer agonisms from dominants. Deception and social plays in primates are known to be related to a higher degree of cognition. In some circumstances, they can be interchanged, although the first remains elusive in the more arboreal South American primates, as in the folivorous howler monkeys (genus *Alouatta*). Here, I report seven records in which subordinate adult males of wild brown howlers (*Alouatta guariba clamitans*) living in two mixed-species groups with black-and-gold howlers (*A. caraya*) and their potential hybrids displayed playful behaviors towards more dominant males from both species in situations of intra- and intergroup and intra- and interespecific disputes over sexual and feeding resources. I performed a total of 1,400 hours of direct observations in a 150-ha forest fragment in southern Brazil, between April 2007 and June 2008. The playful behaviors were successful in buffering agonisms, which were accentuated in their absence. In contrast, these displays were distinct from observed typical social plays, which were symmetric and did not involve sexual or feeding contexts. These findings support the hypothesis that the playful behavior observed was a modification of affiliative behaviors meant to cause dominants to misinterpret or not react to the subordinates' behavior, as predicted by the tactical deception theory. This study widens the number of howler monkey taxa that display these behaviors. At the same time, their effectiveness in evading agonisms during interespecific interactions suggests that these behaviors represent a social regulation present even in wild, mixed groups of howler monkey species.

Keywords: Affiliative behavior; Agonistic behavior; Behavioral flexibility; Hybridisation; Manipulation; Mixed species group.

INTRODUCTION

Animals face conflicting interests in a variety of situations, resulting in potential manipulative communication (Searcy & Nowicki, 2005). They can tactically cheat, mimic, and use others to manipulate or buffer agonism during competitive situations for food and sexual resources. Tactical deception, or manipulation, refers to the capacity of a sender to shift one part of its behavioral repertoire into a deceptive role, depending on the context, with the receiver paying a fitness cost (Whiten & Byrne, 1988; Rubenstein & Alcock, 2019). This is viewed as a conspicuous case of flexible use of behavior to take advantage of conspecific fixed responses (Cluton-Brock, 2009; le Roux et al., 2013). In these cases, cheater individuals can use a series of tactics to a) conceal something from the target individual; b) distract the target's attention from one locus to another; c) cause the target to misinterpret the significance of the agent's behavior; or d) affect the target using other individuals as social tools to the agent's benefit (Whiten & Byrne, 1988).

According to Whiten & Byrne (1988), these deceptions should be used at a lower frequency and in different contexts from those in which animals use the honest version of the behavior, since this would make it more likely that another familiar individual would misinterpret what the acts signify, to the advantage of the actor. Nevertheless, theory predicts that cheating should evolve to avoid detection and punishment, representing an important mechanism for subordinates during competition because it can allow these individuals to escape or buffer some social costs, appeasing tensions when dominants perceive a reduction in their fitness (le Roux et al., 2013).

Most primates live in long-lasting groups; therefore, familiar conspecifics can be the major competitors for access to resources. This situation favours individuals that can offset the costs of competition by using manipulative tactics (Cheney & Seyfarth 1990), although deception of individuals living in intimacy is likely to be subtle and rare (Whiten & Byrne, 1988). Although the frequency of deception correlates with neocortex volume in primates, the use of tactical deception to solve social problems without employing force has been reported in numerous primate species, spanning all major taxonomic groups of this order (Byrne & Corp 2004). Its nature and distribution have shifted to centre stage in attempts to understand social evolution, communication, and mind (Whiten & Byrne 1988). However, deception in monkeys and prosimians can be understood as the product of rapid and extensive learning in a social context, alongside emotional states of anxiety (Kean et al., 2017), rather than mechanisms representing the mental states of others, as appears to be the case in great apes (Byrne & Whiten, 1991; Byrne & Corp, 2004).

Social play, another kind of flexible behavior, is also correlated with the neocortex ratio (Lewis, 2000; Palagi, 2018); it is a prominent feature of primate behavior, most often observed in infants and juveniles. However, social play is also performed by adults and usually tends to be more expressed when animals are in a low-stress setting (Burghardt, 2014; Montgomery, 2014). Social play has been suggested to represent a means of facilitating tolerance and enhancing social skills and the ability of animals to cope emotionally with unexpected situations (Lewis, 2000; Gennuso et al., 2018), which helps them to bear the risk of conflicts that can escalate into severe fighting (Palagi, 2018). Adult social play can have different functions from those of immature individuals, as play between adults has shorter duration (particularly between males) and is more associated with situations of uncertainty in social relationships, courtship between males and females, or a need to solve or prevent disputes between individuals from the same or different groups (Antonacci et al., 2010; Palagi, 2018). Adult social play can also be used to keep the attention of a partner away from a resource, which is an ability to manipulate social situations (Palagi, 2018). In fact, social play rates were associated with a higher frequency of tactical deception in adult primates, supporting adaptive explanations that link both behaviors to adult social challenges (Montgomery, 2014). Moreover, adult primates can mimic infantile behaviors, displaying paedomorphic movements, postures, and vocalisations similar to those of plays as appeasement signals, which operate as de-escalating elements in competitive regimes (Jones, 1980; 1995; Palagi, 2018).

Howler monkeys (genus *Alouatta*), the most folivorous American primates, are arboreal and sedentary. These monkeys are less socially active and invest less in exploration and play than other primate species (Baldwin & Baldwin, 1978). In general, social play in howlers involves mainly juveniles and infants of both sexes, and the participation of adult males is rare (Gennuso et al., 2018). According to Baldwin & Baldwin (1978), adult male howlers rarely participate or physically contact the players. Their appearance at the play scene could be coincidental, and their sudden proximity terminates play.

Interestingly, adult males of mantled howlers (*Alouatta palliata*) were observed to mimic playful, infantilised vocalisations to a more dominant male during approach to a sexually receptive female to copulate, after which they were displaced by the dominant male several times (Jones, 1980). These cases suggest subordinates were trying to cause dominants to misinterpret them using

behaviors similar to play.

Despite the small relative brain sizes of the genus *Alouatta* , as expected from their folivorous low-energy diet (Strier, 2021), other (albeit somewhat old) cases of social buffers, apparenting deceptions in howlers, have been described. Clarke (1998) and Jones (2005) reported cases in which subordinate howlers with an infant approach the dominant males to buffer the dominant's intent to mate with them or to displace them in the feeding context, a case of using infants as social tools. Furthermore, Whiten & Byrnes (1988) reported two individuals in one group of howlers who inhibited their roars until they were in a position to do so with maximal surprise to a second group, gaining preferential access to a resource, which may represent a case of acoustic concealment. Although these cases are rare and anecdotal, it is still important to continually report cases of deceptions to better catalogue and investigate the phenomena (Whiten & Byrnes 1988). This is particularly important in arboreal South American primates since visual and vocal communication can be more difficult to be performed and observed when compared to some of the ground-dwelling African and Asian primates living in open habitats (Jones 1995; Strier, 2021).

Brown howlers (*Alouatta guariba clamitans*) and black-and-gold howlers (*Alouatta caraya*) can live in mixed species groups with their hybrids in the wild along their contact zones in southern Brazil and northern Argentina (Aguiar et al. 2014; Mourthé et al. 2019). A previous study surveyed five groups of mixed howler species (Aguiar et al. 2008) and monitored two of them for behavioral and ecological assessments in the Ilha Grande National Park, Brazil, one of the sympatry sites between the two species. Here, I report seven events of social interactions between male howlers in mixed-species groups, including interspecific interactions, in which subordinate adults of brown howlers used play-like behaviors in what appeared to be manipulative tactics to distract or to buffer agonism from dominants in the context of disputes.

METHODS

STUDY SITE AND SUBJECTS

I followed two neighbouring mixed-species howler groups (Group I and II) comprised of brown and black-and-gold howlers in a 150 ha forest fragment locally known as *Mata do Bugio* in a matrix of pastures in the surroundings of Ilha Grande National Park (left bank of the Upper Paraná River; 23° 22' 52.3" S, 53° 45' 39.6" W), municipality of Icaraíma, state of Paraná, southern Brazil. The forest fragment is a degraded secondary formation of semideciduous seasonal forest at the western limit of the Atlantic Forest domain, one of the known areas of sympatry between the two species (Aguiar et al., 2014). *Alouatta guariba clamitan*s and *A. caraya* are howler species with contrasting sexual dichromatism (Gregorin, 2006), and I taxonomically classified the focal individuals (including their potential hybrids) based on their coat colour, following Gregorin (2006) and Aguiar et al. (2008) — although a recent molecular study showed that some individuals with an apparent pure phenotype of either species could be hybrids (Mourthé et al., 2019).

I followed the groups systematically from dawn to dusk, for four to five days per month, between April 2007 and June 2008, totalling 734 h of direct observations of Group I over 58 days and 664 h of Group II over 54 days. I collected data on activity patterns through scan sampling (Altmann, 1974) every 30 min and recorded all events of social behavior observed occurring in dyads and in group encounters.

Initially, Group I consisted of two adult males (AM1 and AM2) and one adult female of brown howlers, one peripheral subadult male of black-and-gold howler, and one adult female with a hybrid phenotype (AF1), though the group had shrunk to only AM1 and AF1. In this group, AM1 was redder and clearly the dominant male, and AM2 was a browner, younger subordinate individual. AM2 was the individual who received the greatest amount of agonism in his group, almost exclusively from AM1 (78% of all agonism observed in the group, n= 50), mainly in sexual contexts but also during feeding.

Group II comprised two subgroups with fission-fusion social organisation: one subgroup consisted of three adult male brown howlers (AM1, AM2 and AM3), one adult female with a hybrid phenotype and her infant, which was born at the end of the study. AM1 was redder and clearly the dominant among the three males; AM2 was browner, younger, and subordinate; AM3 was more orange and an older male, with several facial cured scars and a more peripheral behavior. AM2 and AM3 received the greatest amount of agonisms (in similar proportions), with fewer agonisms displayed towards AM1. AM2 and AM3 also received agonism from the adult male black-and-gold howler of the group, though they did not display agonism towards him. These agonistic interactions were mainly during sexual contexts but also during feeding. The other subgroup comprised this last adult male (AM1c), one adult female (AFc), and one juvenile of black-and-gold howlers. The acronyms above were provided only for those individuals who were involved in the interactions described next.

OBSERVATIONS

During the entire study, I observed seven records of a kind of playful behavior, which were displayed by three subordinate adult males of brown howlers towards dominant adult males of both species in contexts of potential social conflicts or disputes for sexual or feeding resources in both intra- and intergroup interactions. Each record occurred on different, non-consecutive days.

The behaviors displayed by the subordinates in the seven records were very similar. They consisted of moving slowly and shaking their head repeatedly, with their mouth open and relaxed, vocalizing a soft growl and lightly biting their own hands or branches that were in their way while moving towards a male of higher hierarchy and then trying to touch him and pass around or above him. I observed subordinates performing this behavior immediately before they tried to interact with a female near the dominant or immediately after interacting with a female (or after he fed on a patch of flowers). However, the interactions or feeding bouts were interrupted by the arrival of the dominant male(s) at the scene. The subordinate displayers received no agonisms or playful responses from the dominant males on any occasion, except for one occurrence of a supplantation (see below).

In Group I, I observed one occasion in which the subordinate male (AM2) displayed this behavior towards the dominant male (AM1) as the latter was resting, sitting beside the adult female of the group (AF1). AM2 tried to pass the dominant while displaying the behavior, but the dominant male did not move. After two minutes, AM2 sat and rested beside AF1, between her and the dominant male. Besides the playful behavior, I recorded two events of typical social play between the male brown howlers in this group, both of which were symmetrical. I did not notice any interactions involving females or food either

immediately before or after these two typical playful interactions.

In Group II, I observed six occasions where playful behavior was displayed in situations of apparent competition between males. They were displayed by two subordinate male brown howlers (AM2 and AM3) towards more dominant males. AM2 displayed it three different times towards the adult male black-and-gold howler (AM1c) and once more towards the adult male brown howler (AM1). The older male brown howler (AM3) displayed the behavior two different times, once towards AM1 of its group and again towards the dominant adult male brown howler of the neighbour group (AM1 of Group I) during an intergroup encounter.

AM2 brown howler displayed playful activity towards AM1c black-and-gold howler on two occasions after the former copulated with the AFc black-and-gold howler. The first two times were very similar: AM2 was copulating with her when AM1c came on the same branch, at which point the copula stopped. Immediately, AM2 displayed the behavior towards AM1c, passing by him and leaving the tree. On the third occasion, AM2 displayed and passed by AM1c and approached and touched AFc, which was beside the male black-and-gold howler. AM2 brown howler also displayed this behavior towards the higher-ranking AM1 brown howler when the former was feeding on flowers of a liana in the canopy and the latter came to the same branch. AM2 was supplanted by AM1 after the playful display.

The older male, AM3 brown howler, performed this activity twice towards higher-ranking brown howlers, once towards the dominant brown howler of his group and on another occasion towards the dominant brown howler of a neighbouring group (Group I). AM3 was copulating with AFc black-and-gold howler when AM1 came on the same branch barking, with hackles raised, whereupon the copula stopped. AM3 passed directly by AM1, performing the behavior, and then left the place. Finally, during an intergroup encounter between Groups I and II, AM3 brown howler displayed playful behavior towards AM1 brown howler, the dominant male of Group I. The male brown howlers of both groups were barking in neighbouring trees, except AM3. AM3 left the tree where his group was and went to the neighbour tree and approached the dominant male brown howler (AM1) and the hybrid female (AF1) of the other group, both of which were barking together side by side. AM3 then passed by AM1, performing the behavior, went to the female, and touched her. After touching her, AM3 left the tree rapidly. In Group II, in addition to these playful behaviors, I recorded seven events of typical social play between adult males. All these typical plays were symmetrical, and there were no interactions between these males with females or with food, either immediately before or after the play.

DISCUSSION

The motor pattern of the behaviors displayed by subordinate adult male brown howlers was similar to so-called infantilised behavior with paedomorphic vocalisations observed in *A. palliata* by Jones (1980), who suggested that the incorporations of elements mimicking infantile displays help appeasements in sexual contests. It is noteworthy, then, that the observations of these behaviors in feeding contests in *Mata do Bugio* represent as-yet unreported behaviours since Jones (1980) only observed these patterns in sexual contests. This suggests that subordinate howlers can flexibly use these behavioral shifts during contests over any resource.

In addition, the motor pattern observed here is very similar to elements observed in

typical playful behaviors shown by howlers, like repeated movements, exposing teeth, giving little bites and softening growls, and trying to reach another individual using rapid hand movement. These activities are known to belong to howler's play faces, play invitations, and even play itself (according to the ethograms available in Albuquerque & Codenotti, 2006; Dias & Rangel-Negrín, 2015; de Cunha et al., 2015; Gennuso et al., 2018).

Although adult social play can be used to manipulate behaviors during social challenges (Montgomery, 2014; Palagi, 2018), the contexts and possible functions observed in the present study strongly suggest that those behaviors are not, in fact, play. Unlike the seven records described, the adult social play I observed consisted of symmetrical behaviours and did not involve contexts of disputes over resources. In those seven records, it is more probable that subordinate howlers were using elements of playful behaviors in other contexts. Since these elements have a low probability of escalating to a fight (Jones 2005), they were using them in response to sexual and feeding contests. This may represent an exaptation of affiliative behaviors in stressful situations that aim to avoid aggression from dominant intra- or intergroup competitors, a costly result that folivorous howlers, with their energy-poor diet, should avoid, using ritualization as much as possible (Jones 1980; Strier 2021).

Indeed, the playful behaviors displayed by the subordinates were effective at avoiding hostility (with the possible exception of the case of supplantation in Group II) since the dominant males do not escalate to agonistic behaviors towards them. Interestingly, these behaviors also effectively avoided agonism in dispute interactions between interspecific males living in a mixed-species group. For instance, on the three times when the subordinate male brown howler (AM2) of Group II displayed playful behavior towards the male black-and-gold howler (AM1c) in sexual contexts, the former did not suffer agonism from the latter; however, in other interactions between them involving disputes over resources, the later displayed agonistically against the former (see methods). Although social interactions can be more difficult between species since recognition may be hampered (Moynihan 1968), these interspecific observations and the widening of howler monkey species performing these behaviors suggest these could be patterns in the behavioral repertoire of the genus *Alouatta*.

The use of noncontact displays to resolve agonistic interactions is common in animals, and the displays are mainly threatening (Rubenstein & Alcock 2019). However, the shift of one part of the behavioral repertoire (activities observed in affiliative plays) in a different context (resource disputes) to appease aggression is rarer and could be interpreted as a tactical deception (Whiten & Byrne 1988; Rubenstein & Alcock, 2019). The records described here are consistent with cases that, according to Whiten & Byrne (1988), cause targets (dominant male howlers) to misinterpret the significance of the behaviors of the agent (subordinate male howlers). Although the playful behaviors are clearly serving as buffers to agonisms, I cannot speculate at this time why dominants, the targets/receivers, did not escalate to agonism towards subordinates unless they were indeed deceived. While this is an expected outcome under the theory of tactical deception, the possibility that dominants accepted the displays of the subordinates as submissive cannot be ruled out.

In sum, subordinate adult male brown howlers from the degraded forest of *Mata do Bugio* used playful or mimicked infantile behaviors (*sensu* Jones 1980) to deal with stressful intra- and intergroup resource

disputes with higher-ranking males. This behavioral pattern can be also considered as a mechanism of certain individuals to regulate or facilitate gregarism and social integrity in disturbed habitats where competition can be stronger (Jones 1995). This study expands the cases and taxa in which these potential occurrences of tactical deception are known while also demonstrating that this mechanism of social regulation can be present even in wild mixed groups of howler species.

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