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Breeding Behaviors in the Black Howler Monkey (*Alouatta pigra*) of Belize

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ABSTRACT. Adulterous breeding between a female howling monkey (*Alouatta pigra*) of one troop with a male of an adjacent troop occurred despite territorial defense between the two troops. The specific behaviors are described as well as a synopsis of daily events which occurred between the female and two males from adjacent troops. A discussion of how this interaction and the behavior patterns relate to what is known about breeding in howler monkeys and related species follows.

INTRODUCTION

Breeding behavior in the black howler monkey, *Alouatta pigra*, has not been described. During observations of two troops in Belize I observed a week in which a triadic breeding interaction occurred in which a female bred outside of her troop. Due to the intensity of these interactions, many behaviors, not often seen, were easily observable. These behaviors serve as a basis for a preliminary description of breeding behavior in *Alouatta pigra* which will be compared to breeding behaviors in related species.

METHODS

A field study of two troops of black howler monkeys, *Alouatta pigra*, was carried out in Bermuda Landing, Belize from April 28 to July 14, 1981. A total of 350 hr was spent in contact with monkeys, most of which was spent studying two infants in two troops. During the study of one of these troops (Cashew troop), a female, *Point*, came into estrus. At this time protracted observations were made on her interactions with two males from two different troops, with whom she copulated. Most of these observations took place within 50 ft of the territorial line between the two troops. Over 30 hr were spent observing the breeding interactions.

The Cashew troop was composed of an older dominant male (*One Ball*), a mature younger male (*Dice*), and two adult females, one with a month-old infant (*Spot*), and the other with a juvenile male (*Point*). *Point* was in estrus between May 12–17. The adjacent troop was composed of a male in his prime (*Huevos*), an adult female, a subadult male and a juvenile male.

RESULTS

The situation between the two troops involved a clear case of area territoriality. Although there was some overlap of area usage between the two troops, I saw three cases in which ownership was clear. In each case, the owner troop, finding the visitor troop in their territory,

chased them into their adjacent territory. A definite line with a 3–10-ft gap between trees was accepted as the boundary line. Roaring was commonly heard from both or either troop while on their side of the line.

A number of discrete behavior patterns were noted and will be described below.

Sexual Following

The male, *One Ball*, continually followed *Point*, the estrous female, for six days. He rested very near her, often laying his head on or near her rump. He was attentive to her moves, got up when she did, and paid little attention to eating or other activities. This is very similar to general mammalian pair bonding during estrus.

Male Herding

The resident male's actions were somewhat stereotyped as he pushed his body between the female and her path toward the adjacent territory. He usually ended standing with his shoulder close to and in front of the female's face and chest, effectively cutting off the ambivalent female from going any closer to the male in the adjacent troop. During this movement I never saw the male act aggressive toward the female or physically grab or dominate her in any way other than to block her passage with his body.

Urine Sniffing

As in ungulate species, Glander (1980) noted that *A. palliata* males would sniff urine of females and give a behavior similar to the lip curl or flehmen. In *A. pigra*, I noted urine sniffing by the attentive male during estrus. On a few occasions I saw the male give a chewing response after sniffing the urine. However, I looked closely and never saw a ritualized lip curl or grimace similar to that seen in ungulates or cats. The male, however, was very concerned with smelling the urine and in one case he quickly removed feces from the female's anus with his hand in order to sniff her urine.

Anogenital Rubbing

While sitting on a branch the female would bring her vulva forward, rubbing it on the branch. Both males were seen sniffing the branches where she had been, indicating probable scent marking.

Chin Rubs, Back Rubs and Chest Rubs

Chin rubs were more common in the courtship situation. Both males were noted to push the chin and throat area forward or obliquely forward on the branch. Since there is a known throat gland in *Alouatta* (Eisenberg, 1977; Epple & Lorenz, 1967) this is presumably a scent marking behavior. The female in a few instances rubbed her chin-throat area in a downward motion onto the top of the head of both males. I also saw one instance where a male pushed forward on his chest contacting the branch and rubbing his chest forward on it. Additionally, on one occasion both the resident male and female simultaneously rubbed their backs back

and forth on the branch as though scratching their backs. In this case they may have been rubbing in already deposited scents.

PRECOPULATORY FACING

Eye contact seemed important to the female. At long distances she gazed and tongue flicked at the foreign male who was 20–30 ft away. The female would often try to look the resident male in the face before tonguing or lipsmacking at him and if he would not look at her she would change her position to place her face in front of his face or actually try to pull his face over to her by the side hairs to get him to look at her. These, with tongue flicks often preceded copulatory mounts.

TONGUE FLICKS, LICKING AND LIPSMACKS

I was particularly interested in clear observations on these behaviors as I have seen a great variability in tonguing behaviors in old world monkeys which all seem to have similar conciliatory functions and which seem to have been evolutionarily derived from infantile sucking (HORWICH & WURMAN, 1978). My first view of the tongue extensions led me to believe it was a very different behavior which resembled marmoset tongue extensions (pers. obs., in cotton-topped marmosets; MOYNIHAN, 1970). On closer observation I noted that the tongue was extended as the lower jaw was lowered; in what seemed to be less intense behaviors, the tongue was not extruded and instead the mouth was slowly opened and closed with the tongue barely extended, resembling the slower lipsmacks of old world monkeys when they groom each other. These latter behaviors I termed lipsmacks and they seem to be homologous to those in old world monkeys and are used similarly in distance reducing situations. Lipsmacking with tongue extrusion was also noted in *A. seniculus* (NEVILLE, 1972).

COPULATION

Copulatory mounts usually included the male's grasping the female with his hands and sometimes his feet. The main constancy was his holding her by the shoulder hairs with his hands. Figure 1 shows three postures noted. Each copulation lasted between a half to a minute.

BRANCH BREAKING, BRANCH SHAKING AND SHOULDER HUNCH DISPLAY (LEAP AND REAR; EISENBERG, 1976)

Adults were noted to break off dead branches and let them fall in many situations. This was often done by males unacclimated to humans. During this estrus period it was commonly seen given by both males and seemed to be done temporally with branch shaking displays. In branch shaking the male rounds his back, grasping a branch and rocks back and forth on his hind legs. On occasion he would rise up on his hind legs releasing his hand grips and hunch his head and shoulders forward, rocking again on his hind legs. This seems similar to the golden lion tamarin arch display (RATHBUN, 1979). Piloerection on the shoulders and back were evident. All three behaviors seemed interrelated and aggressive.

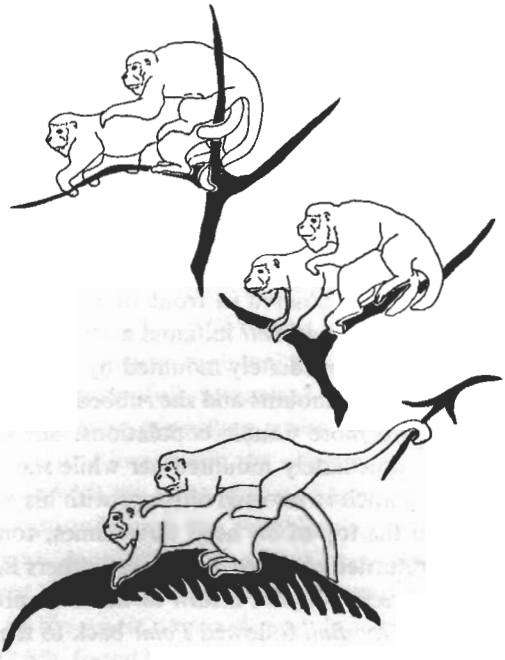

Fig. 1. Three copulation postures.

Gutteral Trill

This vocalization was usually done in conjunction with roaring and especially during territorial encounters. During this courtship, it was frequently noted as an aggressive behavior between the two males. The body was arched, and the whole body especially the chest and belly, moved rhythmically as he vocalized the low uh-uh-uh-uh gutteral trill sounds.

Roaring

Roaring is a complex vocalization which will be discussed in another paper in more detail. Chivers (1969) has done an extensive analysis for *A. palliata*. In this study roaring was definitely used in territorial defense in contrast to Chivers' (1969) explanations of it at Barro Colorado Island. I observed it specifically employed and initiated by the two males during their interactions over the estrous female. Once started it was joined in by other members of both troops.

Greeting Ceremony

Glander (1980) noted this stereotyped behavior done between animals of the same sex. In females, they were highest in frequency during reproductive cycling. Two animals approach one another sniffing each others axillary regions, then sniffing or licking each others genitalia. *Point*, on one occasion when returning from her adulterous liason with *Huevos*, greeted the other troop female in this way.

DESCRIPTION OF TRIADIC INTERACTIONS

May 12—*One Ball* closely followed *Point* sniffing her urinations. The younger male (*Dice*) seemed to move from areas where *Point* was.

May 13—*Dice* was once observed to push his body over *One Ball*'s face perhaps in a greeting ceremony. He tried to engage *One Ball* in play, who responded with an aggressive branch shaking.

May 14—During late afternoon *Point* approached the territory line and exchanged glances with *Huevos*. *One Ball* continually shouldered in front of her. Both males gave aggressive branch shakes and gutteral trills and *One Ball* initiated a roar which both others joined in. Then *Point* crossed the line and was immediately mounted by *Huevos* two times for a minute or less. He sniffed her vulva in between mounts and she rubbed her vulva, tongued at, and presented to *Huevos*, in between two more double copulations. She briefly recrossed the line only to return to *Huevos* who immediately mounted her while she stood on a cohune palm leaf and he held onto a fig tree branch in his own territory with his tail (Fig. 1, bottom). She then faced him and chin rubbed the top of his head three times, tongued at him and again chin rubbed his head. She left, returned and they licked each others faces. He reached for her, she presented and he mounted briefly. On her return to her own area, *One Ball* initiated a roar which *Huevos* joined. Then *One Ball* followed *Point* back to the main part of their territory.

May 15—*Point* continually approached the territory line but was cut off by *One Ball*. He roared and gave shoulder hunch displays. Both he and *Point* rubbed their backs on branches. During the roars both males gave gutteral trills. *Point* vulva rubbed and *One Ball* followed her, sniffing her urine and giving mouth chewing. *One Ball* again initiated a roar which all three participated in and *One Ball* chin rubbed. *Point* then quickly crossed over to *Huevos* who immediately mounted and copulated with her in less than a minute. As others from *Huevos'* troop approached, *Point* returned to her territory and *Huevos* gave a gutteral trill.

May 16—All three animals roared across the line. *Point* was continually cut off from crossing by *One Ball*. He sniffed *Point* and gave shoulder hunch displays, chin rubs and gutteral trills. *Huevos* responded similarly. The courtship procedure changed radically when *One Ball* sniffed *Point*'s vagina, mounted and copulated with her. He gave branch shakes and chin rubs and then sniffed *Point* and copulated again. Following this *Point* no longer attempted to cross the gap or gaze and tongue at *Huevos*, but instead began following and soliciting contact from *One Ball*. She grasped his face as if to make eye contact and sniffed and grasped his penis, and gazed at and nuzzled his face. *One Ball* mounted and copulated with her three times. The last time *Point* presented by crawling under him as he lay on a branch. Following this *Point* vulva rubbed and *One Ball* lipsmacked as she tongued, then presented to him. Later, when across from *Huevos*, *One Ball* sniffed *Point*'s urine, roared and chin rubbed profusely while both full troops joined in roaring. *Point* continually followed *One Ball*, trying to make eye contact with him.

May 17—*Point* followed *One Ball*, tongued and lipsmacked at him, licked his face and rubbed her chin on his head, continually trying to make eye contact with him as she had with *Huevos*. She did this by pulling his face toward her by its side hairs. He clasped her and copulated twice more.

DISCUSSION

Adultery

I use the term adultery without attaching an overly anthropomorphic meaning to it because I felt this interaction to be atypical yet was clearly a stretching of the normal howler social bounds. Carpenter (1934) implies that due to the closed nature of howler troops, breeding across troop lines would not occur, and thus group membership would seem to be a necessary precondition for reproduction (Carpenter, 1965). Although in most primates it is generally the males who change troops and thus function to vary the gene pool, other reproductive strategies may be tried as well. Rudran (1979) noted instances of transient females and noted that red howler females seem to be more mobile than most other primates. Sekulic (in press) observed a lone female who unsuccessfully attempted to enter a troop.

The female in this study was at an opposite extreme. There were many indications that she was secure in her own troop and insecure in the adjacent troop territory. Yet she overcame her ambivalence to copulate with the male of the adjacent troop. Within her own troop she was successfully rearing a juvenile and was participating in allomothering the other infant. Additionally, she was ambivalent about crossing the territory line. When the foreign troop members were with *Huevos*, she crossed briefly and returned to her own territory in response to their approach while in the midst of copulating. Indeed, two weeks later when *Huevos*, whom she had copulated with, found her in his territory, he grabbed her very aggressively and threw her downward. *Spot*, the other female with an infant on her ventrum, came to her defense and lunged at *Huevos*, allowing *Point* to escape as her whole troop retreated across the line.

Male Motivation

One Ball, the dominant resident male, may have been responding to *Huevos* as though he were a subordinant breeding male in his troop by accepting breeding behavior prior to the peak estrus and then breeding the female at the optimum time. Glander (1980) noted his dominant male rejecting the estrous female the first day then following her closely and copulating with her the next day, permitting the beta male opportunity to copulate before and after the midpoint. Jones (1980) also noted dominant males to breed females during peak estrus except in one case where a subordinant male used an infantile appeasement vocalization to attain copulation following his losing a ritual battle with the dominant male.

During breeding interactions in this study the main troop contained one other full adult male, a younger male who showed no interest in the estrous female and perhaps seemed even to avoid her. In one instance I noted his testis had ascended and his genitalia appeared similar to those of an adult female. A few hours later I noticed they were again descended and I could not discern any behavioral situation that was related to the event. In vervets, which display colorful testis with presumable social significance, testis adduction was related to fearful situations and usually occurred in subordinants (Henzi, 1981).

Although grooming was rarely seen (four cases), two of those involved the male, *One Ball*, once grooming the estrous female, and once being groomed by her. Increased grooming of the estrous female was noted both in spider monkeys (Eisenberg, 1973; Klein, 1971) and in marmosets (Kleiman, 1977). Neville (1972) also noted an extended grooming bout in *A. seniculus* which he felt had probable sexual overtones.

VISUAL SIGNALS

The tongue flick was the most obvious and sex related behavior and as CARPENTER (1934) noted, it preceded copulation. If given by both participants it would inevitably lead to copulation. In *A. pigra*, its relation to copulation was similar but I didn't note the rhythmicity but rather just a tongue extension. In *A. caraya* (pers. obs.) and *A. seniculus* (NEVILLE, 1972) a similar tongue protrusion without rhythmic movements were seen. I noted its form to be related to lipsmacking and may be both analygous and homologous to tonguing done in marmosets in which it is related to sexual initiation and copulation (MICHAEL & ZUMPE, 1971), and to lipsmacking in *Lagothrix* (EISENBERG, 1976), and *Cebus apella* and *Ateles* sp. (pers. obs.) done in conciliatory situations. In *Alouatta* it seems more specifically tied to sexuality. In marmosets during sexual actions there is a similar intense staring as well as lipsmacking and rhythmical tongue protrusions (EPPLE in SNYDER, 1974).

The copulatory present is typical of many other primates and the copulatory posture as well. Both the complete (with hind legs on females hips) and incomplete postures [one or both feet on the branch (CARPENTER, 1934)] were observed (Fig. 1). The hands on the female's shoulders and the feet on her hips made the postures different from many old world monkeys. This was also quite different from the spider monkey copulation in which the female sits in the male's lap and he extends his legs over her thighs, locking them in position (KLEIN, 1971; KLEIN & KLEIN, 1971). An intermediate leg positioning was noted in a golden lion marmoset in which the male extended his legs out straight over the female's thighs along her sides (pers. obs.). In *Alouatta*, as noted in spider monkeys and wooly monkeys, there was an increased tendency to lean forward on the arms which appears correlated with larger body size as well as arboreal copulation (EISENBERG, 1973, 1976).

OLFACTORY RELATED BEHAVIORS

The one behavior which was not noted in other new world species was a chin rub on the partner's head. Partner marking may aid in pair bonding in marmosets (EPPLE, 1974) and in howlers it may aid in securing the shorter consort bond. This may occur by overcoming aggression and building up familiarity as a prerequisite for consort behavior (EPPLE, 1976). In this study, out of the context of the estrous period, the strange male, *Huevos*, when he came on *Point*, his previous consort, aggressively grabbed her and threw her down from the branch.

Chin rubbing and chest rubbing were additionally observed in the males in this study, and as in *A. palliata* they seem related to high arousal (EISENBERG, 1976) and aggression between males. NEVILLE (1972) noting rubbing of the face, chin and backs on branches in *A. seniculus*, felt they were scratching rather than marking. The anal rub and chest rub also occur in *Lagothrix* (EISENBERG, 1976). Marmosets show similar chest marking and anogenital rubs and they specifically have gland fields in these areas (EPPLE, 1974). *Alouatta* has a similar sternal area gland complex located, however, in the gular area (EISENBERG, 1977; EPPLE & LORENZ, 1967). Despite the chest rubbing, *A. palliata* does not show a gland in the sternal area (WISLOCKI & SHULTZ, 1925). A captive male *A. caraya* who chin rubbed to a new keeper, showed saliva dribbling onto his beard during intense bouts of chin rubbing.

Chest marking has also been seen in territorial context in *Callicebus moloch* (MASON in EPPLE, 1974) and in *Cebus apella* in conjunction with visual threats and usually by dominant males (DOBRORUKA in EPPLE, 1974).

In old world monkeys MICHAEL and KEVERNE (1970) have established the existence of a chemical which seems to entice copulation. There are observations of anogenital rubs in *A. pigra* and other new world monkeys which suggest a similar pheromone (EPPLE, 1974).

Rolling on the back was noted in an *Alouatta* female after mating (MICHAEL & ZUMPE, 1971), in both sexes of *A. caraya* (pers. obs.) and in *Lagothrix* (EISENBERG, 1976).

VOCALIZATIONS

The main vocalization noted during these interactions was the gutteral trill which seemed to be an aggressive territorial display between males. This sound may be the oodle noted by BALDWIN and BALDWIN (1976) and ALTMANN (1959).

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