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Male Parental Behavior in Black Howler Monkeys (*Alouatta palliata pigra*) in Belize and Guatemala

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ABSTRACT. Male parental behavior was observed in black howler monkeys (*Alouatta palliata pigra*) in Belize and Guatemala from December 1978 to March 1979, with the objective of relating parental behavior to the prevailing monogamous group structure. The results revealed that male parental behavior in *Alouatta palliata pigra* agrees in some respects with reports from the literature on polygamous and polygynous species of *Alouatta*, while in other respects the situation more closely resembles that in monogamous species of non-human primates. Considerable inter-individual variability in male-infant interactions prevailed among the study groups. Male parental behavior in the Belize groups became more prominent with increasing age of an infant.

INTRODUCTION

Male parental behavior has not been well documented for any species of non-human primates, mainly because species that exhibit the greatest amount of this type of behavior are forest dwellers, the study of which is considerably more difficult than that of terrestrial primates (REDICAN, 1976).

Male participation in the rearing of the offspring correlates to some extent with group structure. It is found in all monogamous species, although its extent differs between species and even among groups of the same species (CARPENTER, 1940; CHIVERS, 1971, 1972; EPPLE, 1975a; FOX, 1972, 1974; INGRAM, 1977; MASON, 1966; MOYNIHAN, 1964; REDICAN, 1976). In most polygamous and polygynous species of non-human primates the mother cares exclusively for the infants; exceptions are species such as hamadryas baboons (*Papio hamadryas*) (JOLLY, 1972; KUMMER, 1971) and barbary macaques (*Macaca sylvana*) (DEAG & CROOK, 1971) in which males have been observed to care for infants in somewhat the same way as a mother.

Alouatta lends itself well to the study of the effects of group structure on male parental behavior, since all three major grouping patterns—monogamous, polygamous and polygynous—are known in this genus. However, throughout most of the published reports (ALTMANN, 1959; CARPENTER, 1934, and others), *Alouatta* is referred to as a polygamous species with occasional polygynous groups. Male-infant relationships have not been documented to any degree in the howler literature, and are reported to be generally rather loose. NEVILLE (1972), BALDWIN and BALDWIN (1973) and CARPENTER (1964) all observed that males usually show no reaction to, nor curiosity in young infants. Males exhibited, however, a fairly high degree of tolerance toward young infants and reacted positively in unusual situations. GLANDER (1975), in his studies of *Alouatta palliata* in Costa Rica observed more active participation on the part of the male in the raising of the offspring.

This study was undertaken with the objective to determine whether male parental behavior in monogamous groups of *Alouatta palliata pigra* would resemble that in polygamous and polygynous species of *Alouatta*, or that of monogamous species of non-human primates. In

the absence of comparable quantitative data for other species of *Alouatta* and for monogamous species, comparisons can be only general.

METHODS

Alouatta palliata pigra was studied in the Belice District/Belize and in Tikal/Guatemala for three months, from December 1978 to March 1979. In Tikal low visibility, due to the high and dense vegetation and the howlers' habit of congregating in the uppermost canopy, resulted in few data on the three groups of howlers encountered there. For this reason the Tikal data were not analyzed quantitatively and will be referenced qualitatively where warranted. Visibility in Belize was excellent and permitted collection of precise data.

STUDY AREA—BELIZE

The study was conducted in the Belice district, 60 km west of Belize City, Belize. The 7 km² study area around Bermudian Landing (88° 33.7′ W, 17°32′N) is traversed by the Belize River. The region lies in the Dry Tropical Lowland Zone, has a mean annual rainfall of less than 80 inches, and has a mean annual temperature of more than 24°C (WRIGHT et al., 1959). The wet season lasts from May or June to October, and the transition from summer circulation to the winter pattern is rapid (JENKIN et al., 1976). The coolest temperatures occur between November and January (average 75°F), the warmest from May to September (average 81°F). Dense morning fogs are common from October to February on the middle and upper reaches of the Belize River. These fogs usually disperse by 0900.

The region exhibits a great variety of ecological zones. The howlers were found in gallery forests along the river, in the less disturbed lowland dry forests, on plantations and on large isolated fig trees surrounded by savanna and swampy grasslands. Compared to the dense continuous upper canopy in Tikal, the vegetation in Belize is considerably shorter (10 to 15 m) with the exception of fig trees (*Ficus glabrata*), which reach 40 to 50 m. Fig trees, however, often stand isolated and most have sparse foliage. This circumstance, as well as the fact that the howlers ate newly forming buds, leaving some trees virtually bare of leaves, contributed to the excellent visibility in most areas. Howlers were usually encountered on the following trees: *Ficus glabrata*, *Ficus* sp., *Achras zapote*, *Cecropia peltata*, *Spondias mombin*, *Acacia cookii*, *Acacia angustissima* and *Acacia costaricensis*.

STUDY GROUPS—BELIZE

Thirteen groups of howlers and two solitary males were encountered in the 7 km² study area. Population density was 8.14 howlers per square km with an average group size of 4.4 animals, the sex ratio was 1:1 (Tables 1 & 2). Apart from Group I (polygamous grouping pattern) and Group VI (polygynous grouping pattern), the remaining 14 groups of *Alouatta palliata pigra* in Belize and Guatemala were monogamous. Why the grouping pattern of two of the Belize groups differed, is not known. EPPLE (1975b), MOYNIHAN (1970) and THORINGTON (1968) report incidences of merging between monogamous groups of non-human primates. It is likely that howler groups in Belize have merged after the devastating hurricane that swept the study area four months prior to the study.

Of the 13 groups encountered in Belize, only Group I to VI, containing nine infants alto-

Table 1. *Alouatta palliata pigra* in Belize—Groups with infants.

Group	AM	AF	MJ_2	FJ_2	FJ_1	MI_3	FI_3	MI_2	FI_2	MI_1	Total
I	2	2							1	1	6
II	1	1		1			1				4
III	1	1				1				1	4
IV	1	1	1	2		1					6
V	1	1		1				1			4
VI	1	2		1	1			1		1	7
Total	7	8	1	5	1	2	1	2	1	3	31

AM: adult male; AF: adult female; MJ_2: male juvenile of age class II; FJ_2: female juvenile of age class II; FJ_1: female juvenile of age class I; MI_3: male infant of age class III; FI_3: female infant of age class III; MI_2: male infant of age class II; FI_2: female infant of age class II; MI_1: male infant of age class I.

Table 2. *Alouatta palliata pigra* in Belize—Groups without infants.

Group	AM	AF	MJ_2	FJ_2	FJ_1						Total
A	1	1									2
B	1	1		2							4
C	1	1	2	2							6
D	1	1		1							3
E	1	1			1						3
F	1	1	2								4
G	1	1									2
Solitary	2										
Total	9	7	4	5	1						26
Total Tables 1 & 2	16	15	5	10	2	2	1	2	1	3	57

Abbreviations are the same as in Table 1.

gether (Table 1), were studied in depth. No infants were present in Groups A to G (Table 2). The large number of howler groups within the study area and their habit of howling fairly regularly greatly facilitated locating the groups. Since only 6 of the 13 groups in the study area were with young and each group was different in its age-sex composition, identification of the six groups under observation presented no problem. The home ranges of Groups IV and VI were the only ones to be overlapped. Due to the small size of the groups and the heterogeneous age-sex composition within each group, identification of the individual animals was comparatively easy as well. Apart from the two adult males in Group I and two late female juveniles in Group IV, all animals could be identified individually. The sex of infants and juveniles could be determined easily because the testes in even the smallest male infants observed were fully descended and conspicuously white in colour.

In placing the howler infants into age categories, I used the estimates devised by CARPENTER (1965) (Age cla s I: 0–5 or 6 months; age class II: 5–6 to 10–12 months; age class III: 10–12 to 18–20 months). My own observations of a 10-month-old red howler infant (*Alouatta seniculus*) at the Frankfurt Zoo in Germany and precise age determination of the 6-month-old female infant and the 4-month-old male infant of Group I, as indicated by informants living close by and a film maker who included the group in a wildlife documentary during the time when the infants were born, were helpful in estimating ages of other infants. In accordance with NEVILLE (1972), I judged subadult females by their intermediate size and the intermediate state of the external female genitalia, as well as by their more playful behavior. In agreement with NEVILLE (1972), subadult males could be recognized by their somewhat smaller size as

compared to the adult male, the less extreme development of head and throat anatomy, and their tendency to play more, and to engage less in the characteristic howling in response to certain stimuli.

COLLECTION OF DATA

Data were collected for a total of 477 hr from the six groups with young. Observations were begun at 0500 or 0600 depending on the area where the group was located. Whenever possible, I remained with each howler group for the entire day, following it on its pathways until it settled down for the night. The next day the group was contacted at dawn before it started to move.

The kind, frequency and duration of interactions between infants and adult males have been used as indicators of male parental behavior. It was solicited by infants and/or administered by adult males. Although certain types of interactions do occur between two animals which are at a distance, in this study only interactions involving body contact were considered. For example, a female with her infant frequently sat down close to a male. In this case the proximity between the male and the infant was caused by the female and thus did not reveal any intentions of either male or infant.

Table 3. Social interactions of infant howler monkeys (*Alouatta palliata pigra*).

Categories	Individual interactions
Clinging	clinging ventrally or dorsally while support animal rests
	clinging ventrally or dorsally while support animal moves
Affiliation	sitting in close body contact
	grooming
	hugging
	huddling
	muzzling
	touching
Play	following in close body contact—playful gait
	playing—both animals active
	playing—with part of other group member's body
	climbing across back—playful gait

Data were recorded within each group using the Focal Animal Sampling Method (ALTMANN, 1974). The infant was considered the Focal Animal within each group. It provided a complete record of all parental behavior as it initiated and received interactions. Where more than one infant was present, each infant was considered a focal animal; or, where the activities allowed for it—playing together or both resting in close vicinity—two focal animals were observed simultaneously. The favorable conditions for observation made it possible to collect data on a continuous basis which minimized sampling biases, since activities throughout the day were evenly represented. Due to the great diversity of types of recorded behaviors, they were in this analysis either lumped into one single category or assigned to broad classes of behavior—clinging, affinitive interactions (affiliation) and play (Table 3). Agonistic interactions —2 among a total of 3,139—were not analyzed as a category and will be referred to individually.

A tape recorder was used to record quantitative and qualitative data. Behavioral observa-

tions were made with the unaided eye where possible, otherwise with Bushnell 7×35 binoculars.

RESULTS

Average Patterns of Male-infant Interactions

The percentages of male-infant interactions are based on the total frequency and the total duration of social interactions of infants which occurred within each of the six howler groups in Belize. The average frequency at which interactions occurred between a male and an infant (all six groups lumped) amounted to 16.4%; the average duration amounted to 7.4%. This means that 7.4% of the total time an infant spent interacting in a social manner was spent with a male.

A breakdown of all interactions into three major categories —clinging, affiliation and play (Fig. 1) indicates the way in which males and infants interacted. The resulting percentages are based on all interactions which occurred between males and infants. Clinging interactions between infants and males were few (8.5%) and of short duration (5.4%). An infant was sometimes seen clinging to the back of a male while he was resting. No male was observed carrying an infant.

Associations between males and infants were most clearly characterized by affiliation (50.6% for frequency; 72.0% for duration). Although males often ignored the affinitive approaches of an infant, they frequently responded by holding, hugging and muzzling the infant. The frequency of affinitive interactions between males and infants amounted to slightly more than 50% of the affinitive interactions which took place between mother and infant.

As was the case for clinging and affiliation, play interactions (41.0% for frequency, 22.6% for duration) were usually initiated by the infant. Males were generally tolerant of an infant's playful explorations of parts of his body. Sometimes they got up and left, at other times they

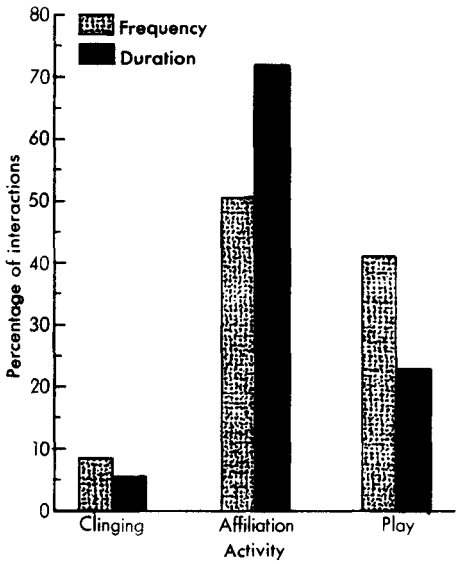

Fig. 1. Average percentage of male-infant interactions.

playfully pulled an infant toward them. Vigorous play interactions, as was common between peers, never occurred between a male and an infant.

INDIVIDUAL VARIABILITY IN MALE-INFANT INTERACTIONS

Individual variability in male-infant interactions among the six howler groups in Belize was considerable. In this analysis the percentages of male-infant interactions are based on the total frequency and the total duration of social interactions which occurred between each infant and its respective group members. Variability in both frequency and duration of interactions existed not only between age classes but also within each age class (Fig. 2).

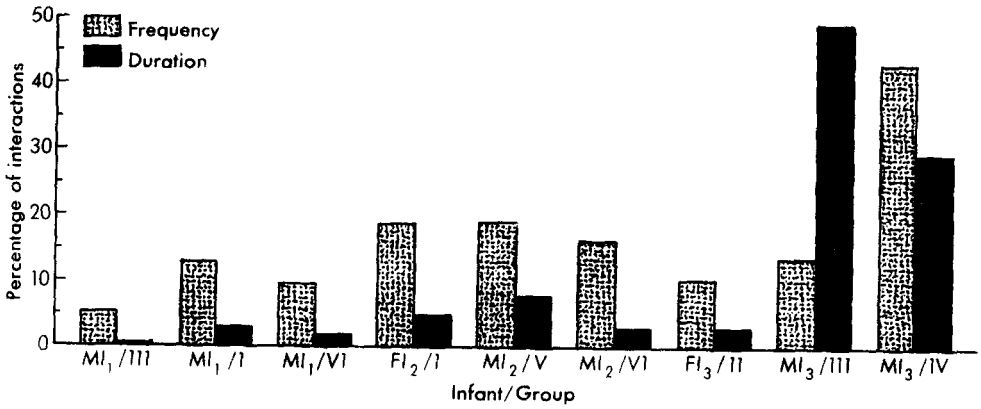

Fig. 2. Within group male-infant interactions.

Qualitative observations indicated that within age class I close contact and active participation on the part of the adult males existed in Group I and to some extent in Group III (the infant in Group III was only 2 months old, while the other infants of age class I were 4 months old). In Group VI the adult male—although generally tolerant to repeated approaches by the male infant$_1$—often left in response to this infant's attempts to interact. On two occa ions the male showed agonistic behavior toward the male infant$_1$ as it and the male infant$_2$ of the same group jumped repeatedly on his back. No such aggression was observed in the other groups.

Within age class II (infants were 6 to 7 months old), the males were seen to actively engage in interactions with the infants in Groups I and V. Again the adult male in Group VI sometimes showed his unwillingness to interact with the infant by moving away as soon as, or shortly after the infant had made physical contact with him.

Patterns of association among infants and males differed considerably in both a quantitative and a qualitative way within age class III (infants were about 12 months old), ranging in duration from 2.8 % (FI_3—Group II) to 49.1 % (MI_3—Group III). Male-infant interactions in Group III were of a more passive type (e.g., sleeping and resting together), while in Group IV more activity was witnessed—touching, hugging, huddling and even grooming, a rare interaction among the Belize howlers. Since a much closer bond had developed between the adult males and the male infants of age class III (Groups III & IV) than between the adult male and the female infant in Group II, it may be questioned whether at this later stage of infancy male infants would associate more closely with adult males than would female infants. The

situation as it existed in Group III in Tikal, contradicts this assumption. In this Tikal group, the adult male was frequently seen to touch the FI_3 and to locomote with it in close body contact. The male was very protective of this infant at all times, especially when it explored the physical environment where a juvenile female spider monkey, which had been traveling for days close to the howler group, frequently tried to take hold of the infant. More research is necessary to verify the extent, if any, to which male howlers interact with male versus female infants.

Change in Male-infant Interactions with Age of an Infant

Figure 3 indicates the average percentage for male-infant interactions within an age class. Each age class contains three infants. Percentages are based on the total frequency and duration of interactions between infants and other group members within a respective age class. The frequency with which male-infant interactions were carried out increased from 11.4% (age class I) to 18.3% (age class II) to 30.2% (age class III). The duration of interactions increased from 2.4% (age class I) to 4.9% (age class II) to 30.1% (age class III). The increases between age classes were tested to be statistically significant (chi square, $df = 1$, $\alpha = .05$, $p < 0.001$ in all cases except for the duration of interactions between age class I and II where $p < 0.01$). The increase is most pronounced in infants of age class III, which no longer depended on their mothers for nutrition and thermoregulation.

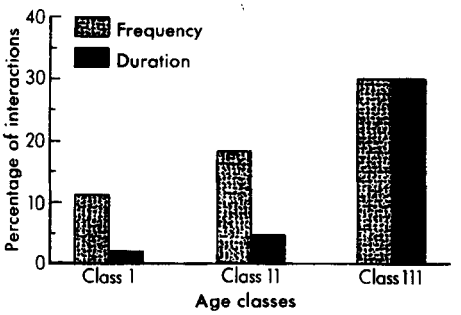

Fig. 3. Male-infant interactions by age classes.

DISCUSSION

Male Parental Behavior in *Alouatta palliata pigra* in Comparison to Other Species of *Alouatta*

Researchers on howler monkeys generally agree that adult males exhibit a high degree of tolerance toward infants but show little active participation during interactions (Altmann, 1959; Baldwin & Baldwin, 1973; Carpenter, 1964; Didur (pers. comm.); Neville, 1972; Shoemaker, 1979). Males are, however, known to interfere actively in case of danger. Carpenter (1964, p. 88) states that "in general, males behave indifferently to young animals, but they may assist in retrieving infants, protect them from predatory animals, and in unusual situations care for an infant in somewhat the same way as a mother." He further ob-

served that despite the rare close physical contact between males and infants, young howlers orient themselves in reference to the adult males.

In the Belize groups the adult males showed both tolerance and accommodative behavior toward infants. Males allowed small infants to jump on their backs, swing on their tails and climb over them many times during explorations of the environment. Howler males in Belize and Tikal were seen at various occasions to display protective behavior. In the Belize Group I both adult males hurried close to the small whining male $infant_1$ which found itself alone in the upper canopy of a large fig tree. The males remained with the infant until the mother returned. In Tikal (Group III) the adult male was always ready to protect the female $infant_3$ at the approach of a juvenile female spider monkey.

Orientation of infants in reference to adult males as observed by CARPENTER (1964) was not recorded quantitatively in the Belize and Tikal groups, since this type of behavior, where visual cues figure prominently, is difficult to assess from a distance. I observed, however, that the male infants of age class III oriented themselves in reference to the adult males, as they followed them during group progressions, and foraged and sat near them.

Although in the above instances we find close agreement between my study groups and other species of howlers, the male howlers in Belize and Guatemala distinguished themselves be engaging more actively in parental behavior. Howler mothers in Belize were seen to deposit infants close to males before beginning to forage in the outermost branches of the trees. The males held the infants between their arms, hugging and muzzling them. The infants always remained near the males until the mother returned. Although most interactions were initiated by infants, males at times approached infants in an affinitive manner. GLANDER (1975, p. 482) remarked that in the groups of *Alouatta palliata* he observed in Costa Rica "adult males frequently investigated the infants and often the infants transferred to the males during this time." He also reported on males baby-sitting infants while mothers left the area.

Variability in male parental behavior in the Belize groups was considerable. In Group VI the disposition of the adult male very much resembles that described by researchers for other species of howlers where the male is known to be tolerant of infants but seldom shows overt interest in them. In the other five howler groups in Belize the adult males showed varying degrees of interest in the infants. In Groups III and IV males interacted with infants frequently and for extended periods of time even exceeding mother-infant interactions in either frequency or duration.

MALE PARENTAL BEHAVIOR IN *Alouatta palliata pigra* IN COMPARISON TO MONOGAMOUS SPECIES

Reports from the literature have shown that active participation in the upbringing of the young and even predominance in this activity on the part of the father is common in monogamous species (REDICAN, 1976). Although variability regarding the degree to which the father participates does exist among species (CRANDALL, 1951; EPPLE, 1975a; REDICAN, 1976) and even among different groups of the same species (EPPLE, 1975a) parental behavior as exhibited by the adult male is integral to the raising of the offspring in monogamous species.

The average percentage of male-infant interactions in the six Belize groups (16.4% for frequency, 7.4% for duration) is high as compared to other species of *Alouatta* (percentages for other howler species are not available), but low as compared to reports from the literature on monogamous species. In the brown-headed tamarin (*Saguinus fuscicollis*) carrying scores

observed by EPPLE (1975a) ranged from 29.87% to 95.63% for the adult male. The difference in this rather loose comparison may be due to the fact that male howlers in Belize and Guatemala were never observed to carry infants, an activity which accounts for a high percentage of male-infant associations in monogamous New World species. Recent studies (KLEIMAN, 1977; LEUTENEGGER, 1973) have shown that the birth weight of the newborn infant in relationship to the mother's weight, is a decisive factor in male care in many monogamous species. MITCHELL (1979) asserts that the larger the infant at birth, relative to the size of the mother, the sooner the male begins to care for the infant. The mother-infant weight relationship in howlers is such that the mother does not depend on the male for carrying the infant. Not only is the howler infant considerably smaller at birth in relation to the mother's size than is the case in other monogamous New World species, but howlers only give birth to one infant at a time, while in other monogamous New World species twins are the rule.

Although the average amount of social interaction of the six Belize groups does not approach male parental behavior as it is known from monogamous species, great individual variability in male-infant interactions exists among the six groups. In Groups III and IV, male-infant interactions far exceed those observed in other groups. In Group III, the male $infant_3$ interacted for a longer total period of time with the adult male (49.1%) than with its mother (32.7%). In Group IV, male-infant interactions were more frequent (43.3%) than interactions between mother and infant (41.8%). The percentages for male-infant interactions within these two groups fall within the range of carrying scores for tamarins given by EPPLE (1975a).

CHANGE IN MALE PARENTAL BEHAVIOR WITH AGE OF AN INFANT

The great range of male parental behavior in non-human primates concerns not only the intensity of male care but also the onset of contact between males and infants. Thus, for example, in marmosets, an adult male has been seen to exhibit parental behavior immediately following the birth of the infants, and, in fact, has been observed to assist during the birth of infants (REDICAN, 1976). The carrying of infants in this species continues even after the infants have been weaned (LANGFORD, 1963; MALLINSON, 1971). EPPLE (1975a) observed that in the brown-headed tamarin (*Saguinus fuscicollis*) the adult males carry the infants more during the first month of their lives than later. In the night monkey (*Aotus trivirgatus*), MOYNIHAN (1964) observed that the mother cares predominantly for the infant during the first few days after birth, after which time the male takes over more actively. WENDT (1964), on the other hand, reported that in a group of cotton top tamarins (*Saguinus oedipus*) the male carried the offspring exclusively during the first 5 weeks of life; later the mother participated in the carry ing. The next offspring, however, remained with the same female for one week after its birth before the male and siblings participated in its care. In other monogamous species, such as gibbons (*Hylobates*) and siamangs (*Symphalangus*), although interactions occur among males and the very young offspring (CARPENTER, 1940), they become more prominent as the infant becomes less dependent on its mother (BERKSON, 1966; CHIVERS, 1971, 1972).

Studies on different species of *Alouatta* have shown that in *Alouatta palliata* (BALDWIN, pers. comm.), *Alouatta seniculus* (NEVILLE, 1972) and *Alouatta caraya* (SHOEMAKER, 1979) the male-infant bond is very loose, and characterized by few interactions that are generally initiated by the infants, with little active participation by the adult male. In all three species, however, a trend has been observed toward an increased number of interactions with the

male as the infant matured. NEVILLE (1972) and CARPENTER (1965) remarked on the higher frequency of interactions between older infants and adult males.

The results of the Belize study indicated that with age of the infants there was a strong trend toward more and longer lasting interactions with males (Figure 3). The infants' greater mobility at a more advanced age was certainly instrumental in the increase of contacts, although the tendency of adult males and females to associate closely already brought very young infants to the vicinity of adult males.

A comparison of male parental behavior in *Alouatta palliata pigra* with other species of *Alouatta* and with monogamous species of non-human primates seems to indicate that male parental behavior in *Alouatta palliata pigra* most closely resembles patterns of parental behavior in gibbons and siamangs in which males interact with very young infants but do so increasingly as the infant matures.

SUMMARY

Male parental behavior in *Alouatta palliata pigra* agrees in some respects with reports from the literature on polygamous and polygynous species of *Alouatta*, especially regarding a male's tolerance to and protection of infants. In the monogamous groups of howlers in Belize, however, males interacted in a more active way with infants than has been reported from other species of howlers. Interactions between males and infants in the Belize groups were mainly of the affinitive type, although play interactions were also common. An infant rarely clung to an adult male and then only when the male was resting.

Inter-individual variability in male parental behavior was considerable among the study groups. While percentages of male-infant interactions in some groups were low, they exceeded mother-infant interactions in others reflecting a situation similar to monogamous species elsewhere. Male-infant interactions increased on the average in both frequency and duration with age of an infant. They were characterized by the virtual absence of agonism.

More quantitative and qualitative data on male parental behavior in relation to the prevailing group structure are required to allow for a more precise comparison between species. This study on monogamous groups of *Alouatta palliata pigra* has clearly indicated, however, that within this species there is a potential for extensive male parental behavior.

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