Brief Report

Received: October 4, 1995

Accepted after revision: May 29, 1996

Folia Primatol 1996;67:152-156

A Preliminary Analysis of the Timing of Infant Exploration in Relation to Social Structure in 17 Primate Species

A.	Adrian	Treves
----	--------	--------

Department of Anthropology, Peabody Museum, Harvard University, Cambridge, Mass., USA

Key WordsInfant development
Adult males
Conspecific threat
Predation
Social structure
Maternal protectiveness
Infanticide

Dr. Adrian Treves, 65 Greenway Terrace, Princeton, NJ 08540 (USA)

Introduction

Independent exploration of the social and physical environment by infant primates is considered to be an important phase in the development of social expertise and foraging aptitude [1-3]. However, infant independence is often reported to be curtailed by maternal protectiveness [4, 5] in possible response to perceived danger [6, 7]. Male and female group members may play roles as protectors or as sources of threat to infants, varying by species or group contexts [8-13]. Few cross-species studies of behavioral development have been published [9, 14] and almost no attempt has been made to relate group composition to variation in infant development. This paper analyzes data in a cross-species comparison of adult male numbers and infant exploration to determine whether resident males generally play a protective or a threatening role within groups. The following two alternative hypotheses are examined.

Hypothesis 1: independent exploration occurs earlier in social groups with multiple adult males because of the protection afforded by these potential group defenders. This prediction rests on the premise that multi-male grouping arises in habitats with high risk of predation because of the added defensive ability of the males [15-18].

Hypothesis 2: independent exploration occurs later in social groups with multiple adult males. This prediction rests on the premise that multi-male group structure implies the presence of one or more males with low paternity certainty and a possible incentive to commit infanticide [8, 19, 20].

Any examination of development rates is likely to be influenced by basic life history variables. Harvey et al. [21, p. 191] indicate that '... postnatal brain development, learning skills, and social maturity may be intimately linked with physical maturity'.

KARGER © 1996 S. Karger AG, Basel

0015-5713/96/0673-0152\$12.00/0 E-Mail karger@karger.ch Fax + 41 61 306 12 34

<http://www.karger.ch>

Table 1. The age at which 25-35% of an infant's time is spent out of arm's reach from its mother, in relation to social structure and developmental indices

Species Age Males Developmental indices References

W66KS

female neonate age at first

BW, kg BW, kg breeding, months

<i>Alouatta nigra</i>	9	2	5.7	0.480	48	10
<i>Ptilocolobus</i>	11	3.5	5.8	0.521 ²	42	22
<i>Colobus</i>	5	1	9.2	0.445	55	22-23
<i>Callicebus</i>	7	1	1.1	n.a.	36	9
<i>Macaca mulatta</i>	12	4.6	3.0	0.496	60	24
<i>Macaca radiata</i>	16	3	3.7	0.404	52 ²	25 ⁴
<i>Papio anubis</i>	16	7.6	13.5	1.068	73 ³	15
<i>Presbytis johnii</i>	10	1.8	12.0	0.422	31	26
<i>Presbytis</i>	10	4.2	11.4	0.422	31	4.27
<i>Lemur catta</i>	7	1	2.5	0.088	24	14 ⁴
<i>Lemur fulvus</i>	13	1	1.9	0.081	28	14 ⁴
<i>Varecia</i>	4	1	3.1	0.108	24	14 ⁴ 28
<i>Aotus trivirgatus</i>	9.5	1	1.0	0.098	29	9
<i>Callimico goeldii</i>	10	1	0.5	0.049	16	29
<i>Erythrocebus</i>	14	3	5.6	0.505	53	30-31
<i>Cercocebus</i>	14	3	3.0	0.325	42	3
<i>Pithecia pithecia</i>	11.5	1	1.4	n.a.	29	32 ⁴

Age = Age in weeks at which the infant spends 25-35% of its time out of arm's reach from its mother; males = mean number of resident adult males; data taken from Smuts et al. [33]; developmental indices: BW = body weight in kg; age at first breeding or sexual maturity taken from Harvey et al. [21] and Ross [34]; n.a. = not available.

¹ The average of *Colobus polykomos* and *Colobus guereza* neonatal body weight is used [21].

² *Macaca mulatta* age at first breeding is used.

³ *Papio cynocephalus cynocephalus* age at first breeding is used.

⁴ Captive studies.

Life history traits which are related to developmental rate (adult female body weight, neonatal body weight and age at first reproduction) are tested first in order to control for confounding variables.

Material and Methods

Data were collected from the literature for 17 primate species (table 1) including: (a) the age, in weeks, at which a quarter to a third of an infant's time is spent out of arm's reach (or greater than 1.3 m) from its mother ('age'); (b) the average number of adult males in a social group of the population in which the infant grew up ('males'), and (c) 3 indices of developmental speed: the mean body weight of adult females, the mean body weight of neonates and the age at first breeding or age at sexual maturity. The range of values used for percent of time out of arm's reach were chosen in order to facilitate the inclusion of wild data sets which rarely provide an exact or standardized measurement. Values for 'males' presented here derive from captive groups, but all results are the same if 'males' is taken from wild studies.

When life history variables were missing from the literature, an average congeneric measurement was used if available (e.g. neonatal weight for *Ptilocolobus badius* was the average of its congeners' values [21]). Including or excluding such interpolated values revealed no significant dif-

ferences. For some species, age at first breeding was available while for others only age at sexual maturity was available. These are highly correlated measures [21] but not necessarily interchangeable. However, I could not discern a bias toward either hypothesis if these were used interchangeably.

Spearman ρ rank correlation was used to assess significance, while log transformation was used to calculate percent of variance in parametric tests. Statistical tests were calculated using Statview 4.1 (Abacus Concepts Inc., Berkeley, Calif., USA, 1992).

Results

Despite the diversity of life history patterns present, no significant influence of adult female body weight ($n = 17$, $p = 0.2$, $p = 0.54$), neonatal body weight ($n = 15$, $p = 0.3$, $p = 0.23$) or first reproduction ($n = 17$, $p = 0.4$, $p = 0.08$) on 'age' was detected among the species in table 1. Having dismissed the possibility of a significant confounding effect, 'males' was tested directly against 'age', which varied between 4 and 16 weeks. 'Males' varied between 1 and 7.6 between species (table 1).

Hypothesis 1 predicts a significant negative relationship between 'age' and 'males'. Hypothesis 2 predicts a significant positive relationship. The rank correlation analysis indicates that the relationship was significantly positive (support for hypothesis 2) and 'males' explained approximately 40% of the variation in 'age' (males $n = 17$, $p = 0.6$, $p = 0.013$). To reduce non-independence of samples, congeneric pairs are averaged for *Macaca*, *Presbytis* and *Lemur* and the test run again ($n = 15$, $p = 0.8$, $p = 0.008$). The patas monkey (*Erythrocebus patas*) and red colobus (*Piliocolobus badius*) are treated as separate genera here. Finally, if one excludes *Papio anubis* because the age in weeks was only estimated [15], the result remains significant ($n = 14$, $p = 0.7$, $p = 0.022$). Restricting the analysis to wild groups yields a regression explaining 50% of the variation (log-transformed $n = 12$, $r^2 = 0.5$, $F = 10.8$, $p = 0.008$), also a significant relationship.

Discussion

The preceding analysis indicates that the age at which an infant spends 25-35% of time away from its mother is delayed by the presence of more males in the social group. If the conjecture underlying this test is correct, this result joins the mounting evidence from wild studies that mother-infant behavior is modified by the threat of conspecific attack [4, 6, 12; Treves and Chapman, unpubl. data] and the present report suggests an index of within-group threat. Silk [25] showed that infants were more likely (76%) to receive contact aggression when they were off their mothers than when they were in ventral contact (24%).

No support was found for the predation avoidance hypothesis which predicts that infant independence is curtailed in species living in smaller groups because of an increased threat of predation. However, it still remains possible that comparisons of different group sizes within the same population would reveal some effect attributable to risk of predation [35].

The data presented here are from varied sources. As some of the investigators did not sample multiple infants nor specifically document maternal behavior, the conclusions of this analysis must therefore be regarded as preliminary. Nevertheless, the results are sufficiently clear to call for more refined longitudinal studies.

154 Folia Primatol 1996;67:152-156 Treves

Acknowledgments

Thanks are extended to Lisa Naughton, Colin Chapman and Dr. R.D. Martin for helpful comments on the manuscript. Support was provided to the author by an NSF Fellowship for Graduate Study.

References

- Altmann J: Baboon Mothers and Infants. Cambridge, Harvard University Press, 1980.
- Hendy H: Social interactions of free-ranging baboon infants; in Else JG, Lee PC (eds): Primate Ontogeny, Cognition and Social Behaviour. Cambridge, Cambridge University Press, 1986.
- Hauser M, Fairbanks LA: Mother-offspring conflict in vervet monkeys: Variation in response to ecological conditions. *Anim Behav* 1988;36:802-813.
- Hrdy SB: The Langurs of Abu. Cambridge, Harvard University Press, 1977.
- Nicolson NA: Infants, mothers and other females; in Smuts BB, Cheney DL, Seyfarth RM, Wrangham RW, Struhsaker TT (eds): Primate Societies. Chicago, University of Chicago Press, 1987, pp 330-342.
- Alberts SC: Vigilance in young baboons: Effects of habitat, age, sex and maternal rank on glance rate. *Anim Behav* 1994;47:749-755.
- Hauser MD: Variation in maternal responsiveness in free-ranging vervet monkeys: A response to infant mortality risk? *Am Nat* 1988;131:573-587.
- Dittus WPJ: The social regulation of primate populations: A synthesis; in Lindburg DG (ed): The Macaques: Studies in Ecology, Behavior and Evolution. New York, van Nostrand Reinhold, 1980.
- Wright PC: Biparental care in *Aotus trivirgatus* and *Callicebus moloch*; in Small M (ed): Female Primates: Studies by Women Primatologists. New York, Liss, 1984.
- Horwich RH, Gebhard K: Relation of allo-mothering to infant age in howlers, *Alouatta pigra*, with reference to Old World monkeys; in Taub DM, King FA (eds): Current Perspectives in Primate Social Dynamics. New York, van Nostrand Reinhold, 1986, pp 66-88.
- Mendoza SP, Mason WA: Parenting within a monogamous society; in Else JG, Lee PC (eds): Primate Ontogeny, Cognition and Social Behaviour. Cambridge, Cambridge University Press, 1986.
- Wasser SK, Starling AK: Reproductive competition among female yellow baboons; in Else JG, Lee PC (eds): Primate Ontogeny, Cognition and Social Behaviour. Cambridge, Cambridge University Press, 1986.
- Whitten PL: Infants and adult males; in Smuts BB, Cheney DL, Seyfarth RM, Wrangham RW, Struhsaker TT (eds): Primate Societies. Chicago, University of Chicago Press, 1987, pp 343-357.
- Klopfer PH, Boskoff KJ: Maternal behavior in prosimians; in Doyle GA, Martin RD (eds): The Study of Prosimian Behavior. New York, Academic Press, 1979.
- Hall KRL, Devore I: Baboon social behavior; in Devore I (ed): Primate Behavior: Field Studies of Monkeys and Apes. Chicago, Holt, 1965.
- Anderson CM: Predation and primate evolution. *Primates* 1986;27:15-39.
- van Schaik CP, Hörstermann M: Predation risk and the number of adult males in a primate group: A comparative test. *Behav Ecol Sociobiol* 1994;35:261-272.
- van Schaik CP, van Noordwijk M: The special role of male *Cebus* monkeys in predation avoidance and its effects on group composition. *Behav Ecol Sociobiol* 1989;24:265-276.
- Hrdy SB: Infanticide among animals: A review, classification and examination of the implications for the reproductive strategies of females. *Ethol Sociobiol* 1979;1:13-40.
- Collins DA, Busse CD, Goodall J: Infanticide in two populations of savanna baboons; in Hausfater G, Hrdy SB (eds): Infanticide: Comparative and Evolutionary Perspectives. New York, Aldine, 1984.

- Harvey PH, Martin RD, Clutton-Brock TH: Life histories in comparative perspective; in Smuts BB, Cheney DL, Seyfarth RM, Wrangham RW, Struhsaker TT (eds): Primate Societies. Chicago, University of Chicago Press, 1987, pp 181-196.
- Struhsaker TT: The Red Colobus. Chicago, University of Chicago Press, 1975.
- Oates J: The social life of black-and-white colobus monkeys, *Colobus guereza*. Z Tierpsychol 1977;45:1-60.
- Southwick CH, Beg MA, Siddiqi MR: Rhesus monkeys in North India; in Devore I (ed): Primate Behavior: Field Studies of Monkeys and Apes. Chicago, Holt, 1965, pp 111-129.
- Silk JB: Mother-infant relationships in bonnet macaques: Sources of variation in proximity. Int J Primatol 1991;12:21-40.
- Poirier FE: The Nilgiri langur (*Presbytis johnii*) troop: Its composition, structure, function and change. Folia Primatol 1969;10:20-47.
- Jay PC: The common langur of North India; in Devore I (ed): Primate Behavior: Field Studies of Monkeys and Apes. Chicago, Holt, 1965, chap 7.
- Rigamonti MM: Home range and diet in red ruffed lemurs (*Variegata variegata rubra*) on the Masoala Peninsula, Madagascar; in Kappeler PM, Ganzhorn JU (eds): Lemur Social Systems and Their Ecological Basis. New York, Plenum Press, 1993, pp 25-40.
- Infant Independence and Social Structure
Folia Primatol 1996;67:152-156
- 155
- Heltne PG, Wojcik JF, Pook AG: Goeldi's monkey: Genus *Callimico*; in Coimbra-Filho AF, Mittermeier RA (eds): Ecology and Behavior of Neotropical Primates. Rio de Janeiro, Academia Brasileira de Ciências, 1981, chap 4.
- Chism J: Development and mother-infant relations among captive patas monkeys. Int J Primatol 1986;7: 49-62.
- Chism J, Rowell TE: The natural history of patas monkeys; in Gautier-Hion A, Bourlière F, Gautier JP, Kingdon J (eds): A Primate Radiation: Evolutionary Biology of the African Guenons. Cambridge, University of Cambridge Press, 1988.
- Savage A, Shideler S, Lasley B: A preliminary report on the behavior and reproductive patterns of captive white-faced sakis (*Pithecia pithecia*); in Vecchio T, Miller A (eds): The 1993 Regional Studbook of the White-Faced Saki. Providence, Roger Williams Park Zoo, 1993.
- Smuts BB, Cheney DL, Seyfarth RM, Wrangham RW, Struhsaker TT (eds): Primate Societies. Chicago, University of Chicago Press, 1987.
- Ross C: The intrinsic rate of natural increase and reproductive effort in primates. J Zool Lond 1988;214: 199-219.
- Anderson CM: Male investment under changing conditions among chacma baboons at Suikerbosrand. Am J Phys Anthropol 1992;87:479-495.
- 156 Folia Primatol 1996;67:152-156 Treves