

(Brown and Zunino, 1994).

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References

- Bicca-Marques, J. C. 1994. Padrão de utilização de uma ilha de mata por *Alouatta caraya* (Primates: Cebidae). *Rev. Brasil. Biol.* 54(1):161-171.
- Brown, A.D. and Zunino, G. E. 1994. Hábitat, densidad y problemas de conservación de los primates de la Argentina. *Vida Silvestre Neotropical* 3(1):30-40.
- Cabrera, A. 1939. Los monos de la Argentina. *Physis* 16:3-29.
- Crockett, C. M. and Eisenberg, J. F. 1987. Howler variations in group size and demography. In: *Primate Societies*, B. B. Smuts, D. L. Cheney, R. M. Seyfarth, R. W. Wrangham and T. T. Struhsaker (eds.). pp.54-67. The University of Chicago Press, Chicago.
- Emmons, L. H. 1990. *Neotropical Rainforest Mammals. A Field Guide*. The University of Chicago Press, Chicago.
- Neris de Colman, N. N., Placci, G., Ruiz, J. C. and Zunino, G. E. 1994. Panel de expertos en monos caraya. Informe Final. Entidad Binacional Yacireté, Ayolas, Paraguay. 16pp.
- Rumiz, D. I. 1987. Ecología poblacional de *Alouatta caraya* en el norte de la Argentina. Tesis de Doctorado. Universidad Nacional de La Plata, Buenos Aires, 100pp.
- Rumiz, D. I. 1990. *Alouatta caraya*: Population density and demography in northern Argentina. *Am. J. Primatol.* 21(4):279-294.
- Rumiz, D. I., Zunino, G. E., Obregozo, M. L. and Ruiz, J. C. 1986. *Alouatta caraya*: Habitat and resource utilization in northern Argentina. In: *Current Perspectives in Primate Social Dynamics*, D. M. Taub and F. A. King (eds.), pp:175-193. Van Nostrand Reinhold, New York.
- Rylands, A. B., Mittermeier, R. A. and Rodríguez Luna, E. 1995. A species list for the New World primates (Platyrrhini): Distribution by country, endemism, and conservation status according to the Mace-Lande system. *Neotropical Primates* 3(suppl.):113-164.
- Zunino, G. E. 1986. Algunos aspectos de la ecología y etología del mono aullador negro (*Alouatta caraya*) en hábitats fragmentados. Tesis de Doctorado, Universidad de Buenos Aires, Buenos Aires, 152 pp.
- Zunino, G. E. 1989. Hábitat, dieta y actividad del mono aullador negro (*Alouatta caraya*) en el noreste de la

Argentina. *Bol. Primatol. Latinoamericano* 1(1):74-97.

Zunino, G. E. and Ruiz, J. C. 1995. Reintroducción y translocación de primates en la Argentina: Antecedentes, riesgos y beneficios. In: *Simposio: Primatología en Argentina, Resúmenes. X Jornadas Argentinas de Mastozoología*, pp.77-78. Sociedad Argentina para el Estudio de Los Mamíferos (SAREM), 14-17 November, 1995, La Plata, Argentina.

TEMPORAL DIVISION OF LABOR IN A PRIMATE: AGE-DEPENDANT FORAGING BEHAVIOR

Introduction

Division of labor based on age, or size may reflect the reproductive condition of individuals in social groups. In 1967, West proposed the general hypothesis that hierarchical relations may be advantageous to both dominants and subordinates and that individuals of low rank may be inferior reproductives who benefit genetically from associations with and contributions to reproductively superior individuals. Since increasing age or size eventually entails decreasing reproductive value (V_x), several authors have noted that the display of social behavior, such as foraging behavior that benefits all members of a group, should increase with age as the benefits from individual (selfish) reproduction decline (e.g., West-Eberhard, 1975; Hrdy and Hrdy, 1976). As individual reproductive value decreases, benefits (genetic or other) from assisting the reproduction of conspecifics (social behavior) may increase because costs (genetic or other) of social behavior decrease with decreased benefits from individual reproduction. In order to test this hypothesis, I studied the relationship between adult female age, dominance rank, reproductive value, and social foraging behavior (food search and pursuit) for adult female mantled howler monkeys (*Alouatta palliata* Gray).

Subjects and Methods

During an extended period of study at Hacienda la Pacifica, Cañas, Guanacaste, Costa Rica, I studied two marked, aged groups of mantled howler monkeys in two tropical dry forest habitats (see Jones, 1980; Table 1). For this species, age and dominance rank are negatively correlated in both sexes (Jones, 1978, 1980).

Foraging was operationally defined as the behavioral series: feed-rest-move (at least 100m) - feed, by a unit of more than three adults. These criteria were adopted in order to standardize measurement and to eliminate periods of food search within unusually large patches

and by consort pairs. I identified which females in the primary study groups initiated foraging sequences and analysed these observations by age.

My null hypothesis held that the frequency of foraging by females of any age class would be proportional to the total number of females who foraged in an age class. Two of the 15 females in one group (both young adults) were never observed to direct foraging sequences and are excluded from analysis. Three females were aged on the basis of physical and behavioral traits other than tooth wear, and assignment to age classes for these females was made independent of the present analysis. Two of these females were observed from sub-adult through adult growth and classified as young adults; a third female, classified as middle-aged, was the mother of a sub-adult and a juvenile offspring, a highly unlikely combination for any other age class (see Glander, 1980). In my analysis of the second group (eight adult females), two young adult immigrant females were never observed to forage socially and were excluded from analysis. The pattern of results reported here would remain unaffected by alternative treatments of the raw data.

A monthly foraging rate for each forager was computed by dividing the frequency of foraging by the female's number of months resident in a group, a period of time varying from 10-14 months since some females emigrated during the study. These rates were compared with a female's age class, on the one hand, and dominance rank, on the other, to assess the relationship

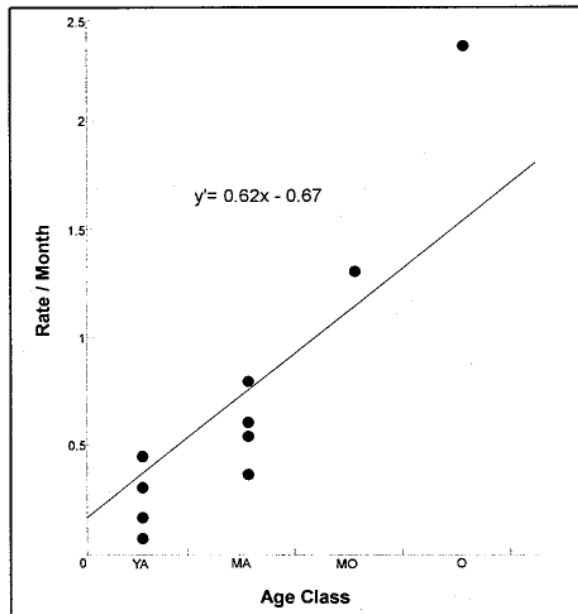


Figure 1. Social foraging rate as a function of age for young adult (YA), middle-aged (MA), middle-aged to old (MO) and old (O) female howlers. Each point represents one adult female except where asterisk indicates two.

Table 1. Age class, estimated age in years, number of females in each age class (N), observed (O) and expected (E) frequencies of social foraging, and cumulative chi square (χ^2) values for a test of the null hypothesis.

Age class	N	O	E	(O-E) ² /E
Young adult (5-7)	5	15	42.4	17.71
Middle-aged (7-10)	5	35	42.4	1.29
Middle-aged to Old (10-15)	1	18	8.1	12.11
Old (15+)	1	33	8.1	76.54
Total	12	101	101.0	107.65

between the display of social foraging behavior and rank, and reproductive value (V_x , population data in Malmgren, 1979, Table 23; equation after Wilson and Bossert, 1971) where the relative contribution to future generations of an individual of a given age is quantified.

Results and Discussion

Table 1 presents the results of my analysis for the first group of foraging frequency as a function of female age, including expected frequencies. Computing "goodness of fit" led to an unequivocal rejection of the null hypothesis ($P \leq 0.001$, $\chi^2 = 107.64$, $df = 3$). Thus, old age and foraging frequency are significantly related. Young adult females initiate foraging significantly less than expected on the basis of their numbers ($P \leq 0.001$), suggesting that such individuals are relatively "selfish" or are conserving time and energy, possibly for reproduction or competition. Table 1 also shows that the middle-aged to old female foraged more than expected by chance ($P \leq 0.01$), and this female succeeded the oldest and lowest ranking female as the most frequent forager when the old female emigrated in 1977 (personal observation).

Additional observations support the reliability of the above patterns. The oldest female in the second group foraged more frequently than any other ($P \leq 0.001$, $\chi^2 = 17.29$, $df = 2$). Similarly, the relationship between foraging rate and age class (Fig. 1) yields a significant positive correlation ($r_s = +0.629$, $p \leq 0.05$). Related to this, the correlation between foraging rate and dominance rank (Fig. 2) is significant but negative (i.e., the higher the foraging rate, the lower the dominance rank, $r_s = -0.63$, $p \leq 0.05$). Thus, the initiation of foraging is significantly associated with female age and dominance rank.

It was hypothesized above that the expression of social behavior should increase with increasing age since reproductive value (Fig. 3) decreases with age and with it the benefits from selfish reproduction. Fig. 3 shows the reproductive value curve for the population of howler monkeys at Hacienda da Pacifica. Comparing Fig. 3 with Figs. 1 and 2, consistent with expectation, a strong negative association appears to exist between reproductive value and rate of foraging. Reproductive

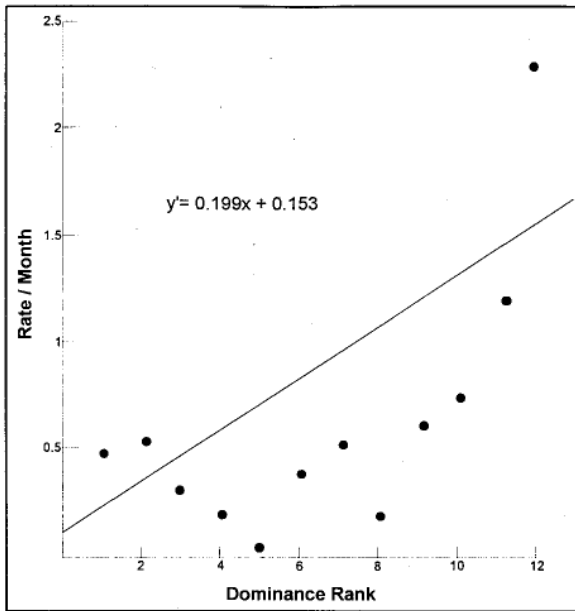


Figure 2. Social foraging rate as a function of individual dominance rank; each point represents one adult female. Note that low numbers mean high rank.

value in the four adult age classes is negatively and significantly correlated with social foraging rate/month ($r_s = -0.95$, $p \leq 0.02$). These results support the view that increasing age or size eventually entails decreasing reproductive value and that the display of social behavior should increase with age as the benefits from individual (selfish) reproduction decline.

What features of the howlers' environment might favor temporal division of labor? On 52 occasions, I was able to record the specific resource upon which foraging sequences terminated. Forty-four (85%) of these sequences terminated on ephemeral food, while eight (15%) sequences terminated with feeding on mature leaves ($P \leq 0.001$, $\chi^2 = 49$, $df = 1$). Thus, the initiation of foraging sequences appears to be associated with food, the local distribution of which is temporally uncertain; new leaves, flowers, and fruit. The old female initiated 21 of the 52 (40%) bouts, 20 of these for ephemeral food.

An old female's presumed experience with the mosaic of her home range might enhance her efficiency as a forager so that her foraging activity may yield an energetic and nutritional gain to other group members. Temporal uncertainty of preferred food resources may favor individuals that are the beneficiaries of the foraging activity of others when reproductive value is low. Division of labor through differential social roles may be a function of relative reproductive value, and behavioral roles may be understood within the context of life history patterns.

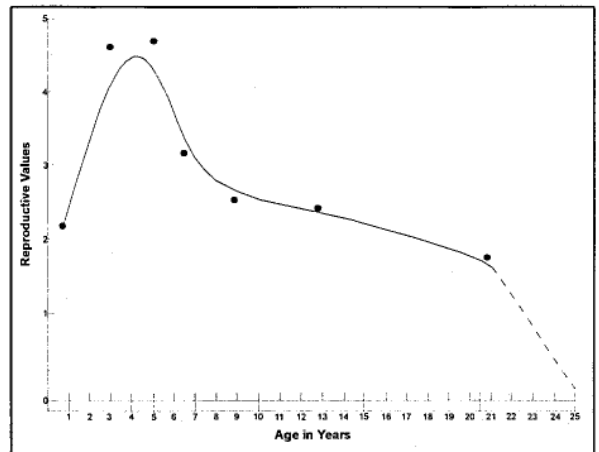


Figure 3. The reproductive value (V_x) curve for the howler population at Hacienda La Pacifica, Cañas, Guanacaste, Costa Rica. Reproductive value was computed for the mid-point of each age class since discrete ages could not be determined year-by-year.

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References

- Glander, K.E. 1980. Reproduction and population growth in free-ranging mantled howling monkeys. *Am. J. Phys. Anthropol.* 53:25-36.
- Hrdy, S. B. and Hrdy, D. B. 1976. Hierarchical relations among female hanuman langurs (Primates: Colobinae, *Presbytis entellus*). *Science* 197:913-915.
- Jones, C. B. 1978. Aspects of reproductive behavior in the mantled howler monkey, *Alouatta palliata* Gray. Dissertation, Cornell University, Ithaca, New York.
- Jones, C. B. 1980. The functions of status in the mantled howler monkey, *Alouatta palliata* Gray: Intraspecific competition for group membership in a folivorous neotropical primate. *Primates* 21:389-405
- Malmgren, L. A. 1979. Empirical population genetics of golden mantled howling monkeys (*Alouatta palliata*) in relation to population structure, social dynamics, and evolution. Ph.D. Dissertation, University of Connecticut, Storrs.
- West, M. J. 1967. Foundress associations in polistine wasps: Dominance hierarchies and the evolution of

- social behavior. *Science* 157:1584-1585.
- West-Eberhard, M. J. 1975. The evolution of social behavior by kin selection. *Quart. Rev. Biol.* 50:1-33.
- Wilson, E. O. and W. H. Bossert. 1971. *A Primer of Population Biology*. Sinauer Associates, Stamford, CN.

PRELIMINARY RECORDS OF COMMON MARMOSETS (*CALLITHRIX JACCHUS*) FROM THE SETE CIDADES NATIONAL PARK, PIAUÍ, BRAZIL

Common marmosets (*Callithrix jacchus*) are endemic to northeastern Brazil and live in a variety of habitat types (Rylands *et al.*, 1993). Previous research on the behavior and ecology of this species has been restricted to the semi-deciduous coastal forests of Permambuco, Paraíba, and Rio Grande do Norte (e.g., Alonso and Langguth, 1989; Digby and Barreto, 1993; Hubrecht, 1984; Scanlon *et al.*, 1989). However, the majority of the common marmoset geographic range encompasses the very different vegetation found in the interior of Brazil. Here we report on preliminary surveys of a marmoset population in the northeastern Brazilian state of Piauí.

Vegetation of the Brazilian Northeast

The northeastern interior is dominated mainly by two types of vegetation: the *cerrado* (savanna forest) and the *caatinga* (dry thorn scrub). The *cerrado* covers over 2.01 million km² within Brazil and is second only to the Amazon forest in the area it covers (Rizzini *et al.*, 1988). The term *cerrado* (*sensu lato*) encompasses a wide range of subtypes of xeromorphic vegetation from the *campo limpo* (open grasslands) to the *cerradão* (dense savanna forests). Trees are semi-deciduous with broad and rigid leaves and thick bark that allows them to survive frequent savanna fires (Eiten, 1972). The *caatinga* covers an additional 0.91-1 million km² and is characterized by a semi-arid climate. Herbs and grasses grow in the *caatinga* only during the rainy season, and vegetation is xerophytic or deciduous (Rizzini, 1977; Rizzini *et al.*, 1988). The flora of the Brazilian *cerrado* is estimated to include 7,000 species compared to the 60,000 species of the Amazon flora and 2,000 species of the flora found in the northeastern *caatinga* (Castro, 1994).

The Study Site

Surveys were conducted at the Sete Cidades National Park in the municipalities of Piri-piri and Piracuruca, Piauí (04° 05'-09'S, 41° 30'-45'W; alt. 100-300 m). The park encompasses 6,221 ha and includes a small hostel,

restaurant, and administrative offices. The primary tourist attractions in the park are a series of dramatic rock formations and rock paintings (Brazil, IBDF/FBCN, 1979).

The park exists in a *cerrado-caatinga* transition zone resulting in a mosaic of habitats. In relatively level areas with good drainage, plant species characteristic of the *cerrado* predominate [e.g., "lixreira" (*Curatella americana*), "barbatimão" (*Stryphnodendron coriaceum*), "cascudo" (*Terminalla fagifolia*), "faveira-de-bolota" (*Parkia platycephala*), and "piqui" (*Caryocar coriaceum*)]. In areas with poor drainage (and subject to flooding) open grassland is found, and along stream beds, riparian forests of the *cerradão*. Mixed into many of these habitats are species characteristic of the riparian forests [e.g., "jatobá-de-mata" (*Hymenaea courbaril* var. *stilbocarpa*), "pau-marfim" (*Agonanadra brasiliensis*), and "pau-pombo" (*Sclerolobium paniculatum* or *Tapirira guianensis*)] and species characteristic of *caatinga* [e.g., "sabiá" (*Mimosa caesalpiniiifolia*), "pau-d'arco-de-sete-folhas" (*Tabebuia aurea*), "aroeira" (*Miracrodruon urundeuva*), "macambira" (*Bromelia laciniosa*), and "xique-xique" (*Pilosocereus gounellei*) (Barroso and Guimarães, 1980).

Marmoset Surveys

Informal surveys were carried out during two periods: July 1994 (three days; eight surveys of 2-5 hours duration) and July 1995 (17 days, total of 66 hours of surveys). Surveys involved one to four observers in five different areas within the park. Particular attention was paid to locating and identifying gum-producing plants bearing characteristic marmoset gouge-holes.

Direct sightings or indirect evidence of common marmosets were found in three areas. In Area 1, a patch of *cerradão* with no standing water, a group of at least three individuals was sighted during the 1994 survey. Vocalizations were heard in this same general area in 1995. Though the area contained trees known to be gum sources for this species [e.g., "cajuí" or cashew (*Anacardium occidentale* var. *microcarpum*)], no trees with gouge-holes were found. In Area 2, pristine riparian forest in a section of the park closed to tourists, three gum trees were found with gouge marks typical of those created by the marmosets (see below). Area 3 consisted of a semi-disturbed gallery forest adjacent to the park office and hostel. Here, a marmoset group containing at least seven individuals was followed for 9.5 hours over 10 days. The group consisted of three adults (at least one male and one female), two juveniles (estimated at 6-7 months of age based on size and pelage), and two infants (estimated at about one month of age). During the brief observation period animals used approximately