- Lönnberg, E. 1941. Notes on members of the genera *Alouatta* and *Aotus. Ark. Zool. 33A*, 10: 1–44.
- Martins, E. S., Ayres, J. M. e do Valle, M. B. R. 1988. On the status of *Ateles b. marginatus* with notes on other primates of the Iriri river basin. *Primate Conservation* (9): 87–91.

BODY WEIGHTS BEFORE AND AFTER FIRST

PREGNANCIES OF IMMIGRANT ADULT FEMALE MANTLED HOWLING MONKEYS (*Alouatta palliata*) IN COSTA RICA

> Evan L. Zucker Margaret R. Clarke Kenneth E. Glander

Introduction

For female primates, as in other mammals, successful reproduction depends upon the proper sequencing of endocrine events (e.g., hypothalamic, pituitary, and ovarian hormone secretions), as well as the physical capacity to support, energetically, the developing fetus (or fetuses) through gestation and lactation (see Bercovitch, 1987; Bercovitch et al., 1998; Serio-Silva et al., 1999; Tardif and Jaquish, 1997). Ontogenetically, one physical requirement for viable first pregnancies appears to be the attainment of a minimum total body weight (Bercovitch and Berard, 1993) or amount of body fat (Schwartz et al., 1988). For mantled howling monkeys (Alouatta palliata), these ontogenetic, physical requirements for successful reproduction are in addition to the social challenges facing females, who emigrate from their natal groups as juveniles, and following a period of time as solitary individuals (one month to two years), immigrate into other groups as young adults (Clarke and Glander, 1984; Glander, 1980, 1992; Jones, 1980; Scott et al., 1978). In order to remain as permanent members in new groups, these immigrant females must become dominant to resident females, a process that can take up to one year (Jones, 1980; Zucker and Clarke, 1998).

Immigrant female howling monkeys give birth to their first offspring, on average, after 19.7 months of residency in a new group (Zucker et al., submitted), meaning they do not conceive their first infant until they are in the group for nearly 14 months (gestation length = 186 days; Glander, 1980). One hypothesized explanation for this apparent delay in reproduction is that they are not fully physically mature at the time of immigration. To assess this hypothesis, we present here (a) the body weights of immigrant female mantled howling monkeys, (b) comparisons of immigrants' weights with the weights of adult female residents, and (c) the body weights of immigrants before and after their first pregnancies. As immigrants are younger than residents, their weights were expected to be less, initially, than the residents. Thus, we are examining the body weights of female mantled howling monkeys from soon after their immigrations (prepregnancy) until after their first births (post-pregnancy).

Methods

Data Set

Howlers were weighed after capture for morphometric, physiological and dental microwear studies at Hacienda La Pacifica, Guanacaste Province, Costa Rica (see Glander et al., 1991; Teaford and Glander, 1996). Body weights for 13 immigrant females, who entered Groups 2, 7 and 19 between 1978 and 1992, were extracted from these records. Group 2 inhabits upland forests, while Groups 7 and 19 inhabit riverine forest. Group 2 has been observed since 1985 (Zucker and Clarke, 1998), Group 7 since 1970 (Glander, 1980), and Group 19 since 1980 (referred to as "Cabina" group by Clarke et al., 1986; see Figure 1 in Glander, 1992, for the locations of these groups on the ranch). Body weights for 36 females resident in these groups were obtained at approximately the same time as were the weights for these immigrants. While secondary dispersal occurs, it is rare (see Glander, 1992). Thus, it can be assumed that nearly all immigrant females are nulliparous. During this time span, three pregnant females entered these groups and another entered with a dependent infant (Zucker et al., submitted); data for these females are not included here.

Body weights for 8 of these 13 females were obtained after the births of their first infants, approximately two years after their capture and weighing as immigrants. Changes in weight were assessed with a correlated samples t-test. Comparison of immigrants' weights with residents' weights was done with an independent groups t-test. Changes in body weights also are expressed in terms of percent increase or decrease.

Results

Immigrants vs. Residents

The 13 immigrants had a mean weight of 4.22 kg (s.d. = 0.30), whereas the 36 resident females of these groups had a mean weight of 5.00 kg (s.d. = 0.65). The immigrants were significantly lighter than the residents (t = 4.16, df = 47, p<0.001). Their weights were approximately 85% of those of the older residents. The weights of immigrants and residents are presented in Table 1. For nine of the 13 immigrants, the body weights of all other adult females in the group were available. In 7 of these 9 cases, the immigrant female was lighter than all other females in the group.

Pre- and Post-Pregnancy Weights of Immigrants

Body weights were obtained for eight of the immigrants soon after they gave birth to their first infants, approximately two years after joining their respective groups. These females showed a significant increase over their pre-pregnancy weights (mean = 4.99 kg; t = 3.84, df = 7, p = 0.003, one-tailed test; see Table 1). Post-pregnancy weights were 16.25% higher than pre-pregnancy weights (range 11% to 32%). One of the eight females, however, weighed less after her first pregnancy than before, losing 5% of her pre-pregnancy weight (see Table 1). This was the only pregnancy and birth this female was known to have. Comparison of the post-pregnancy weights of the eight immigrant females with the weights of resident females indicated no significant difference (t = 0.18, df = 43, p>0.05).

Discussion

These data show that soon after the time of their immigration, female mantled howling monkeys were significantly lighter than resident females, supporting the hypothesis that they were not fully mature, physically, at this stage of their lives, and that they were competing for group membership at a physical disadvantage. However, within two years, and after their first infants were born, females who had competed successfully for group membership increased their body weights by approximately 16%, and their weights were no longer significantly different from those of resident females. Post-partum female Anubis baboons (Papio anubis) lose weight during lactation, weighing 7% less than cycling females (Bercovitch, 1987). If mantled howlers experience patterns of weight changes similar to the baboons, then the post-pregnancy weights reported here for howlers would actually be lower than what these females would weigh when lactation ceases and estrous cycles resume. Bercovitch (1987) further suggested that females might need to surpass a postlactational weight threshold before estrous cycles resumed and subsequent pregnancies occurred.

Bercovitch *et al.* (1998), in their study of captive, provisioned rhesus monkeys (*Macaca mulatta*), found that body weights of young, nulliparous females were predictive of first conceptions: those that conceived weighed significantly more than those that did not. This difference in body weight persisted for at least another year, until these females were four years old, although their subsequent weight did not differ as a function of parity; primiparous females increased their weight by an average of 31% over the next year, while nulliparous females increased their weight by an average of 25% (Bercovitch et al., 1998). The average weight gains by both subsets of rhesus females were greater than those noted for mantled howlers at La Pacifica (16%), but the overall patterns of weight gain were similar. The difference in the amount (or percentage) of weight gained likely reflects species and ecological (management) differences. Rhesus monkeys are seasonal breeders, unlike mantled howlers, so nulliparous females would have until the onset of the next breeding season to increase their weights before the energetic demands of gestation occurred. Primiparous females, likewise, would have longer to reach the weight needed for post-lactational ovulation. Low estrogen levels during periods of acyclicity would also contribute to higher body weights in these rhesus (e.g., Kemnitz et al., 1989). The magnitude of the difference between mantled howlers and rhesus monkeys might also stem from ecological differences; while conceptions could occur at any time of the year for howlers, they face greater seasonal variations in food and nutrient availability than would the provisioned rhesus monkeys studied by Bercovitch et al. (1993). The howler body weight data obtained and used here were not controlled for possible seasonal differences (wet vs. dry).

Comparative growth and development data for New World monkeys are not as readily available as they are for Old World monkeys. Pre- to post-pregnancy body weights of captive, primiparous squirrel monkeys (*Saimiri sciureus*; N = 16), a New World species, also increased significantly (L. Williams, unpubl. data), although the magnitude of the average increase (6.6 %) was not as large as seen in mantled howlers or rhesus monkeys. For this sample of squirrel monkeys, the range of increase was 3.7% to 23.9%, but four of the monkeys showed decreases in their pre- to post-pregnancy weights (losses of 0.5% to 6.0%). While a decrease was noted in one howling monkey, these limited data indicate that post-lactational

Table 1. Immigrant females' body weights, weight gains and residents' mean weights

Female	Group	Entry year	Pre- pregnancy weight (kg)	Post- pregnancy weight (kg)	% change	Group mean weight (kg)	Group s.d.	No. of resident females
APRICOT	7	1978	4.05	4.74	17	4.34	0.99	5
LILAC	7	1989	4.50	5.00	11	5.40	0.28	2
FIONA	7	1990	4.00	5.25	32	4.85	0.58	6
CLEO	7	1990	4.40	4.20	-5	4.75	0.64	6
ARUBA	7	1992	4.80	5.00	4	5.25	0.73	9
OREG	2	1986	3.80	N/A	N/A	4.15	0.16	4
JQ	2	1989	4.00	N/A	N/A	4.60	0.46	3
WISTERIA	2	1991	4.30	N/A	N/A	4.60	0.49	2
SAGE	2	1991	4.20	N/A	N/A	4.60	0.42	2
AZALEA	2	1992	3.90	N/A	N/A	4.80		1
RUBY	19	1980	4.06	5.11	26	4.22		1
GARNET	19	1989	4.70	5.90	26	5.20	0.89	3
LAPIS	19	1989	4.20	5.00	19	5.40	0.61	3
Mean			4.22	4.99	16.25			
S.d.			0.30	0.44	12.40			

-Notes: Group mean weight refers to the resident females' mean weights obtained at the same time as the immigrants' weights; numberof residents contributing to this mean is indicated in the right-most column "N/A" denotes "not available " weight loss in squirrel monkeys might be a more common phenomenon.

Successful reproduction is obviously necessary for sustaining wild populations of nonhuman primates. While the conservation status of howlers is "low risk" (Crockett, 1998), the structure of the La Pacifica population of howlers has changed over the past decade. The total number of monkeys has remained essentially unchanged, but the number of groups has increased; thus, average group size has declined (Clarke and Zucker, 1994; Clarke et al., submitted). In contrast, the protected mantled howler population at Santa Rosa National Park (also in Guanacaste Province) has increased over the comparable time period (Fedigan et al., 1998). For several groups at La Pacifica, emigration and immigration routes appear to have been affected by deforestation and associated canal construction. In one group that has been studied extensively (Group 2), and whose immigrants were included in the present study, the incidence of immigration has decreased (Clarke et al., in press). With the habitat changes, it might take immigrating howler females longer to reach the necessary minimum weight for successful reproduction (or threshold for resumption of cycling post-partum), thus decreasing their potential lifetime reproductive success and reducing the actual number of offspring produced by lengthening interbirth intervals. Applying this scenario to any primate species, decreased habitat quantity or quality could have detrimental effects on reproduction by slowing the rates at which females attain threshold weights necessary for reproduction.

Acknowledgments

This research was supported, in part, by NIH Grant RR00164 to the Tulane Regional Primate Research Center. Sources of support for the dental microwear work can be found in Teaford and Glander (1996). We thank Mark Teaford for his contributions to the study of the La Pacifica howlers and Jennifer Conkerton for assistance with the tabulation of body weight data. Larry Williams (University of South Alabama's Squirrel Monkey Breeding and Research Resource) kindly provided unpublished pre- and postpregnancy body weight data for squirrel monkeys. We also thank the management of La Pacifica for their continued support and permission to work at this site. Some of these data were included in a poster presentation at the 1998 meeting of the American Association of Physical Anthropologists, Salt Lake City, UT (USA).

Evan L. Zucker, Department of Psychology, Loyola University, New Orleans, Louisiana 70118, USA, e-mail: <zucker@loyno.edu>, **Margaret R. Clarke**, Department of Anthropology, Tulane University, New Orleans, Louisiana 70118, USA, e-mail: <mrclarke@tulane.edu>, and **Kenneth E. Glander**, Department of Biological Anthropology and Anatomy, Duke University, Durham, North Carolina 27708, USA, e-mail: <glander@acpub.duke.edu>.

References

- Bercovitch, F. B. 1987. Female weight and reproductive condition in a population of olive baboons (*Papio anubis*). *Am. J. Primatol.* 12: 189–195.
- Bercovitch, F. B. and Berard, J. D. 1993. Life history costs and consequences of rapid maturation in female rhesus macaques. *Behav. Ecol. Sociobiol.* 32: 103–109.
- Bercovitch, F. B., Lebron, M. R., Martinez, H. S. and Kessler, M. J. 1998. Primigravidity, body weight, and costs of rearing first offspring in rhesus macaques. *Am. J. Primatol.* 46: 135–144.
- Clarke, M. R., Collins, D. A. and Zucker, E. L. In press. Responses to deforestation in a group of mantled howlers (*Alouatta palliata*) in Costa Rica. *Int. J. Primatol.*
- Clarke, M. R., Crockett, C. M., Zucker, E. L. and Zaldivar, M. submitted. Changes in the mantled howler population of Hacienda La Pacifica, Costa Rica, between 1991 and 1998.
- Clarke, M. R. and Glander, K. E. 1984. Female reproductive success in a group of free ranging howling monkeys (*Alouatta palliata*) in Costa Rica. In: *Female Primates: Studies by Women Primatologists*, M. F. Small (ed.), pp.111– 126. Alan R. Liss, New York.
- Clarke, M. R. and Zucker, E. L. 1994. Survey of the howling monkey population at La Pacifica: A seven-year follow-up. *Int. J. Primatol.* 15: 61–73.
- Clarke, M. R., Zucker, E. L. and Scott, N. J., Jr. 1986. Population trends of the mantled howler groups at La Pacifica, Guanacaste, Costa Rica. *Am. J. Primatol.* 11: 79–88.
- Crockett, C. M. 1998. Conservation biology of the genus *Alouatta. Int. J. Primatol.* 19: 549–578.
- Fedigan, L. M., Rose, L. M. and Morera Avila, R. 1998. Growth of mantled howler groups in a regenerating Costa Rica dry forest. *Int. J. Primatol.* 19: 405–432.
- Glander, K. E. 1980. Reproduction and population growth in free-ranging mantled howling monkeys. *Am. J. Phys. Anthrop.* 53: 25–36.
- Glander, K. E. 1992. Dispersal patterns in Costa Rican mantled howling monkeys. *Int. J. Primatol.* 13: 415–436.
- Glander, K. E., Fedigan, L. M., Fedigan, L. and Chapman, C. 1991. Field methods for capture and measurement of three monkey species in Costa Rica. *Folia Primatol.* 57: 70–82.
- 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.
- Kemnitz, J. W., Gibber, J. R., Lindsay, K. A. and Eisele, S. G. 1989. Effects of ovarian hormones on eating behaviors, body weight, and glucoregulation in rhesus monkeys. *Horm. Behav.* 23: 235–250.
- Schwartz, S. M., Wilson, M. E., Walker, M. L. and Collins, D. C. 1988. Dietary influences on growth and sexual maturation in premenarchial rhesus monkeys. *Horm. Behav.* 22: 231–251.
- Scott, N. J., Jr., Malmgren, L. A. and Glander, K. E. 1978. Grouping behavior and sex ratio in mantled howling

monkeys. In: *Proceedings of the Sixth Annual International Congress of the International Primatological Society*, D. J. Chivers and W. Lane-Petter (eds.), pp.183–185. Academic Press, London.

- Serio-Silva, J. C., Hernandez-Salazar, L. T. and Rico-Gray, V. 1999. Nutritional composition of the diet of *Alouatta palliata mexicana* females in different reproductive states. *Zoo Biol.* 18: 507–513.
- Tardif, S. D. and Jaquish, C. E. 1997. Number of ovulations in the marmoset monkey (*Callithrix jacchus*): Relation to body weight, age and repeatability. *Am. J. Primatol.* 42: 323–329.
- Teaford, M. F. and Glander, K. E. 1996. Dental microwear and diet in a wild population of mantled howling monkeys (*Alouatta palliata*). In: *Adaptive Radiations of Neotropical Primates*, M. A. Norconk, A. L. Rosenberger and P. A. Garber (eds.), pp.433–449. Plenum Publishing, New York.
- Zucker, E. L. and Clarke, M. R. 1998. Agonistic and affiliative relationships among adult female mantled howlers (*Alouatta palliata*) in Costa Rica over a four-year period. *Int. J. Primatol.* 19: 433–449.
- Zucker, E. L., Clarke, M. R. and Glander, K. E. submitted. Latencies to first births by immigrating adult female howling monkeys (*Alouatta palliata*) in Costa Rica.

FOOD RESOURCES AND THE SURVIVAL OF A GROUP OF HOWLER MONKEYS (*Alouatta palliata mexicana*) IN DISTURBED AND RESTRICTED HABITAT AT LOS TUXTLAS, VERACRUZ, MEXICO.

> F. Gómez-Marin, J. J. Veá E. Rodríguez-Luna, F. García-Orduña D. Canales-Espinosa, M. Escobar and N.Asensio

Introduction

In recent decades, a gradual transformation and disappearance of primate habitat has taken place worldwide, placing an increasing number of species in danger of extinction. Mexico, at the northern limit of Neotropical primate distribution, is one of the areas where primates are potentially under the greatest threat. At present, researchers have only a very general idea of the distribution, biology and ecology of the Mexican primates *Ateles geoffroyi vellerosus, A. g. yucatanensis, Alouatta palliata mexicana* and *A. pigra.* There is still a great deal to be learnt (Rodríguez-Luna *et al.,* 1996a).

Primates are profoundly affected by growing pressure from human activity, as well as the implementation of inappropriate development policies that largely ignore environmental consequences. The main pressures affecting the primates and their habitat in south-eastern Mexico are "slash and burn" farming techniques to create cattle pasture (Guevara *et al.*, 1997) or agricultural land for crops (for example, sugar cane and maize), fires, logging and the construction of rural and urban infrastructure (such as dams and highways). The hunting of primates for food and their capture for sale as pets also threaten groups surviving in increasingly small forest fragments (Paré *et al.*, 1992; Peres, 1997). These small groups remaining in forest patches may also be more susceptible to disease and genetic problems. These threats have led to a recent reassessment of the conservation status of the four Mexican primate taxa, prompting the World Conservation Union (IUCN) to list two of them (*Alouatta palliata mexicana, Ateles geoffroyi yucatanensis*) as threatened species (Hilton-Taylor, 2000). As new field studies are developed, it will be necessary to revaluate the Mexican primates to determine their conservation status more accurately.

In the Los Tuxtlas region A. palliata is found in San Martín Tuxtla Volcano, in Sierra Santa Marta, in San Martín Pajapan and in the fragments of forest surrounding these three areas (Fig. 1). These areas make up the core of the recently established Los Tuxtlas Biosphere Reserve (Presidential Decree in Diario Oficial de la Federación, 23 November 1998). The A. palliata population is in numerous isolated groups in this area. Besides the destruction and fragmentation of their habitat, the main threat is hunting, and although still surviving, there is an urgent need for plans and conservation measures to ensure the long-term survival of these groups (Rylands et al., 1996/1997). To address this, a Conservation Assessment Management Plan (CAMP) workshop was held (Rodríguez-Luna et al., 1996a) at Puebla (México). Its recommendations led to a Population and Habitat Viability Assessment (PHVA) for Alouatta palliata mexicana, which included a simulation of the survival of populations using ecological and demographic parameters (Rodríguez-Luna et al., 1996b).

Factors which must be considered in the conservation and management of primates in fragmented habitats include population densities, home range boundaries and foraging strategies (e.g., minimum foraging area required to maintain a group). A number of estimates for the minimal forest area required have been suggested for both continuous and fragmented habitat (Estrada and Coates Estrada, 1996). These data are useful when estimating the carrying capacity of a particular habitat, but values may vary according to the characteristics of each and the pressures from indirect and direct human activities such as hunting (Neville et al., 1988). These variations explain the different estimates obtained in this study, and it is therefore difficult to define the carrying capacity of any given habitat and/or the minimum area required by a group of this species, as small changes in environmental conditions and anthropogenic pressure can cause significant differences in the demography of primate groups. The incidence of illness and other factors (injuries, loss of variability, genetic defects, behavioral abnormalities) in population regulation also remains unclear, especially in fragmented habitats (Jones, 1994).

Estrada and Coates Estrada (1994) showed the negative effects of habitat fragmentation on the viability and size of the monkey groups living in areas of dense vegetation