SHORT ARTICLES

BODY WEIGHTS OF ADULT FEMALE *ALOUATTA PALLIATA* IN COSTA RICA INCREASE WITH AGE

Evan L. Zucker
Margaret R. Clarke
Kennneth E. Glander

Introduction

Body weights are often used as correlates of general health, as well as being predictive, perhaps, of future reproductive success (Trivers and Willard, 1973; Bercovitch *et al.*, 1998). For female nonhuman primates, the long-term monitoring of body weights constitutes an integral part of the study of life histories (Harvey *et al.*, 1987). With respect to female mantled howling monkeys (*Alouatta palliata*), they emigrate from their natal groups as juveniles (Glander, 1980, 1992; Scott *et al.*, 1978), as do males, later immigrating into other social groups after a period of living alone. In order to stay in these new social groups, immigrating females must become dominant to all resident females, a process that can take up to a year (Jones, 1980; Glander, 1992; Zucker and Clarke, 1998). As group membership is a competitive process, the sizes (weights) of immigrant females might contribute to their competitive abilities and eventual successful immigrations. Newly immigrant females weigh less than resident females; but after two years, this difference disappears (Zucker *et al.*, submitted).

This process of juvenile emigration from natal groups, with subsequent immigration into other groups as young adults, results in reversed, age-graded hierarchies for each sex (Clarke and Glander, 1984; Jones, 1980; Zucker and Clarke, 1998). The most dominant individual of each sex is typically the youngest, while the least dominant is the oldest, usually having the longest tenure in the group (Clarke and Glander, 1984; Jones, 1980; Zucker and Clarke, 1998). Thus, age and status are inversely (negatively) related, unlike the positive relationship common in Old World genera, such as *Macaca* and *Papio*; that have been more extensively studied with respect to physical growth and development (Altmann *et al.*, 1977; Bercovitch, 1987; Bercovitch *et al.,* 1998; Rawlins *et al.*, 1984; Small, 1981).

In this report, we present body weight data for adult females, which have successfully immigrated and resided in one social group at Hacienda La Pacifica, Guanacaste Province, Costa Rica. These females were residents between 1985 and 1993, during which time various age and sex classes were the subjects of behavioral and physiological studies.

Methods

Study Site and Subjects

Hacienda La Pacifica, located 5 km northwest of Cañas, in Guanacaste Province, Costa Rica, is a 1,980-ha ranch (Glander, 1992) in the lowland tropical dry forest zone (Holdridge, 1967). The majority of adult mantled howlers on the ranch have been captured and marked for reliable identification (Scott *et al.*, 1976; Glander *et al.*, 1991; Glander, 1992). Upon capture, all monkeys were weighed, measured, and tattooed, and adult females were palpated to detect pregnancies (Glander, 1980, 1992). Adults are marked with unique, color-coded leg chains (males) or collars and tags (females). Individuals captured for the first time are aged, based on dental characteristics (Pope, 1966). Monkeys have usually been captured during the months of February and July.

Study of Group 2 at La Pacifica began in 1985, after census work in 1984 provided the group's demography (Clarke *et al.*, 1986). During the 9-year period covered in this report (1985–1993), mean group size was 17.3 monkeys (sd = 3.8), including an average of 8.4 adult females (sd = 1.6). This group inhabits an L-shaped home range of upland forest (see Fig. 1 in Glander, 1992, for a map of the ranch showing the location of this group). Home range size was estimated to be 24 ha (Zucker *et al.*, 1996), although this was decreased by approximately 10% in 1991 following deforestation related to the construction of a major canal system through La Pacifica and other parts of Guanacaste Province (Clarke *et al.*, 2002).

Data Set

Six adult females were captured and marked in 1985. In 1986, four more adult females were captured and marked, including two females believed to be recent immigrants. Two marked adult females from 1985 were not present in 1986. Thus, beginning in 1986, all adult female residents in this group were marked and identifiable. In calculating the mean weight of adult females in this group, the first weights obtained for these 10 females (1985–1986) were used, in addition to the first weights obtained for the subsequent six immigrants. Only the body weights of nonpregnant females are included.

Longitudinal assessment of body weights became possible after all of the adult females in Group 2 were marked. Weights for 12 females which were in the group for a minimum of two years are presented here, with multiple weights available for eight of them. As we have minimized the number of times animals in this group are captured, weights are not available for all individuals in all years of study. After the initial two years, weights of some females were obtained in 1989, 1991, 1992, and 1993. Animals new to the group were captured for permanent marking, as were residents which needed damaged or lost collars, tags, or chains to be replaced.

The affiliative and agonistic interactions of the adult females in Group 2 were studied systematically between 1988 and 1992 during portions of June, July, and/or August (Zucker and Clarke, 1998). Thus, dominance relationships of the 7–9 females in the group during this period are also known, and results generally fit the expected reversed, age-graded hierarchy, although the hierarchies were variable over time. Yearly dominance ranks are given in Zucker and Clarke (1998, Table III).

Results

Taking into account only the first weights, the mean body weight for the 16 females, which were residents in Group 2 at some time between 1985 and 1993, was 4.09 kg (sd = 0.49; range 3.18–5.10 kg). Using all body weights obtained during the study period for these 16 females (n = 26), the mean body weight of an adult female was 4.30 kg (sd = 0.53; range 3.18–5.70 kg). Yearly means and standard deviations are presented in Table 1.

Multiple body weight measurements were available for eight Group 2 females. Seven of them increased their weight over time. The last body weights of these females were, on the average, 16.46% greater than their first weights, with increases ranging from 4.65% to 40.67% (sd = 14.98%). The female who lost weight experienced a decrease of 3.92% over two years. Weights over time for the older females in the group are shown in Figure 1a, while weights for the younger females are shown in Figure 1b. It is evident that the females' weights increased over the years, regardless of length of tenure in the group. Taking into account the number of years in the group, the mean increase per year was 3.64% (sd = 2.72%) for the seven females that showed increases. For mantled howlers, status decreases with increased tenure in the group (Clarke and Glander, 1984; Glander, 1980; Jones, 1 80; Zucker and Clarke, 1998), so there would be an inverse relationship between status and body weight.

Discussion

Adult female mantled howling monkeys increased their body weights throughout their lives, although the proximate causes of these changes have not yet been assessed in this sample (or population). Increases could be due to increased bone growth and overall size, decreased lean body mass, increased amounts of fat, or changes in bone densities (see Schwartz and Kemnitz, 1992).

During the latter portion of the study period, construction-related deforestation produced some major changes in the group's home range (Clarke *et al.*, in press) and, despite the loss of a major *Spondias* tree and a number of other fruit trees, body weights of the adult females continued to increase, regardless of their specific age or social status. Mean daily path length increased following deforestation (Clarke *et al.*, 2002), so these weight increases occurred even with increased activity, and were not due to decreased activity that might accompany increased age.

The weight increases with age described for this one group of howlers might not be found in groups consuming different diets or living in different microhabitats, such as those inhabiting the riverine forests at La Pacifica. Howlers in the drier, upland forests spend more time feeding than do the howlers living near the rivers (Teaford and Glander, 1996), which could be compounded further by increased feeding time per day during the dry season by the upland groups. The volume of food consumed, which would contribute to body weight, might not reflect the nutritional value of the food, or alternatively, the relationship between volume and nutritional value could vary seasonally. Intergroup differences

Table 1. Adult female *Alouatta palliata* at Hacienda La Pacifica, Guanacaste Province, Costa Rica. Ages, years weighed, yearly means, and standard deviations.

Female	1985	1986	1989	1991	1992	1993
Burgundy	9-R[*]					
Cherry	15-R					
Goldenrod	12-R					
Indigo	6-R	7-R				14-R
Marigold	9-R					
Violet	18-R		22-R			
Oregano		4-I				
Pansy		12-R	15-R			
RC		9-I	12-R			16-R
Tulip		19-R				25-R
Chicory			11-I	13-R		
JQ			4-I			
Sage				4-I		6-R
Wisteria				5-I		7-R
Azalea					4-I	
Bamboo					20-I	
Mean (kg)	3.85	4.08	4.70	4.47	4.35	4.56
Sd	0.55	0.21	0.70	0.38	0.64	0.11
N	6	5	5	3	2	5

[*] Numbers indicate estimated age, in years; "R" = resident in group, "I" = recent immigrant.

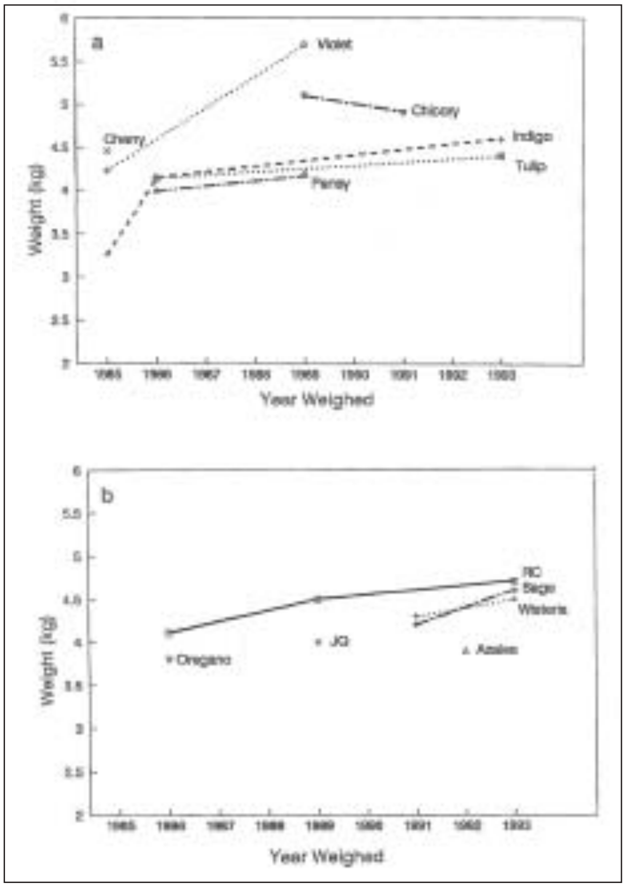

Figure 1. Weights over time of adult female howling monkeys in Group 2 at Hacienda La Pacifica. Weights of older females are shown in (a) and younger females in (b).

in the consumption of different food types were found even within microhabitats (Teaford and Glander, 1996).

Studies of rhesus monkeys (*Macaca mulatta*) provide some comparable data relating body weight to status, although differences in the life histories and social systems of these two species produce different patterns. For rhesus females living in an outdoor field cage, Small (1981) found a significant positive correlation between rank and fat index (composite fat score from skinfold measurements/body weight). Higher fat indexes for high ranking females were attributed to preferential access to food, resulting in them being more healthy. For mantled howlers, immigration patterns produce an inverse relationship between status and weight, although this is clearly confounded by age. In Small's (1981) study, the ages of the higher ranking females were not given, nor was the upper age limit of the adult females studied, although no significant relationship was found between fat index and age (Small, 1981).

Cross-sectional data for provisioned rhesus monkeys on Cayo Santiago, in Puerto Rico, indicated that age and weight were positively related for adult females until they were approximately 13 years old, then weight declined gradually (Rawlins *et al.*, 1984, Table II). In this study by Rawlins *et al.*, sample sizes were quite small for females over six years old. With larger sample sizes, Schwartz and Kemnitz (1992) corroborated this curvilinear pattern, finding that weight increased over the first 14 years, then decreased. Females over 20 years old were significantly lighter than other adult females (Schwartz and Kemnitz, 1992). Thus, howlers and rhesus differ during the latter portion of adulthood in this relationship between age and weight. Rhesus females decrease in weight as they approach their twenties, whereas the weights of howler females continue to increase. The sample of La Pacifica howlers included two females (Violet and Tulip) over 20 years old (Table I), which continued to increase in weight during their twenties. Testable hypotheses about these species' differences during latter adulthood might center on differences in activity levels, quality and types of foods eaten, psychosocial stresses, and/or physical forces associated with arboreal (howler) versus more terrestrial (rhesus) ways of life.

Acknowledgments

This research was supported in part by NIH Grant RR00164 to the Tulane Regional Primate Research Center. Some of the capturing and weighing of monkeys was done in conjunction with dental microwear studies; see Teaford and Glander (1996) for sources of support for that work. We thank Jennifer Conkerton for assistance with data tabulation, the management of La Pacifica for their continued support and permission to work at this site, and the Hagnauer family for all their assistance in numerous ways over the many years. Some of these data were presented 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, LA 70118, USA, e-mail: <zucker@loyno.edu>, **Margaret R. Clarke**, Department of Anthropology, Tulane University, New Orleans, LA 70118, USA, e-mail: <mrclarke@tulane.edu>, and **Kenneth E. Glander**, Department of Biological Anthropology and Anatomy, Duke University, Durham, NC 27708, USA, e-mail: <glander@duke.edu>.

References

Altmann, J., Altmann, S. A., Hausfater, G. and McCuskey, S. A. 1977. Life history of yellow baboons: Physical development, reproductive parameters, and infant mortality. *Primates* 18: 315–330.

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., 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.

Clark, M. R., Collins, D. A. and Zucker, E. L. 2002. Responses to deforestation in a group of mantled howlers (Alouatta palliata) in Costa Rica. *Int. J. Primatol.* 23: 365–381.

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.

Glander, K. E. 1980. Reproduction and population growth in free-ranging mantled howling monkeys. *Am. J. Phys. Anthropol.* 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.

Harvey, P. H., Martin, R. D. and Clutton-Brock, T. H. 1987. Life histories in comparative perspective. In: *Primate Societies*, B. B. Smuts, D. L. Cheney, R. M. Seyfarth, R. W. Wrangham and T. T. Struhsaker (eds.), pp.181–196. University of Chicago Press, Chicago.

Holdridge, L. R. 1967. *Life Zone Ecology*. Tropical Sciences Center, San José.

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.

Pope, B. L. 1966. The population characteristics of howler monkeys (*Alouatta caraya*) in northern Argentina. *Am. J. Phys. Anthropol.* 24: 351–360.

Rawlins, R. G., Kessler, M. J. and Turnquist, J. E. 1984. Reproductive performance, population dynamics and anthropometrics of the free-ranging Cayo Santiago rhesus macaques. *J. Med. Primatol.* 13: 247–259.

Schwartz, S. M. and Kemnitz, J. W. 1992. Age- and gender-related changes in body size, adiposity, and endocrine and metabolic parameters in free-ranging rhesus macaques. *Am. J. Phys. Anthropol.* 89: 109–121.

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

Scott, N. J., Jr. Scott, A. F. and Malmgren, L. A. 1976. Capturing and marking howler monkeys for behavioral research. *Primates* 17: 527–533.

Small, M. F. 1981. Body fat, rank, and nutritional status in a captive group of rhesus monkeys. *Am. J. Primatol.* 2: 91–95.

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.

Trivers, R. L. and Willard, D. E. 1973. Natural selection of parental ability to vary the sex ratio of offspring. *Science* 179: 90–91.

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.

Zucker, E. L., Clarke, M. R., Glander, K. E and Scott, N. J. Jr. 1996. Sizes of home ranges and mantled howler social groups at La Pacifica, Costa Rica: 1972–1991. *Brenesia* 45/46: 153–156.

VARIATIONS IN GROUP SIZE IN WHITE-FACED SAKIS (*PITHECIA PITHECIA*): EVIDENCE FOR MONOGAMY OR SEASONAL CONGREGATIONS?

Shawn M. Lehman
Waldyke Prince
Mireya Mayor

Introduction

There are few longitudinal data on the social structure and behavior of white-faced sakis (*Pithecia pithecia pithecia*). Synecological studies have found that they tend to live in small groups of 2–4 animals (Buchanan *et al.*, 1981; Mittermeier, 1977; also Oliveira *et al.*, 1985, who studied the golden-faced subspecies, *P. p. chrysocephala*), which have led some researchers to suggest that white-faced sakis are monogamous (e.g., Napier and Napier, 1986; Robinson *et al.*, 1986; Dunbar, 1988). Besides group size, support for monogamy in white-faced sakis comes from field studies in which males and females responded in a territorial manner to loud calls during vocal playback experiments (Rosenberger *et al.*, 1997).

Data from historic accounts and recent surveys indicate that some groups of white-faced sakis contain more than four individuals. There have been reports as early as the mid-19th century of groups with 6–10 members (Schomburgk, 1848; Schomburgk, 1876). More recent field accounts confirm that some groups have more than one adult member of each sex (Buchanan, 1978; Oliveira *et al.*, 1985; Kinzey and Norconk, 1993; Gleason and Norconk, 1995; Ryan, 1995; Norconk *et al.*, 1997; Norconk *et al.*, 1998), leading to suppositions that this species may not be monogamous. It has been suggested that groups with more than four animals may represent seasonal congregations of smaller groups (Buchanan, 1978; Fleagle and Meldrum, 1988). Therefore, it is not surprising that Rosenberger and coworkers (1997) recommended that