# ARTICLES

## DEVELOPMENTAL STAGES IN THE HOWLER MONKEY, SUBSPECIES *ALOUATTA PALLIATA MEXICANA*: A NEW CLASSIFICATION USING AGE-SEX CATEGORIES

**Cristina Domingo Balcells**[1], **Joaquím José Veà Baró**[1]

[1]*Centre Especial de Recerca en Primats. Universitat de Barcelona. Gran Via de les Corts Catalanes, Barcelona, Spain. cdbalcells@atmacaucho.com*

### Abstract

We present a new classification of age-sex categories for the mantled howler monkey *Alouatta palliata*. This classification includes only those physical and behavioral characteristics that can be distinguished under field conditions, with the goal of being able to infer the approximate age of monkeys in the wild. Our classification is based on data collected *ad libitum* during monthly censuses of 8 groups of *A. p. mexicana* in a fragmented landscape on the "Los Tuxtlas" Biosphere Reserve at the northern limit of this species' distribution. Our new classification system contains 10 categories that can be compared directly to existing classification schemes to facilitate cross-site studies. We compare the results of our study to the currently used classification system which was based on more southern populations of *A. palliata* in Panamá and Costa Rica.

**Key Words:** Age-sex categories, *A. palliata*

### Resumen

Presentamos una nueva clasificación de categorías de edad-sexo para los monos aulladores *Alouatta palliata*. Esta clasificación incluye solamente aquellas características físicas y comportamentales que pueden ser distinguidas en condiciones de campo, con el propósito de poder inferir la edad aproximada de los monos en estado silvestre. Nuestra clasificación está basada en datos colectados *ad libitum* durante censos mensuales de 8 grupos de *A. p. mexicana* en un paisaje fragmentado el la Reserva de la Biósfera "Los Tuxtlas" en el límite norte de distribución de esta especie. Nuestro nuevo sistema de clasificación contiene 10 categorías que pueden ser comparadas directamente con esquemas de clasificación existentes para facilitar lo estudios de diferentes sitios. Comparamos los resultados de nuestro estudio con el sistema de clasificación actualmente utilizado el cual se basaba en poblaciones de *A. palliata* más sureñas en Panamá y Costa Rica.

**Palabras Clave:** Categorías sexo-edad, *A. palliata*

### Introduction

The study of ontogeny is essential to evolutionary anthropology and primatology since it allows for the comparison of developmental and growth strategies among species. Within a given species, establishing life stages allows one to understand the degree of variability in the development and maturation patterns found in different populations (Neville *et al.*, 1988). Furthermore, for a wide range of primatological studies it is crucial to be able to determine the main developmental stages of the individuals of a species and estimate their age based on their characteristics. For this purpose, the sequence of dental eruption and the length of the long bones are considered to provide the most accurate information (baboons: Phillips-Conroy and Jolly, 1988; howlers: DeGusta and Milton 1998; De Gusta *et al.*, 2003; vervet monkeys: Bolter and Zihlman, 2003; chimpanzees: Zihlman *et al.*, 2004). However, for the analysis of hard tissue it is necessary to examine the individual directly and in the majority of field studies this may not be feasible, may be costly, or may even be harmful to the primates. As such, standardized classifications for each species are useful as they allow the ages of the individuals and their developmental stage to be estimated based only on morphological and behavioral characteristics that are observable from a certain distance.

In demographic and ethological studies these classifications can be used to describe the group composition, age at sexual maturity or migration, morphological and behavioral changes associated with these processes or to examine the influence of ecological constraints on the different developmental stages in a primate population (Bolter and Zihlman, 2003). On the other hand, depending on the physical and behavioral criteria that are applied, the assessment of these stages can vary within a species or even within a population (Bramblett, 1980). Additionally, genetic variation within and between populations has been frequently identified as a cause of differences in the development of individuals (Arendt, 1997). The habitat niche can also modify the growth and development pattern of different populations of the same species (Bolter and Zihlman, 2003). Geographic variation as well as altitudinal and latitudinal, temperature and precipitation gradients, often create genetic clines in growth and development rates (Arendt, 1997). In contrast, when and how to grow, mature and reproduce depend on the state of the organism, including its physiological condition and the associated ecological costs (Gotthard, 2001), which in turn depend on the environment, the risks of predation and resource availability.

For the mantled howler monkey *(Alouatta palliata)* there are few published classifications that define developmental stages by age based on observable characteristics. The most used systems differentiate between immature individuals and adults, or between a few different stages of development (Table 1) and are based on data for the southern populations of howlers from Barro Colorado Island (BCI), Panamá (Carpenter, 1934, 1965) and from Costa Rica (Glander, 1980; Clarke, 1990). These classifications have been used extensively to classify wild howler monkeys by their age throughout their wide distribution. Mantled howlers are found from southern Mexico through Central America and part of Colombia and Ecuador. Despite being one of the most studied New World primate genera, *Alouatta* species' systematic relationships remain unclear (Cortés-Ortiz *et al.*, 2003), and subsequently, it is unknown whether this genetic differentiation has any influence on the development of individuals or the relation between age and external changes. Here we present a new system of classification in age-sex categories for the mantled howler monkey in its most northern distribution, in the region of Los Tuxtlas, Mexico. We compare and discuss our results with the current classification systems from Panamá and Costa Rica.

## Methods

### *Study site*

This study was carried out in a fragmented landscape of disturbed tropical rainforest, located in southern Veracruz, Mexico. The area is within the buffer zone of the Los Tuxtlas Biosphere Reserve (18°34', 18°37'N and 95°02', 95°08'W; elevation in the study area: 25–400 m a.s.l.). The climate is warm and humid (Soto and Gama, 1997) with a mean annual temperature of 25° C and annual precipitation of 4710 mm (EBT, Los Tuxtlas Biology Station, 1996–2005). The dry season occurs from January or February to May and the rainy season is from June to December or January (EBT, 1996–2005), with strong winds from the north from November to February (Soto and Gama, 1997). Currently, there are no large predators, such as jaguar or harpy eagle, in the zone, although there have been reports of attempted attacks by tayra on a troop of howlers (Asensio and Gómez-Marín, 2002).

### *Data collection*

Eight groups of howler monkeys were monitored over a total of 23 non-consecutive months in daily sessions of 6 to 8 hours starting at sunrise. Each group was visited several times each month to ensure reliable observations. Data

**Table 1.** Classification of *A. palliata* by age-sex category.

| Class | Carpenter,1934[a] | Carpenter,1965[b] | Glander,1980[c] | Clarke,1990[d] |
|---|---|---|---|---|
| **Infant 1** | < 1 mo | 0–5/6 mo | ≤ 2 days | 0–3 mo |
| **Infant 2** | 6 mo | 5/6–10/12 mo | 2–21 days | 3–6 mo |
| **Infant 3** | 12 mo | 10/12–18/20 mo | 21–90 days | 6–12 mo |
| **Juvenile 1** | 18 mo | 20–30 mo | 3–6 mo | 12–20 mo |
| **Juvenile 2** | 21 mo | 30–40 mo | 6–30 mo | 20–36 mo |
| **Juvenile 3** | 36 mo | 40–50 mo | - | - |
| **Subadult female** | - | - | 30–48 mo | - |
| **Subadult male** | - | - | 30–48 mo | - |
| **Adult female** | - | >50 mo | >48 mo (first birth approx. 43 mo) | >34–36 mo sexually mature |
| **Adult male** | - | >50 mo | >48 mo | >36–40 mo sexually mature |
| **Characteristics taken into account** | Estimated weight, hair color, relation to mother, play | Estimated weight, hair color, relation to mother, play | Weight, genitalia, hair, transport | Travel, relation to mother and non-mother, play |
| **Methods** | Observations in the wild (approx. 8 months) and in captivity (n = 3). Collections (n = 4). | Modified data from 1934. | Discontinuous observations of one group from 1970–78. Capture (weight, measures, palpation). | Observations of 6 females and 5 males over 22 months, focused on socialization patterns between sexes. |

[a, b] Subspecies *A. palliata aequatorialis*. Data from Barro Colorado Island (BCI), Panama (9°8 N, 79°49 W), tropical rain forest.
[c, d] Subspecies *A. palliata palliata*. Data from La Pacífica, Costa Rica (10°28 N, 85°07 W), dry tropical deciduous forest.

were collected from October 2003 to November 2005 by two teams, each with a researcher and a field assistant, who made every effort to apply homogeneous criteria, as described below. At the beginning of the study there were a total of 20 immature in the eight groups and over the observation period there were 20 births that could be assigned to a specific month. All the animals observed were individually recognized by their natural markings typical of the subspecies. Their identification cards were kept up-to-date throughout the study, and complemented with drawings, photographs and videos. To follow individual development, during each session the observation date and the particular characteristics of the individual at that moment were recorded on each card *ad libitum*. Most of the morphological and behavioral characteristics used in previously established classification systems were included. *Morphology:* color and length of fur, relative body structure and size, appearance of the genitals, head shape. *Behavior:* relationship with the mother, presence/absence of sexual behavior, type of locomotion, feeding and play. The characteristics are listed in Table 2 of the Results section.

*Estimating the age corresponding to different developmental stages in howlers*

Once the field work had been completed, "time lines" were drawn for each individual that was born during the study and therefore of known age. We call the representation of the age in months of each monkey its "time line", and used these together with morphological and behavioral changes that occurred as the study progressed to describe each stage. Using the characteristics recorded, a life stage was assigned to each individual for each observation, applying each of the existing classification systems presented in Table 1. This made it possible to compare the degree of agreement between these classification systems with respect to the assigned stage and in comparison with the animal's real age. Owing to discrepancies detected, the classifications were modified and a new one was created that homogenized the criteria and fit the data of our study. Then, this new system was used to estimate the age of the 20 immature that were present in the first census of the study. Using our pilot classification system, the life stage was assigned to each individual for each observation based solely on the animal's characteristics. In one column the age range estimated using this classification was noted, and in another column the age range estimated at the first observation of the individual according to its characteristics was noted, and to this age we added the elapsed months for the subsequent observations. Finally, agreement between the columns was compared to test whether the classification and the estimated ages fit. Applying this method systematically, we were able to estimate the age ranges for the life stages leading up to maturity.

## Results

Using the time lines, we present the development of the 40 immature studied (Fig. 1). The category corresponding

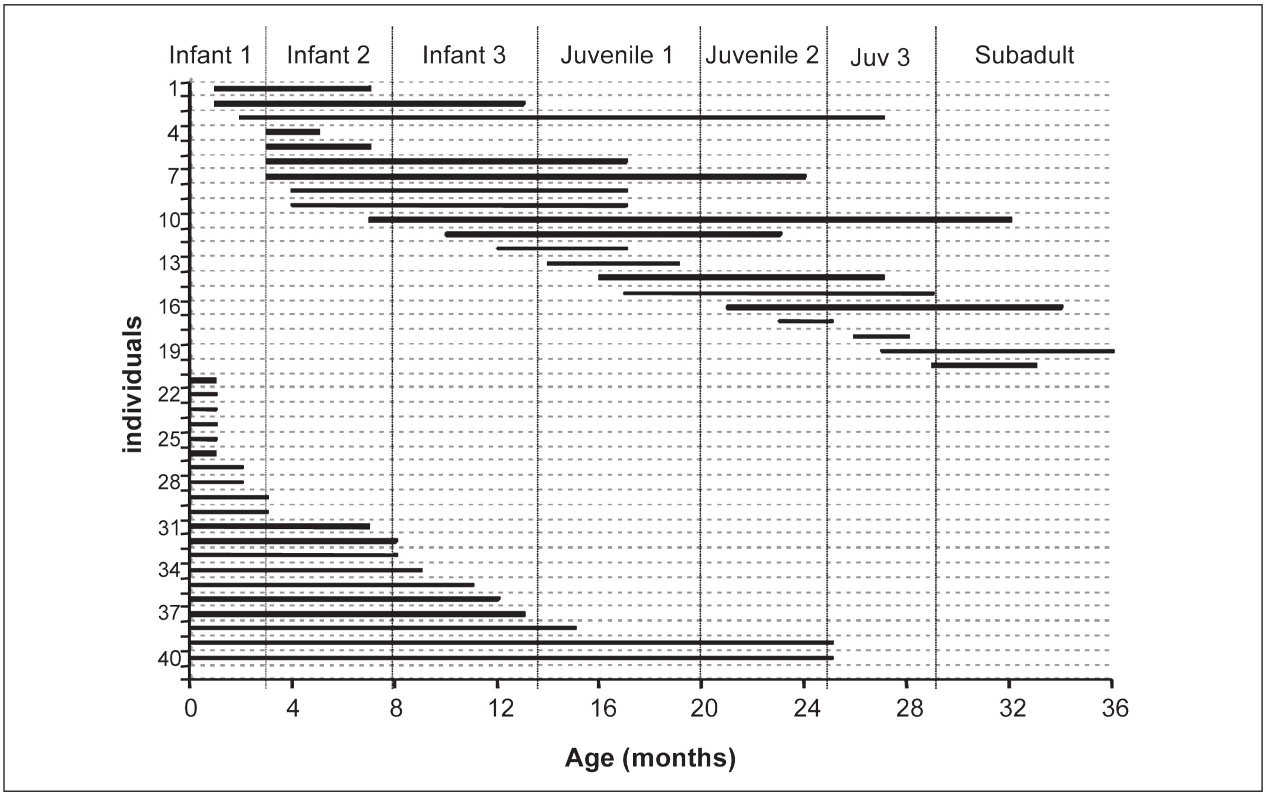

**Figure 1.** Time lines for the 40 immature individuals studied (see text). The category corresponding to the age in months is shown for each individual, applying the classification scheme proposed in this study. Time lines starting at zero (individuals 21–40) correspond to the 20 individuals that were born during the observation period. Lines 1–20 represent immature already present at the beginning of the study.

**Table 2.** Age-sex classification of the Los Tuxtlas howler monkeys (*Alouatta palliata mexicana*).

| Class | Infant 1 | Infant 2 | Infant 3 |
|---|---|---|---|
| **Age (months)** | 0–2/3 | 3/4–7/8 | 8/9–13/14 |
| **Morphology** | Very short silvery gray coat, changing to yellowish to light brown. Extremities and head proportionally more developed than the body. | Short gray-brown to dark brown fur. No mantle. Body proportional to extremities. | Short brown fur, no mantle or beard. |
| **Locomotion and relation with mother** | Carried ventrally by the mother during locomotion, sometimes dorsally. During rest, may try to explore surroundings very close to its mother without letting go of her. | Carried dorsally by the mother or sporadically ventrally during locomotion (especially during rest or during short movements by the mother when she gets up while the baby is feeding or during suspensory locomotion.) Rests with the mother and starts to explore nearby surroundings alone, but stays close to the mother. | Carried dorsally by the mother during long or difficult locomotion and also alone, following the mother, becoming more independent about own locomotion which is quick and abrupt. When on the mother's back, the baby on the base of her tail and tends to wrap its tail around hers. Rests with the mother. |
| **Feeding** | Only suckles. | Suckles and towards the end of this stage begins to try solid food (at approx. 6–8 months). | Suckles, but eats increasingly more solid food as it grows. |
| **Other behaviors** | Other females and juveniles show interest in these infants. Sporadically allomaternal behavior can be observed, with the baby being carried by other individuals. | Begins to play with other infants and juveniles, always in close proximity to its mother. | Plays much of the time and is generally tolerated by adult males. |

**Table 2.** ***cont'd.*** Age-sex classification of the Los Tuxtlas howler monkeys (*Alouatta palliata mexicana*).

| Class | Juvenile 1 | Juvenile 2 | Juvenile 3 |
|---|---|---|---|
| **Age (months)** | 14/15–19/20 | 20/21–24/25 | 25/26–28/29 * |
| **Morphology** | Coat similar to that of the adult in color, but shorter, particularly on the head and sides of the body. Light colored fur on the sides, but without long fringes. No beard and no fur on the sides of the face, giving the head the shape of a small triangle. Body lengthening. | Fur similar to that of the adult in color, but slightly shorter, particularly on the head and sides of the body. Mantle developing; fur light colored and longer on the sides. Larger in size than Juvenile 1 and the body is longer, and its shape more defined. | Fur similar to that of a young female adult in length and color. Slightly smaller than subadult and adult females and easily confused with same in the field. Sex organs not clearly visible. |
| **Locomotion and relation with mother** | Generally rests in contact with or near the mother. Independent, quick, agile locomotion; often follows the mother when the troop moves as a unit. | Independent adult locomotion. At the beginning of this stage juveniles may stay near a female (the mother), but do not generally rest in contact with her. At the end of this stage it is difficult to know who the juvenile's mother is. | Independent adult locomotion. It is impossible to know who the juvenile's mother is. |
| **Feeding** | Still suckles when the mother is resting, but eats mainly solids when the group is foraging. | No longer suckles, only forages. | Adult feeding habits. |
| **Other behaviors** | Plays a lot with other immatures. Generally very well tolerated by adult males and can play with them. Stage at which the emigrations begin **. | Emigration stage**. Often elusive solitaries. If this juvenile remains in the group, it is very independent. Still actively plays with other individuals of its cohort and with infants. | Final emigrations **. Often elusive solitaries. Is totally independent if it stays in the group. Still actively plays with other individuals of its cohort and with infants. |

* The age limit probably depends on the sex of the individual.
** See text for more details.
*** As estimated by other authors (see Table 1), no precise data from this study.

**Table 2.** ***cont'd.*** Age-sex classification of the Los Tuxtlas howler monkeys (*Alouatta palliata mexicana*).

| Class | Subadult female | Subadult male 3 | Adult female | Adult male |
|---|---|---|---|---|
| **Age (months)** | 28/29–35 | 31/32 to 48 months, approx. *** | >36/40 | >48 |
| **Morphology** | Adult coat, with a long light colored mantle. Juvenile in appearance. Hair around face a little shorter than that of adult females and, in general, the face is smoother and rounder than that of adults. Slightly smaller in size than a fully adult female, confusable with a stage 3 juvenile, but the vulva is clearly visible, although small and closed. | Adult coat, with mantle. Secondary sex characteristics developing: beard, lengthening and slight partitioning of head, testicles begin to descend and the scrotum changes from black to white with many black spots. 31/32 months (scrotum not pendulous and genital area black, but with the definite profile of a male). | Dark brown coat, hair longer around the face with a long light colored mantle. Full size. More robust than previous stages. | Dark brown coat, hair longer around the face with a long light colored mantle. Full size. Secondary sex characteristics fully developed. Scrotum fully pendulous and white, sometimes still has the remains of some black spots. |
| **Locomotion** | Independent. | Independent. | Independent. | Independent. |
| **Feeding** | Adult feeding habits. | Adult feeding habits. | Adult feeding habits. | Adult feeding habits. |
| **Other behaviors** | Usually elusive solitaries. If they stay in the group they play actively and appear to have a low hierarchical rank. They do not copulate. Nulliparous. | Often elusive and solitary. Begins to howl at the end of this stage when the testicles have descended. | First estrus and copulation at approximately 35 months old, and first birth at 41 months ** (considering: approximately 6 months for gestation). | Alone or with the group. Howling. Actively copulates when he has access to females. Threatening behavior such as standing on his hind legs and arches body. Occasionally fights with other males. |

* The age limit probably depends on the sex of the individual.
** See text for more details.
*** As estimated by other authors (see Table 1), no precise data from this study.

to the age in months is shown for each individual throughout the study, from the first observation to end of the last observation at the end of the study or when the animal disappeared, either because it died or emigrated. To simplify interpretation, adult categories are not included in the figure and the time lines are drawn as continuous, even though all individuals were not observed during all the months (*e.g.* sample gaps or emigration-immigration events, see Balcells, 2008 for further details on the groups and individuals history). The complete classification by age-sex categories fit to our Los Tuxtlas population is summarized in Table 2 where the distinguishing characteristics for each stage and the estimated age range are listed. The classification we propose is constructed based on those listed in Table 1. There are 10 categories; more than those proposed by other authors, but they can easily be grouped together when required because of the data or the study. We suggest that the maximum number of categories be used to obtain a more accurate estimate of age based on characteristics that are easy to record in the field over a reasonable amount of observation time. On the other hand, any classification of a continuous temporal process is arbitrary and because of this, under field conditions we frequently find individuals that are difficult to assign to one or another of two adjacent categories; these i-ii transition stages (*e.g.* Infant 2–3) can be read in Table 2 as n/n+1.

Some important behavioral events in the lives of primates are of interest when comparing individual's age with external appearance. Howlers usually leave their natal group before reaching maturity (Glander, 1992). Accordingly, there is notable migratory activity in our study population at the group level (Balcells, 2008), and the individuals in the juvenile and subadult categories are often solitary and secretive. In Los Tuxtlas natal emigration generally occurs when the sex of the individual is not externally detectable under field conditions (see also Clarke *et al.*, 2007, for evidence of juvenile monomorphism in *A. palliata*). As such any difference in migration age and behavior between the sexes is not easily distinguishable without later long term follow-up. During our study, we were able to observe only two individuals and determine their sex after they had emigrated. Individual 10 (Fig. 1) returned to his group and was identified as a Subadult male (according to our classification system), having abandoned the group at 27–29 months of age. Individual 15 emigrated at 20–22 months old and later was identified as a small solitary Subadult female behaving evasively. Our data suggest that emigration can occur in any of the three juvenile stages (25% Juvenile 1, 37.5% Juvenile 2 and 37.5% Juvenile 3, *n*=8 observed disappearances of immatures in age of non-dependency from mother) and 3 to 4 of the migrations coincided with the birth of a sibling.

In addition to migration, weaning and first reproduction are also key periods in the lives of howlers. During our study, we were only able to infer the age of one female (individual 19, Fig.1) when she first gave birth, at between 39 and 42 months of age; as calculated for a gestation period of 6 months (Cortés-Ortiz *et al.*, 1993; Glander, 1980), and that first estrus and copulations occur at around 35 months. For males, the beginning of reproductive activity probably depends on social aspects that give them access to the females, but during our study we were not able to observe this process. With respect to feeding, complete weaning in Los Tuxtlas was observed at the end of the Juvenile 1 stage, at 18–20 months of age. It is common to observe a Juvenile 1 (from 15 to 19 months old) still suckling opportunistically when the mother is resting, although during this stage it appears that individuals are no longer dependent on their mother for food, because they can survive as solitaries and some individuals leave the natal group before reaching 15 months of age.

## Discussion

*Comparison of classification systems*

The classification systems analyzed here for age-sex categories of *Alouatta palliata* coincide with each other to differing degrees. On the one hand, Carpenter's (1965) classes have wide age ranges and very advanced ages for the accompanying physical and behavioral characteristics when compared with other systems, including the one we propose for Los Tuxtlas and an earlier one by the same author from 1934. The age assigned for individuals with similar characteristics can differ by as much as 15 months, in spite of being classified as the same morphological stage (*e.g.* Juvenile 1 is 3–6 months old according to Glander, 1980 and 20–30 months according to Carpenter, 1965). Glander (1980) also proposes a wide range of ages for Juvenile 2 (6–30 months), that would include Carpenter's (1934) Juvenile 1 and 2 stages (in both characteristics and age), and from the end of Infant 3 to Juvenile 3 for the system we propose for Los Tuxtlas. In general, our classification system is similar, with certain differences, to the systems of Carpenter (1934) and Clarke (1990). Carpenter (1934) classifies as Juvenile 3 those individuals with characteristics similar to those of the Subadult stage in the Los Tuxtlas classification system. Clarke's (1990) classification proposes age ranges that are very similar to those of our system, although she assigns an age of 20 to 36 months to Juvenile 2, and includes individuals that we would classify as Juvenile 3 and Subadult in this stage. However, for some studies it might be interesting to differentiate between individuals that begin to exhibit sexual traits and the juveniles that do not yet show any external evidence of their sexual identity given that these stages are associated with physiological and social changes. Additionally, differentiating between these stages allows a closer fit to the estimated range of ages for the individuals in the pre-maturation stages that are critical to group dynamics (Glander, 1992).

As regards key events during the development of howler monkeys, there is greater consensus. From our data, sexual maturity in females occurs at approximately 36 months and the first birth occurs at 43 months. This agrees with reports by Glander (1980) and Clarke (1990). According to Clarke (1990) weaning occurs during Juvenile 1 (18 months) in females, while males become independent earlier, both in locomotion and feeding. Carpenter (1934) agrees with this, and although in 1965 he said weaning occurs during Juvenile 1, a much older age is assigned (20–30 months). Glander (1980) does not specify any age for weaning. In Los Tuxtlas, complete weaning was observed at the end of Juvenile 1, at 18–20 months old when individuals can emigrate and survive without suckling, and this coincides with the findings of Carpenter (1934) and Clarke (1990). Finally, the emigration age in males is 12–20 months according to Clarke (1990), while females emigrate at 22–24 months. Our data suggest that the birth of a sibling is an important factor for triggering emigration, and emigration tends to occur before the sex of the individual can be identified and so any difference associated with the sex of the individual is difficult to discern at the time of emigration. More data are required to determine whether there are differences between the sexes or individuals in emigration age, and to broaden our understanding of the factors that might produce any differences observed.

*Genetics, environment and development*

Although growth rates are genetically imprinted, they are phenotypically plastic (Laurila *et al.*, 2001), and a function of the adaptive balance between the costs and benefits associated with development (Gotthard, 2001). In two populations of captive macaques, differences were found in growth rates that could be attributed to their different origins, the different climates of the centers, different social structure or genetic profile (Vancata *et al.*, 2000). Also, in langurs the socio-ecology of the species interacts with its development patterns (Washburn, 1942). In baboons, as a result of improved nutrition, growth rate varies among groups during the same year and for the same group in different years (Strum, 2005). In vervets, reproductive maturity is early compared to that of baboons and is considered an adaptation to unpredictable food sources (Rowell, 1977). On the other hand, the early consumption of solid food in indris could reduce maternal investment (Godfrey *et al.*, 2004). However, in some Platyrrhini (*Aotus, Callicebus, Saimiri, Callimico, Saguinus, Leontopithecus, Cebuella* and *Callithrix*), ecological and social factors, such as predation and competition for food do not appear to adequately explain the differences observed in infant development and growth rates (Garber and Leigh, 1997). In howlers, the lack of consistency in the age classifications within each geographic area prevents us from asserting that environmental differences significantly affect the development strategies of the populations. Although the forage available to the different populations studied might offer differing nutritional value owing to differences in habitat and vegetation (Table 1), this factor probably does not have a significant influence on development (at least for field observations). Howler monkeys can restrict their energetic expenditure behaviorally (Milton, 1980) and, owing to their highly folivore and generalized diet, are capable of using different resources, even in disturbed habitats (Rodríguez-Luna *et al.*, 2003; Cristobal and Arroyo, 2007). For the same reason, the effects of intra- or interspecific competition in habitats with limited resources are mitigated (Van Schaik, 1989).

On the other hand, howler monkeys are not subject to severe predation pressure in any of the study sites because of their large size and the decrease in the populations of potential predators; hence this factor is also not likely to exert a significant influence at present. Finally, latitude does not appear to have an important effect on the rate of development of *A. palliata*, given that there are no consistent differences between the Mexican and more southern populations, in spite of the fact that latitude might be important in fish and amphibians (Duponchelle and Legendre, 2000). It is, however, worth mentioning that in a study using 7 microsatellites for different populations of *A. palliata* in Mesoamerica, Cortés-Ortiz (2003) found a marked decrease in the genetic variation of the populations from south to north where *A. p. mexicana* (from Mexico) was the least variable population, followed by *A. p. palliata* (from Costa Rica), and the population of *A. p. aequetorialis* (from Panamá) had the greatest variation. Even though populations of *A. p. mexicana* do not appear to be facing any detrimental effects owing to the reduction in the genetic variation, this fact could cause differences between populations and should be considered when making comparisons between different populations (subspecies). The incorporation of molecular data in demographic-behavioral studies of different populations would help to reveal the effect of the loss of genetic variation in the ontogenetic development of howler monkeys.

### *The consequences of using different criteria*

According to Neville *et al.* (1988), the use of different criteria for classifying wild *Alouatta palliata* individuals can interfere with the comparison and interpretation of the results obtained by different authors over a wide variety of studies. In demographic studies, not considering subadults as a separate class could result in an underestimation of the number of juveniles or reproductive adults in the censuses. Similarly, certain individuals would be considered as infants or juveniles depending on the classification system. Therefore, it is necessary to keep in mind which classification system has been applied to evaluate the evolution of populations for censuses that use the number of immatures per reproductive female (Heltne *et al.*, 1976). Even purely behavioral and socio-ecological studies (*e.g.* daily activity pattern, diet, play, socialization) that use distinct age classifications to compare behavior patterns between categories of individuals can lead to contradictory conclusions as a result of the criteria applied. The same problem occurs in studies for which it is necessary to infer the age of the individuals in order to prepare life tables, evaluate relative mortality for each stage and age, infer the birth month of the individuals, time of weaning, reproduction or migration.

Our results indicate the need to unify the criteria for classification by age-sex categories for mantled howler monkeys, and to identify consistent differences between populations with different characteristics. Further long term studies are needed in Los Tuxtlas, Mexico and the other places where this species is found.

## Acknowledgements

We are grateful to B. Hervier and S. Vegas for providing data and to C. Pérez for participating in long hours of field work. We thank the Los Tuxtlas Biological Station-UNAM for climate information. For valuable comments on a previous version of the manuscript we thank L. Cortés-Ortiz, P.A.D. Dias and J. Cristóbal-Azkarate. CD Balcells was supported by Floquet de Neu scholarship 1st ed. and from the Ministry of External Affairs in Mexico. For infrastructure support we thank the Ministry of Education and Science of Spain BSO2002-03340 and SESJ2005 1562/PSIC, and E. Rodríguez-Luna of Universidad Veracruzana, Mexico. The research complied with protocols approved by the appropriate institutional animal care committee of SEMARNAT-the Mexican Office for the Environment and Natural Resources, and adhered to the legal requirements of Mexico.

## References

Arendt, J. D. 1997. Adaptive intrinsic growth rates: An integration across taxa. *Q. Rev. Biol.* 72: 149–177.

Asensio, N. and Gómez-Marín, F. 2002. Interspecific interaction and predator avoidance behavior in response to tayra (*Eira barbara*) by mantled howler monkeys *(Alouatta palliata)*. *Primates* 43: 339–341.

Balcells, C. D. 2008. Efectos de la fragmentación del hábitat en la evolución demográfica del mono aullador (*Alouatta palliata mexicana*). Doctoral thesis, Universitat de Barcelona, Barcelona, Spain.

Bolter, D. R. and Zihlman, A. L. 2003. Morphometric analysis of growth and development in wild-collected vervet monkeys (*Cercopithecus aethiops*), with implications for growth patterns in Old World monkeys, apes and humans. *J. Zool., Lond.* 260: 99–110.

Bramblett, C. A. 1980. Model for development of social behavior in vervet monkeys. *Dev. Psychol.* 13: 205–223.

Carpenter, C. R. 1934. A field study of the behavior and social relations of howling monkeys (*Alouatta palliata*). *Comp. Psychol. Monogr.* 10 (2): 1–168.

Carpenter, C. R. 1965. The howlers of Barro Colorado Island. In: *Primate Behavior*, I. De Vore (ed.), pp. 250–291. Holt, Rinehart & Winston, New York.

Clarke, M. R. 1990. Behavioral development and socialization of infants in a free-ranging group of howling monkeys (*Alouatta palliata*). *Folia Primatol.* 54: 1–15.

Clarke, M. R., Zucker, E. L., Ford, R. T., and Harrison, R. M. 2007. Behavior and endocrine concentrations do not distinguish sex in monomorphic juvenile howlers (*Alouatta palliata*). *Am. J. Primatol.* 69:477–484.

Cortés-Ortiz, L., Bermingham, E., Rico, C., Rodríguez-Luna, E., Sampaio, I., and Ruiz-García, M. 2003. Molecular systematics and biogeography of the Neotropical monkey genus, *Alouatta*. *Mol. Phylogenet. Evol.* 26: 64–81.

Cortés-Ortiz, L. 2003. Evolution of Howler Monkeys, Genus *Alouatta.* Dissertation, University of East Anglia, Norwich, England.

Cristóbal-Azkarate, J. and Arroyo-Rodríguez, V. 2007. Diet and Activity Pattern of Howler Monkeys (*Alouatta palliata*) in Los Tuxtlas, Mexico: Effects of Habitat Fragmentation and Implications for Conservation. *Am. J. Primatol.* 69:1–17.

De Gusta, D. and Milton, K. 1998. Skeletal pathologies in a population of *Alouatta palliata*: behavioral, ecological, and evolutionary implications. *Int. J. Primatol.* 19(3): 615–650.

De Gusta, D., Everett, M. A., and Milton, K. 2003. Natural selection on molar size in a wild population of howler monkeys (*Alouatta palliata*). *P. Roy. Soc. Lon. B. Bio.* 270: 15–17.

Duponchelle, F. and Legendre, M. 2000. *Oreochromis niloticus* (Cichlidae) in Lake Ayame, Côte d'Ivoire: life history traits of a strongly diminished population. *Cybium* 24(2): 161–172.

Garber, P. A. and Leigh, S. R. 1997. Ontogenetic variation in small-bodied New World primates: implications for patterns of reproduction and infant care. *Folia Primatol.* 68(1): 1–22.

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 (4): 415–435.

Godfrey, L. R., Samonds, K. E., Jungers, W. L., Sutherland, M. R., and Irwin, M. T. 2004. Ontogenetic Correlates of Diet in Malagasy Lemurs. *Am. J. Phys. Anthropol.* 123: 250–276.

Gotthard, K. 2001. Growth strategies of ectothermic animals in temperate environments. In: *Animal Developmental Ecology*, D. Atkinson and M. Thorndyke (eds.), chapter 15. BIOS Scientific Publishers Ltd, Oxford.

Heltne, P. G., Turner, D. C., and Scott, N. J. Jr. 1976. Comparison of census data on *Alouatta palliata* from Costa Rica and Panama. In: *Neotropical Primates: Field studies and conservation*, R. W. Thorington and P. G. Heltne (eds.), pp. 10–19. National Academy of Science, Washington DC.

Laurila, A., Pakkasmaa, S., and Merilä, J. 2001. Influence of seasonal time constraints on growth and development of common frog tadpoles: a photoperiod experiment. *Oikos* 95: 451–460.

Milton, K. 1980. *The foraging strategy of howler monkeys. A study in primate economics.* Columbia University Press, New York.

Neville, M. K., Glander, K. E., Braza, F., and Rylands, A. B. 1988. The howling monkeys: genus *Alouatta*. In: *Ecology and behavior of Neotropical primates,* A. M. Russell, R. A. Mittermeier, A. B. Rylands, A. Coimbra-Filho and G. A. B. Fonseca (eds.), pp. 349–453. World Wildlife Fund, Washington DC.

Phillips-Conroy, J. E. and Jolly, C. J. 1988. Dental eruption schedules of wild and captive baboons. *Am. J. Primatol.* 15: 17–29.

Rodríguez-Luna, E., Domínguez-Domínguez, L. E., Morales-Mávil, J.E. and Martínez-Morales, M. 2003. Foraging strategy changes in an *Alouatta palliata mexicana* troop released on an island. In: *Primates in Fragments: Ecology and Conservation,* L. K. Marsh (ed.), pp 229–250. Kluwer Academic/Plenum Publishers, New York.

Rowell, T. 1977. Variation in age at puberty in monkeys. *Folia Primatol.* 27: 284–296.

Soto, A. and Gama, L. 1997. Climas. In: *Historia Natural de Los Tuxtlas*, E. González-Soriano, R. Dirzo and R. C. Vogt (eds.), pp. 7–23. UNAM, Mexico DF.

Strum, S. C. 2005. Weight and age in wild olive baboons. *Am. J. Primatol.* 25 (4): 219–237.

Vancata, V., Vancatová, M. A., Chalyan, V. G., and Meishvilli, N. 2000. Longitudinal study of growth and body mass changes in ontogeny in captive rhesus macaques (*Macaca mulatta*) from the Institute of Medical Primatology, Sochi. *Variability and Evolution* 8: 51–81.

Van Schaik, C. P. 1989. The ecology of social relationships amongst female primates. In: *Comparative Socioecology: The Behavioural Ecology of Humans and Other Mammals*, V. Standen and R. A. Foley (eds.), pp. 195–218. Blackwell Scientific Publications, Oxford.

Washburn, S. L. 1942. Skeletal proportions of adult langurs and macaques. *Hum. Biol.* 14: 444–472.

Zihlman, A., Bolter, D., and Boesch, C. 2004. Wild chimpanzee dentition and its implications for assessing life history in immature hominin fossils. *P. Natl. Acad. Sci.* 101(29): 10541–10543.