CHAPTER TEN

An Exploratory Analysis of Developmental Plasticity in Costa Rican Mantled Howler Monkeys (*Alouatta palliata palliata*)

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INTRODUCTION

The genus *Alouatta* (howler monkeys) is the most widely distributed platyrrhine genus, occupying a broad range of biogeographic regimes (Groves, 2001; Crockett, 1998; Curdts, 1993). It has been postulated by several authors that the ecological success of howlers is in part a function of phenotypic plasticity (phenotypic variation expressed by reproductive individuals throughout their lifetimes: Crockett and Eisenberg, 1987; Jones, 1995a,b,c, 1997a, 2002,

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2003a, 2005; Crockett, 1998; Horwich *et al.*, 2000; Clarke *et al.*, 2002a; Silver and Marsh, 2003; Pavelka *et al.*, 2003; Kowalewski and Zunino, 2004; also see Jones, 1978, 1981; Kinzey and Cunningham, 1994; Strier, 1992, 1996; Brockmann, 2001; Jones and Agoramoorthy, 2003; Reader and Laland, 2003). Phenotypic plasticity is thought to be favored in response to environmental heterogeneity (changes in abiotic or biotic events over time and space), optimizing genotypic and phenotypic success in conditions of uncertainty and/or risk (Meyers and Bull, 2002; Lewontin, 1957; also see West-Eberhard, 1979, 2003).

Numerous studies document plasticity in the feeding responses exhibited by howlers. Glander (1975), for example, showed within- and between-season differences in plant selectivity by Costa Rican mantled howlers (*A. palliata palliata*). Studying *A. seniculus* and *A. pigra*, de Thoisy and Richard-Hansen (1997) and Ostro *et al.* (2000), respectively, reported changes in food and site selectivity before and after translocation. These studies support Crockett's (1998: 549) suggestion that the success of howlers is facilitated by "their ability to exploit folivorous diets" and a broad range of habitat types.

Research documenting seasonal peaks in births for some howler species in some habitats also provides evidence for phenotypic plasticity in these monkeys. Jones (1980a,b) showed that mantled howler groups in deciduous habitat of Costa Rican tropical dry forest environment (Frankie *et al.*, 1974) exhibited birth seasonality, but that birth seasonality was not evident for groups occupying riparian habitat. Similarly, Fedigan *et al.* (1998) documented birth seasonality in mantled howlers occupying deciduous habitat of tropical dry forest in Guanacaste, Costa Rica. Studying *A. pigra* (the black howling monkey), Brockett *et al.* (2000) provided evidence for birth seasonality at one semideciduous forest site in Belize where a significant proportion of females appeared to adjust the timing of gestation with peaks in preferred food. In their report on *A. caraya* (the black and gold howler) in Argentina, Kowalewski and Zunino (2004) documented birth seasonality in riparian forests of Argentina and an absence of birth seasonality on a nearby island; and Crockett and Rudran (1987) showed a peak in births for red howlers (*A. seniculus*) in the more heterogeneous of two Venezuelan habitats. Strier *et al.* (2001) did not detect birth peaks for brown howler monkeys (*A. fusca clamitans*) in the Atlantic Forest of Brazil. Brockett *et al.* (2000) concluded that the reported patterns of howler gestation and birth were likely to be a function of differential patterns of rainfall, possibly as condition-dependent and/or facultative responses to the availability of limiting resources, as suggested by Kowalewski and Zunino (2004).

Crockett (1998) stressed the importance of bisexual dispersal as a plastic response to local conditions for howlers. Mesoamerican *A. palliata*, for example, exhibit variations in dispersal patterns as a function of dominance rank (Jones, 1980a) and habitat perturbation (Clarke *et al.*, 2002a; see Jones, 1999, 2004; Estrada *et al.*, 2002). Additional features of howler species reflecting phenotypic plasticity are demonstrated by results showing effects of group and/or population size (density) on relative reproductive success (the mean number of immatures:females per female group size (*A. palliata*: Jones, 1996a; *A. pigra*: Horwich *et al.*, 2001a)) and variations in the number of males in a group (Horwich *et al.*, 2001b).

Recently, within-species variation in howler behavior and social organization was highlighted by Wang and Milton's (2003) work showing that characteristics of the dominance hierarchy of mantled howlers (*A. palliata aequatorialis*) in Panamanian semideciduous lowland tropical forest may differ from the same features in howlers inhabiting tropical dry forests of Costa Rica (Jones, 1978, 1980a,b; Glander, 1980). Wang and Milton's (2003) study documents a relaxed dominance hierarchy in their subjects on Barro Colorado Island, contrasting with the linear hierarchies documented for the mantled howlers in Costa Rican tropical dry forest (Jones, 1978, 1980a; Glander, 1980). These results strengthen the interpretation that differences in habitat (e.g. dispersion and/or quality of limiting food resources; rainfall) may explain observed differences in morphology, behavior, and sociosexual organization within howler species. This chapter describes the results of an exploratory study of habitat differences in chest circumference for female mantled howler monkeys (*A. palliata palliata*) and proposes that the findings are a result of developmental plasticity, a component of phenotypic plasticity whereby between-individual variation(s) in fixed traits result(s) from differences in environments encountered during development.

METHODS

The concepts employed in this chapter have recently been reviewed by Piersma and Drent (2003), West-Eberhard (2003), and Meyers and Bull (2002) (also see Sultan and Spencer, 2002; Kingsolver *et al.*, 2002). As pointed out by Piersma and Drent (2003), definitions for terms and concepts related to phenotypic plasticity are not standardized in the literature, and different fields may utilize different meanings for the same words or phrases. One factor retarding standardization between the social and biological sciences is that definitions in the latter disciplines are generally derived from population genetics, a field that few social scientists have studied, and a field promoting analysis at the population rather than the individual level. Concepts related to quantitative genetics, however, are common to both behavioral genetics (a field studied by many social scientists, especially psychologists) and population genetics. Thus, potential exists for a common vocabulary in this domain of investigation.

Study Site: Hacienda La Pacífica

The study site was Hacienda La Pacífica, Cañas, Guanacaste, Costa Rica, a lowland cattle ranch comprising approximately 13.3 km^2 of pastureland, agricultural fields, and forest fragments at the time of the surveys reported in the present chapter (early- to mid-1970s; see Malmgren, 1979). Details of the study site can be found elsewhere (e.g. Clarke *et al.*, 2002b; Clarke and Zucker, 1994; Clarke *et al.*, 1986; Malmgren, 1979; Glander, 1975). Hacienda La Pacífica is situated within tropical dry forest environment whose natural components include riparian and deciduous forest habitats (Frankie *et al.*, 1974; see Jones, 1996b). Riparian and deciduous habitats are seasonal with flower and fruit activity occurring primarily during the dry season, November through April (Frankie *et al.*, 1974). In the deciduous forest, leaf fall is synchronized for most trees during early to mid dry season. Most trees in the riparian forest retain their leaves throughout the year, displaying a phenological pattern similar to wet forest sites in Costa Rica (Frankie *et al.*, 1974). Riparian habitat, with higher humidity and greater proportion of evergreen vegetation, is most likely characterized by a higher level of primary productivity compared to deciduous habitat (G. W. Frankie, pers. comm., 2004), although quantitative data are lacking.

A third habitat, irrigation, is discussed in this chapter. Irrigation habitat is a degraded secondary deciduous habitat surrounding irrigation ditches at the ranch. Irrigation ditches were constructed consequent to anthropogenic perturbation for the purposes of farming and cattle ranching (see Clarke *et al.*, 1986). To my knowledge, irrigation habitat has not previously been discriminated in other reports based upon research at Hacienda La Pacífica. In this report, irrigation habitat is presumed to be more stressful than riparian or deciduous habitats for mantled howlers based upon the lower proportion of leaf cover and presumed desiccating effects. These assumptions, although untested, are consistent with assumptions made by other primatologists reporting from the field (e.g. Ravosa *et al.*, 1993; Hunt and McGrew, 2002).

The climatological features (e.g. patterns of temporal and spatial autocorrelations of rainfall: see Jones, 1997b) throughout Central America are very similar (Rand and Rand, 1982). These characteristics are a component of (abiotic) environmental heterogeneity which is thought to be a major force in the selection of phenotypic plasticity (see, for example, Sultan and Spencer, 2002). It is argued in this chapter, however, that local rather than global features of the environment are most likely to influence developmentally plastic features of the phenotype, a position consistent with recent discussions (see Kingsolver *et al.*, 2002; Piersma and Drent, 2003; West *et al.*, 2002).

Mantled howlers have been systematically studied at Hacienda La Pacfica since early 1970s, most notably by faculty and students of the Organization for Tropical Studies (OTS). When the present data were collected, approximately 16 howler groups occupied the ranch on variably sized forest fragments (Malmgren, 1979), and no other non-human primate species inhabited the ranch with the exception of the occasional *Cebus* vagrant. The organismic data on which this paper are based are extracted from the censuses conducted in the early- to mid-1970s by Dr. Norman J. Scott, Jr. (US Fish and Wildlife Service, Retired) and his assistants, including the present author.

Animals: *Alouatta palliata*

Mantled howlers, with a maximum body weight of approximately 7 kg (Wolfheim, 1983), are distributed throughout the forests of Middle America and the Pacific coast of northern South America (Groves, 2001). Populations are generally structured into highly communal, polygynandrous (multimale–multifemale) groups, though social organization may include polygynous and "age-graded" varieties of sociosexual architecture (Crockett and Eisenberg, 1987). Howlers are classified as diurnal, arboreal folivores (primary consumers), and are herbivorous primates, preferring new leaves, fruit, and flowers (Glander, 1975; Milton, 1980; Crockett and Eisenberg, 1987; Jones, 1996b). This chapter emphasizes data for adult female mantled howling monkeys.

Field Procedures

Morphometric data (weight (g), length of body (mm), length of tail (mm), pubis width (mm), length of arm (mm), and chest circumference (mm)) were collected from marked and aged (see Scott *et al.*, 1976; Malmgren, 1979; also see Glander *et al.*, 1991; Glander, 1993; Jones, 1980a) animals (127 adult females and 36 adult males). Age was determined by tooth wear (Scott *et al.*, 1976), whereby age class 1 was estimated to be 5–7 years old; age class 2, 7–10 years old; age class 3, 10–15 years old; and age class 4, >15 years old. Subjects were censused and measured (Malmgren, 1979; Scott *et al.*, 1976) in three discriminable habitats on the ranch: riparian (canopy cover estimated at 65–100%), deciduous (canopy cover 40–75%), and irrigation (canopy cover 10–45%). Some animals were followed by radio-tracking (AVM Instrument Company, 810 Dennison Drive, Champaign, IL 61820, USA), necessitated by the extrusion of lime stone aggregated upon a rough landscape, features of the deciduous habitat interfering with location of study groups. Some sample sizes differ in the present report ($N = 127$) and that of Jones (2003b; $N = 120$), because the number of valid cases (cases without missing data) was not the same for all the analyses. Data were analyzed with EcStatic software (Chalmer, 1990), and all tests are two-tailed with α set at 0.05.

PREVIOUS RESULTS FOR THE RELATIONSHIP BETWEEN CHEST CIRCUMFERENCE AND HABITAT IN MANTLED HOWLERS AT HACIENDA LA PACIFICA

A previous report (Jones, 2003b) on the present sample of adult male and female mantled howlers showed that there was no significant difference between habitats in the proportion of each of four age classes represented in the sample. For males, there was a significant negative correlation coefficient between *habitat* and *weight* ($r = -0.4224$, $p = 0.004$, $N = 35$) and a significant negative correlation between *habitat* and *chest circumference* ($r = -0.3273$, $p = 0.024$, $N = 35$). For both the comparisons, *weight* and *chest circumference* were smallest in the irrigation habitat. For females, a significant correlation coefficient was found between *habitat* and *chest circumference* ($r = -0.1851$, $p = 0.021$, $n = 119$). An analysis of variance (ANOVA) comparing male weight with habitat yielded a nearly significant finding (riparian > deciduous > irrigation), but female weight did not differ with habitat (Table 1).

Table 2 displays the means and standard deviations of chest circumference (CC) in all three habitats for both sexes. An ANOVA for the data in Table 2 showed a significant between-habitat difference for females (Table 3) but not for males, and a Newman–Keuls post-test demonstrated that CC was significantly smaller for females in irrigation habitat relative to CC for females in riparian or deciduous habitats (irrigation < riparian, deciduous;

Table 1. Weights (g) of adult male and female mantled howler monkeys in three habitats in the present survey. Null hypothesis was riparian = deciduous = irrigation

Sex	Riparian	Deciduous	Irrigation
Males[a]	5912.00 ± 594.53, $n = 10$	5755.45 ± 586.33, $n = 11$	5333.13 ± 621.17, $n = 15$
Females[b]	4530.91 ± 419.45, $n = 44$	4554.57 ± 407.18, $n = 37$	4439.44 ± 396.05, $n = 39$

See Jones (2003b) and text for further discussion.

[a] $F_{2,23} = 3.1413$, $p = 0.056$.

[b] $p > 0.05$.

Table 2. Means and standard deviations of chest circumference (CC: mm) for adult males and females in the present survey. The null hypothesis was riparian = deciduous = irrigation

Sex	Riparian	Deciduous	Irrigation
Males[a]	328.40 ± 12.14, $n = 10$	328.64 ± 15.67, $n = 11$	316.64 ± 13.45, $n = 14$
Females[b]	289.59 ± 13.94, $n = 44$	291.03 ± 13.13, $n = 37$	283.28 ± 13.45, $n = 39$

See Jones (2003b) and text for further discussion.

[a] $p > 0.05$.

[b] See Table 3.

Table 3. A source table (ANOVA) of adult female chest circumference (CC: dependent variable) × habitat (independent variable)

Source	SS	df	MS	F	p
Habitat[a]	1318.46	2	659.23	3.5986	0.0304
Residual	21,433.5068	117	183.1921		
Total	22,751.9667	119	191.1930		

See text and Jones (2003b) for further information.

[a] Irrigation × riparian (♀♀): $p < 0.05$ (Newman–Keuls test (Chalmer, 1990)). Irrigation × deciduous (♀♀): $p < 0.05$ (Newman–Keuls test (Chalmer, 1990)).

riparian = deciduous; Figure 1). This finding, the only significant comparison yielded by all morphometric analyses for females, may be indicative of differential (energy) investment to cardiovascular function(s) as has been reported for Indian children (Sundaram *et al.*, 1995). Comparable analyses for males yielded no significant results.

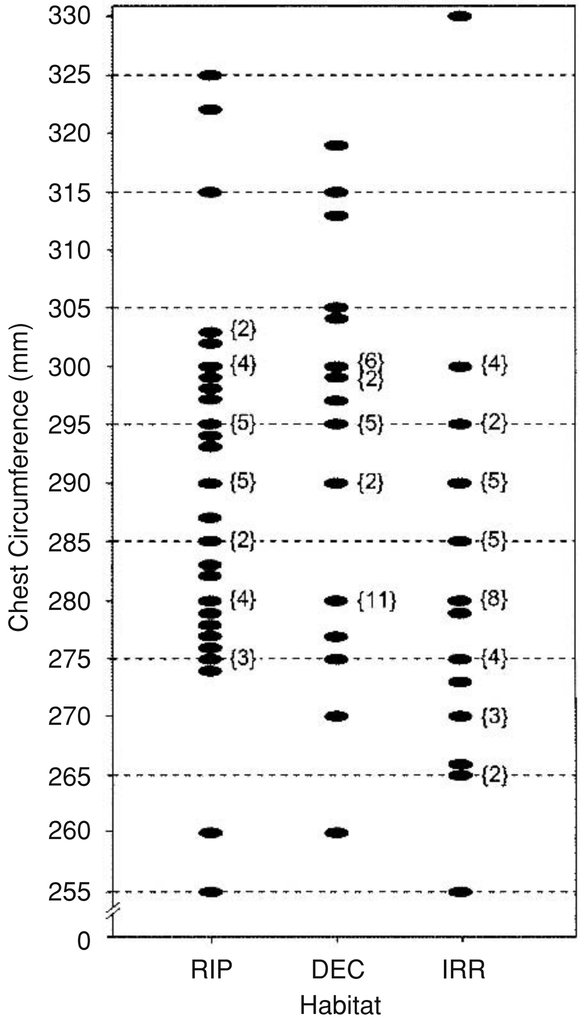

Figure 1. Distribution of chest circumference (CC: mm) × habitat (riparian = RIP; deciduous = DEC; irrigation = IRR) for adult female subjects in the present study ($N = 127$). Numbers in parenthesis = number of females in the sample with the specified chest circumference. See text for further explanation.

CORRELATIONS IN MORPHOMETRIC CHARACTERS AND BETWEEN-HABITAT DIFFERENCES FOR ADULT FEMALE CHEST CIRCUMFERENCE: PUBIS WIDTH RATIO

Table 4 displays correlation coefficients for CC relative to four other morphometric characters for adult females. The strongest correlation is a negative nonsignificant one shown for CC and pubis width (P). A further test evaluated the

Table 4. Correlation coefficients (r), sample sizes (N), and significance level (p) comparing female chest circumference (mm) with four other morphometric characters for females, pubis width (mm), arm length (mm), total body length (mm), and tail length (mm). Note that total sample size is divided between three habitats (riparian, deciduous, and irrigation)

	Pubis	Arm	Body	Tail
Chest	$r = -0.1225$, $N = 120$, $p = 0.091$	$r = -0.0829$, $N = 120$, $p = 0.184$	$r = 0.0340$, $N = 120$, $p = 0.356$	$r = -0.0376$, $N = 120$, $p = 0.342$

See Jones (2003b) and text for further discussion.

possibility that a tradeoff exists between CC and P in primate females inhabiting irrigation habitat. A test of this possibility showed no significant correlation coefficients between CC and P in riparian ($r = 0.0758$, $p = 0.313$, $n = 44$) and deciduous ($r = -0.0063$, $p = 0.485$, $n = 37$) habitats. In irrigation habitat, however, the correlation coefficient between CC and P was highly significant ($r = -0.3895$, $p = 0.005$, $n = 39$), indicative of a tradeoff.

The ratio between chest circumference and pubis width (CC:P; Figure 2) was calculated for each female subject. The resulting ANOVA comparing CC:P by habitat showed no significant relationships. Based on the results displayed in Tables 2 and 3, it is expected that, in future studies with larger sample sizes and correction for sources of error (discussed below), CC:P in irrigation habitat

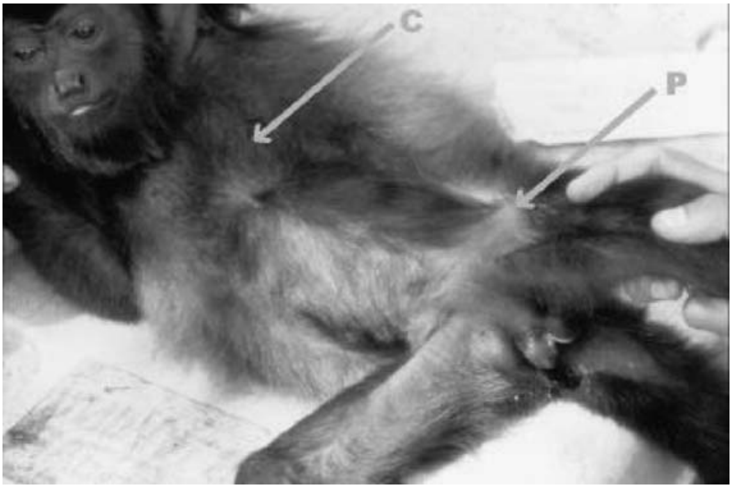

Figure 2. Anesthetized adult female mantled howler monkey (*Alouatta palliata mexicana*) showing approximate location of chest (C) and pubis (P). Juan Carlos Serio Silva©.

(Mean = 0.6962, SD = 0.06, $n = 39$) will be shown to be significantly smaller than the same ratio in the remaining habitats, riparian (Mean = 0.7045, SD = 0.05) and deciduous (Mean = 0.7193, SD = 0.06).

The above expectations rest upon two assumptions. The first assumption is that energy is limiting for an individual so that an increase in energy investment to one structure or function implies a decrease in energy investment to one or more alternative structures or functions. The second assumption is that significant differences exit between the three habitats discriminated in this study, possibly differences in primary productivity. A tentative test of this idea using Malmgren's (1979) estimates of adult density (adults/km^2) for 10 groups showed that mean adult density in riparian habitat was 312.5 ($n = 2$), for deciduous habitat, 159.4 ($n = 5$), and for irrigation habitat, 211.33 ($n = 3$) ($F_{2,7} = 5.3641$, $p < 0.0387$). A Newman–Keuls post-test (Chalmer, 1990) showed that adult density in both deciduous and irrigation habitats was significantly smaller than adult density in riparian habitat ($p < 0.05$) but did not differ from each other ($p > 0.05$). These limited findings indicate that the riparian habitat supports a higher density of adults and may be more productive. Additional research is required to determine the phytogeochemical differences among these three habitats and to test their proposed ontogenetic consequences for mantled howler females.

WITHIN-HABITAT VARIATION IN CC:P RATIO FOR ADULT FEMALE MANTLED HOWLERS

Within-habitat variation in CC:P ratio was assessed for adult females. For these treatments, an ANOVA compared CC:P for each group in each habitat. Statistical analysis showed within-habitat variation to be highly significant for each habitat analyzed separately (riparian: $F_{5,120} = 7.67$, $p = 0.00001$, 6 groups; deciduous: $F_{5,120} = 4.67$, $p = 0.0006$, 6 groups; irrigation: $F_{3,122} = 4.80$, $p = 0.0034$, 4 groups). Interestingly, then, within-habitat variation in CC:P ratio was greater than between-habitat variation, suggesting that, for adult females, positively assortative habitat selection (i.e. a female moving from one riparian habitat to another) is not occurring or is not marked at La Pacfica.

DISCUSSION

The present findings suggest that allocation of energy to CC is more plastic than allocation of energy to P, presumably because functions associated with

P (locomotion, birth) contribute more than pulmonary function, on average, to survival and/or reproduction (see Lloyd, 1987). The negative trend found in the present results cannot be explained by variations in P as a function of habitat since Jones (2003b) found no statistically significant habitat × character comparisons for any morphometric measurement except CC. Adult females in irrigation habitat, then, had a smaller, though not statistically significant, chest circumference relative to pubis than the same ratio for adult females in the other habitats, suggesting a developmental tradeoff between these two body parts and indicative of the relative importance (conservation) of pubis size for females.

Are CC and CC:P Endogenously or Exogenously Induced?

Environmental heterogeneity will prevent individuals from responding *optimally* to any set of conditions since heterogeneity will decrease the accuracy of responses, on average (Meyers and Bull, 2002; Piersma and Drent, 2003). Several authors (e.g. West-Eberhard, 2003; Sih, 2004) have pointed out that developmental plasticity, including tradeoffs in the relationships between growth and development of body parts, may represent facultative adjustment to local conditions (e.g. diet: see Emlen, 1997). Since howlers demonstrate a significant degree of plasticity in their feeding tactics and strategies (e.g. Silver and Marsh, 2003; Fuentes *et al.*, 2003; Zunino *et al.*, 2001; Milton, 1980; Glander, 1975; also see Kowalewski and Zunino, 2004), it will be important to investigate in future the extent to which variations in body mass and sizes of body parts reflect autonomous (endogenous) factors (e.g. geneotype, physiology) and/or exogenous ones (e.g. climate, competition for limiting food of varying dispersion, and/or quality).

Both endogenous (e.g. somatic or physiological perturbations) and/or exogenous (e.g. abiotic or social perturbations) induction of plastic responses may lead to differential allocation of an organism's resources (energy). A tradeoff between chest circumference and pubis width assessed in the present chapter may represent such a case. Although the present report advances the interpretation that CC and CC:P vary as a function of developmental plasticity, future studies will need to identify the functional relationship, if any, between CC and P (F. Nijhout, pers. comm., 2004). For example, if CC and P vary as a function of developmental plasticity, then we expect that changes in endogenous and/or exogenous factors, possibly food dispersion, quality, and/or nutritional status, will be causally related to variations in these morphometric characters. However, if CC and P vary as a function of some third variable, then any association between them is expected to be purely correlational, not causal. The "original Darwinian dilemma" (F. Nijhout, pers. comm., 2004) in interpreting structures that correlate negatively requires resolution for the present observations.

As a partial test of alternative explanations for the pattern of results presented here, it will be necessary to survey and measure the population at discrete intervals over time (C. P. Groves, pers. comm., 2004). Other important *caveats* to the methods and interpretations of the present results entail possible sampling error introduced by inter-investigator error (i.e. measurements were recorded by more than one researcher: Scott *et al.*, 1976), error introduced by surveys taken over a several year period (Scott *et al.*, 1976), and error resulting from the observation that most home ranges of these monkeys overlap more than one habitat type. Future studies need to eliminate, to control, or to correct for these potentially confounding effects and to confidently evaluate hypothesized differences in primary productivity between riparian, deciduous, and irrigation habitats. Furthermore, in order to employ statistical regression on morphometric factors as a function of habitat, it will be instructive in future to measure habitat (food dispersion and quality) with a continuously distributed variable, such as amount of forest cover and resource productivity *for each group*. Such an assessment seems particularly important since a high level of within-habitat variability was shown. Finally, the potential for habitat selection by female mantled howlers is in need of empirical support by radio-tracking dispersing females in order to determine rates of dispersal for irrigation habitat relative to these rates for riparian and deciduous habitats and the fates of dispersing females. Alternatively, within-individual (e.g. variations in genotype) and/or other within-habitat effects (e.g. local competition for limiting food resources) may explain the tendency for females with relatively smaller chest circumference to be clustered in irrigation habitat.

Competition among Body Parts in the Development and Evolution of Mantled Howler Monkeys

Studies with invertebrates (Stern and Emlen, 1999; Nijhout and Emlen, 1998; Emlen and Nijhout, 2001; also see Plaistow *et al.*, 2004) have shown that changes in the relative growth of bodily structures represent competition among body parts for energy and that these responses are apparently under hormonal control. Stern and Emlen (1999) pointed out that there are parallels between insects and vertebrates in the proposed mechanisms for control of body part growth. These authors also pointed out that, similar to insects, some vertebrate body parts grow relative to overall body size. For female mantled howler monkeys in the present sample, Jones (2003b) found no significant relationships between weight, on average, and habitat (see Glander, this volume, for a discussion of individual variation in body mass). Thus, overall body size alone (weight) did not account for the results described in this paper, supporting arguments that assessment of mortality in addition to assessment of body size is required for valid estimation of life-history features (see Stearns, 1984, 1992; Jones, 1998).

Stearns (1984: 694) suggested that life-history evolution is a function of "extrinsic age- and size-specific shifts in mortality rates that interact with . . . the intrinsic constraints and potentials of organisms." Pubis width, then, may be conserved because of costs to reproduction or survival occasioned by a smaller (threshold) pubis size (see Ridley, 1995). Research on a number of vertebrate species has demonstrated ontogenetic changes in body parts in association with the utilization of new habitats (see Shubin and Dahn, 2004). Future studies of female mantled howlers should measure differential reproductive success of individuals of different size, body proportions, genotype, and behavior within and between habitats. These considerations lead to the hypothesis that pubis size for female mantled howlers is a conservative character, presumably due to the constraints of birth and/or locomotion (see Fleagle, 1999: 34) and that smaller chest circumference of females in the irrigation habitat represents a plastic response to local conditions. The effects of chest circumference on reproductive output or mortality in riparian and deciduous habitat and of decreased chest circumference on these life-history parameters in irrigation habitat remain unclear.

Thresholds of Patch Quality as Generators of Dispersal and Phenotypic Plasticity

Results of the work presented in the present report and in Jones (2003b) demonstrate that metapopulation effects (i.e. genetic and/or phenotypic effects of habitat fragmentation) between the variably sized forest fragments at Hacienda La Pacfica have not prevented females residing on patches of irrigation habitat from exhibiting, on average, CC or CC:P smaller than females residing in either riparian or deciduous habitats. Extending a previous theoretical treatment by Moran (1992), Sultan and Spencer (2002; see Kingsolver *et al.*,

2002) have formulated an elegant model showing that phenotypic plasticity in morphological and other traits may be favored where dispersal occurs at sites differing in the relative frequencies of "environments" (e.g. relative frequencies of riparian, deciduous, and irrigation habitats).

Interestingly, Sultan and Spencer (2002: 279–280) show that, in the presence of dispersal, fixation of the plastic genotype may occur even when its fitness is lower than that of other genotypes as long as its costs are small and responsive to local conditions (e.g. competition for food or other limiting resources). As pointed out above, it will be important for primatologists to assess the costs as well as the benefits of phenotypic plasticity (see, for example, Sih, 2004). If a tradeoff is occurring between CC and P for adult female mantled howlers, one would expect that cardiopulmonary function is being compromised for these individuals in the most stressful habitat (i.e. smaller CC in irrigation habitat relative to adult females in riparian or deciduous habitats, Figure 1). This putative cost to females may represent a cost for a female residing in irrigation habitat. If females are "energy maximizers" (Schoener, 1971), then female mantled howlers in irrigation habitat at Hacienda La Pacfica may be exhibiting plasticity in resource (energy) allocation at a measurable cost to survival or reproduction. As Kingsolver *et al.* (2002) conclude, research is needed to verify the predictions of Sultan and Spencer's (2002) model. These authors' conclusions suggest that it will be important to obtain estimates of dispersal rates for primates (see Pope, 1992; Hanski, 2001), to compare and contrast populations varying in levels of plasticity, to evaluate the extent to which thresholds of plastic responses are sensitive to local compared to global conditions, and to conduct simulations and field experiments to manipulate the sizes and connectivity of habitat patches.

SUMMARY

The topic of developmental plasticity is fundamentally related to life-history evolution (West-Eberhard, 2003), in particular, patterns of survival and reproduction. Jones (1997b) employed matrix analysis (see Alberts and Altmann, 2003) of Scott's census data with age structure for mantled howlers at Hacienda La Pacfica to estimate life-history parameters including survivorship, fecundity, and mortality. The suite of life-history traits described by this author (e.g. low survivorship in more than one age class, iteroparity, relatively small reproductive effort) is consistent with the view that mantled howlers, and possibly other members of the genus, express tactics and strategies minimizing costs to fecundity. Since changes in CC and/or CC:P are irreversible morphological changes, it is proposed that female mantled howlers are capable of responding to local conditions with mechanisms of developmental plasticity, a within-individual strategy compatible with the life-history strategy of mantled howlers (Meyers and Bull, 2002; Table 1; see Ravosa *et al.*, 1993). Further research is required to test alternate hypotheses for the present results (e.g. natural selection (C. P. Groves, pers. comm.; F. Nihout, pers. comm.)) and to examine the possibility that there is a threshold of response to locally stressful conditions in irrigation habitat exhibited by female howlers and manifested as developmental plasticity in CC and CC:P.

The present report is consistent with the program of Stearns *et al.* (2003: 311) expressed in the following statement: "Alternative explanations for characteristic male and female growth schedules, and the consequences of the patterns seen in each species . . . all call for investigation across the spectrum of primate social systems." The study of the functional ecology, including physiological ecology and developmental plasticity, of primates is in its early stages (Milton, 1998; also see Strier, 1992; Ravosa *et al.*, 1993; Crockett, 1998; Reader and Laland, 2003: 20–21; Jones, 2005), investigations which are likely to occupy laboratory and field investigators for many years. This body of research will have important implications on primate and other mammalian development, energetics, life history, evolution, and conservation, as it involves an understanding of growth, survival, and reproduction relative to environmental regimes.

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