

Chapter 5

Demographic and Morphological Perspectives on Life History Evolution and Conservation of New World Monkeys

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5.1 Introduction

As an order, primates are distinguished by several features of their life histories from other mammals. These include late achievement of sexual maturity, low female reproductive rates and potentially very long lives (Martin 1990). New World primates present a diverse array of life histories and social organizations (Ross 1991; Garber and Leigh 1997). In this chapter we explore primate life history variation relative to demography and development. We also note how an appreciation of life history and particularly the relations between life history, morphology, and demography can contribute solutions to vexing conservation problems.

Our interest in these questions comes at a critical moment in life history theory because much of this body of theory is undergoing important revisions. The traditional theoretical viewpoint arranges primate taxa along a continuum of “fast vs. slow” life histories. Primates with “fast” life histories bear young over short gestation periods. These young have brief infant and juvenile periods to begin reproducing at small sizes and young ages. Following these fleeting stages, animals with “fast” life history expect short adult lifespans. A “slow” life history species manifests an opposing set of attributes, with long pre- and postnatal developmental periods, large adult size, with few but protracted reproductive events. This paradigm or general theory of life history has been extremely productive in characterizing variation across the primate order. However, recent studies reveal serious deficiencies with this idea in understanding important variation in growth patterns and life history variables (Pereira and Leigh 2003). Furthermore, we maintain that a perspective of “fast” versus “slow” life histories is a heuristic that, unfortunately, inhibits the investigation and understanding of important variation in primate life histories and demography. This idea also hinders development of effective conservation programs.

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In this chapter, we review several areas in which a life history approach can enhance our perspectives on the biology of New World monkeys, with important implications for conservation efforts. Specifically, we briefly discuss demographic modeling in order to understand basic population processes in New World monkeys. These analyses show that even very limited data can provide critical insights into population dynamics. In addition, we discuss how these basic data can provide insights into understanding threats to populations. The data available for long-term, detailed demographic analyses are not yet available for Neotropical primates, except in a few important cases (Strier and Mendes this volume; for example see Crockett 1996; Rudran and Fernandez-Duque 2003 [*Alouatta seniculus*]; Strier et al. 2001 [*Brachyteles hypoxanthus*]). However, studies of primate life histories, even those that have analyzed rudimentary data, can provide information for basic demographic models. Our second objective is to consider how patterns of morphological development impact the course of life history. Traditionally, morphological analyses have been considered independent of both demographic analyses and conservation efforts. However, our morphological studies reveal considerable potential for morphology in understanding how life histories, and thus the basic demographic properties of populations, evolve (Garber and Leigh 1997; Pereira and Leigh 2003; Leigh 2004; Leigh and Blomquist 2007). Finally, attention to both modeling and morphology permits us to bring the concept of reaction norms to bear on conservation questions, along with ideas about genetics and conservation. In all, our contribution stresses the many, but often underappreciated, ways in which a life history perspective, by incorporating demographic models and ontogenetic data, can aid in understanding adaptation and solving conservation problems.

5.2 Demographic Models

5.2.1 Demography

The study of the size, structure, and distribution of populations and their dependence on vital rates of birth, death, and migration—is central to life history theory, providing ways in which ideas about life history can be linked directly to patterns of selection and to conservation concerns about the status of threatened primate populations. Most importantly, demography utilizes powerful quantitative tools to understand how population size and composition change. Demographic analyses can take many forms, ranging from broad approximations of population change to detailed analyses of the relations between individual reproductive performance and phenotypes (Kruuk et al. 2002). On the side of conservation concerns, one approach, *population viability analysis*, is an especially powerful tool. Such approaches are finding broad applications (Young and Isbell 1994; Strier 2000a), but we emphasize Caswell's (2001) thorough treatment of these techniques. He identifies central questions facing researchers and policy-makers developing conservation plans, including the following:

Is the population really declining? Is it declining more than that could be considered normal (i.e. outside the boundaries of what might happen given group structure and inter-annual patterns)? Defining the scope of demographic problems for a population is of obvious interest. The IUCN (2001) definitions of endangerment are based on population size, their degree of fragmentation, and estimated rates of decline.

What part(s) of the life cycle could be impacted to cause the population to decline? This may include factors such as increased emigration, mortality during specific phases of life, depressed fertility, and later maturation. Weighting their importance is key to targeting variables for management.

What are the immediate causes of these changes in the life cycle? Many factors could be involved in changing the lifecycle. For example, infant mortality may be higher because of increased numbers of displaced males raising levels of infanticide; females may have fewer live offspring because of nutritional stress, heavy parasite loads, or inbreeding depression.

What are the ultimate causes, and what can be done about them? Loss or fragmentation of required habitat, hunting, introduction of parasites or other novel environmental factors could be implicated.

A prominent example of how these questions can be answered with rudimentary species-average life history information is provided by conservation efforts on behalf of the loggerhead sea turtle (*Caretta caretta*; see Crouse et al. 1987; Crowder et al. 1994, 1995). Human disturbance through unintentional capture and death in fishing nets, the destruction of nesting sites on beaches, and mortality of eggs and hatchlings all impact loggerheads as well as other sea turtle species. Traditional conservation practices focused on protecting beach habitat, eggs, and hatchlings. However, demographic models demonstrated that neither doubling fertility nor increasing hatchling survival to 1.0 (no death) would induce population growth. Instead, modeling showed that increasing adult survival provided the most effective way to yield a healthy population (Crouse et al. 1987; Crowder et al. 1994, 1995).

At first glance, these questions and analyses seem only loosely related to the kinds of interspecific differences in socioecology and average life history frequently analyzed in the primate life history literature (e.g., Ross 1991; Lee and Kappeler 2003). Thus, such data seem to have limited significance for understanding conservation problems, mainly because such variables are seen as the outcome of long-term and species-specific evolutionary process, with little relevance to microevolutionary processes confronted by most field primatologists. However, a demographic model of the average life history has considerable power to identify variables with the greatest effects on population growth rates. For primates, these are typically survival variables (*see below*). Whether or not these variables can be easily manipulated in a favorable manner through changed land-management or other interventions is a separate, and often much more difficult, question. Such a question involves phenotypic and genetic variation in life history traits as well as covariation among such traits. Robust demographic data are rare for primates, mainly as a result of their long lifespans, and relatively few researchers have prioritized such data (e.g., Rudran and Fernandez-Duque 2003; Strier et al. 2006), at least in research predating the emergence of the major conservation threats facing primates. Primatologists play important roles in all of the steps of this process and must offer useful information for setting policy.

5.3 Simple Demographic Models for New World Monkeys

In an effort to provide some basic information on the connections among demography, conservation, and life history we explored a simple demographic model for a set of New World monkeys. This analysis provides an example of how demographic models can be used with primates even when data are very limited. One result of these models is a ranking of importance of the life history parameters for each species. Knowing which aspects of the life history impact population growth rate the most establishes baseline information for conservation programs to target these life history traits. The model relies on published data on average age of maturation, litter size, inter-birth/litter intervals, and maximum lifespan (Table 5.1). A mixture of captive and wild data was used, though wild data were prioritized when available. In the absence of survival data for these species we simulated average values for adult and juvenile rates. Because the comparative data available are thin, we utilized a very simple demographic model from Charlesworth (1980). The variables investigated can be measured relatively simply, and are commonly utilized in life history analyses. These are reported averages for species, so the data cannot address questions about variation within a species. Our model takes the form of an equation (Equation 1) exploring relations among key demographic parameters:

$$l_{\alpha} b \frac{\lambda^{-\alpha}}{1 - P \lambda^{-1}} = 1 \quad (5.1)$$

Specifically, the terms in this model are: α , female age of first reproduction in years; l_{α} , percentage of newborns surviving to age α ; b , birth rate (litter size/interlitter interval) $\times 0.5$; P , annual survival rate of adult females; and λ , finite rate of increase—population growth rate. Data are input for l_{α} , b , P , and α and λ is solved for by iteration. In other words, values are substituted for λ until one that satisfies the equation (i.e., makes it equal to 1) is found. Survivorship terms (l_{α} and P) were simulated over a range of values (0.05 to 0.90 at intervals of 0.05 for l_{α} , and 0.5 to 0.995 at intervals of 0.005 for P). The resulting set of data includes non-functional life histories (e.g., extremely low survivorship) and parameter combinations that are very unlikely for these primate species. To correct this, we deleted simulated life histories based on three criteria. First, the combination of l_{α} and P had to yield survivorship to maximum recorded lifespan of between 10 and 1 percent. This ensures that the rates selected are reasonable for the species, given what little is known about their lifespans. Second, only combinations in which average sub-adult survival ($l_{\alpha}^{(1/\alpha)}$) was less than or equal to adult survival (P) were used. This is a typical pattern of most mammals and holds for those primates on which there is data. We only accepted sets of values that yielded λ less than 1.30. Higher values would indicate population growth rate higher than 30% per year, which is undoubtedly outside the capability of any primate species, for an extended period of time. Furthermore, the simulated values are intended to be averages. After culling the simulated data, between 74 and 304 life histories were available for each species shown in Table 5.1. Simulated life histories for all but one species included values that would result in both increasing

Table 5.1 Life history data used in study of elasticities of population growth rate to life history traits based on Equation (5.1). Data were selected to roughly capture the breadth of life history and taxonomic variation in New World monkeys. All variables are measured in years except litter size. Species are listed with phylogenetic relatives (Schneider 2000)

Species	Litter size	Inter-litter interval	Age of first reproduction	Maximum lifespan	Data type
<i>Brachyteles hypoxanthus</i>	1	3	9	35	wild ^a
<i>Ateles paniscus</i>	1	2.7	7.1	22	free-ranging ^b
<i>Alouatta palliata</i>	1	1.8	3.6	19	wild & free-ranging ^b
<i>Pithecia pithecia</i>	1	1	2.1	36	captive ^c
<i>Cebuella pygmaea</i>	2	0.6	1.9	18.6	captive ^d
<i>Callithrix jacchus</i>	2	0.4	1.3	20	captive ^d
<i>Callimico goeldii</i>	1	0.4 ^e	1	22.5	captive ^d
<i>Leontopithecus rosalia</i>	2	0.9	1.5	31.6	wild & captive ^d
<i>Saguinus oedipus</i>	1	0.9	1.5	26.2	wild & captive ^d
<i>Cebus apella</i>	1	1.6	7	45.1	wild & captive ^f
<i>Saimiri sciureus</i>	1	1	2.5	30.2	wild & captive ^f
<i>Aotus trivirgatus</i>	1	1	5	21.2	wild & captive ^g

^a Strier et al. 2006. Estação Biológica de Caratinga.

^b Di Fiore and Campbell 2007. Barro Colorado, La Pacifica and Santa Rosa.

^c Harvey and Clutton-Brock 1985. Maximum lifespan reported on captive animals in AnAge online database <http://genomics.senescence.info/>

^d Digby et al. 2007 and AnAge database. Age of first reproduction data are for first ovulatory cycles are thus minima for first births. ILI for *Saguinus* and *Leontopithecus* are from wild populations.

^e Harvey and Clutton-Brock 1985.

^f Jack 2007 and maximum lifespan from AnAge database.

^g Fernandez-Duque 2007 and maximum lifespan from AnAge database.

and decreasing populations ($\lambda > 1$ and $\lambda < 1$). The aberrant species (*Callithrix*) had values ranging from 1.015 to 1.297.

To compare the effect on population growth rate (λ) of a change in any of the model terms we used elasticities calculated through implicit differentiation of the model given in Equation 1. These formulae are provided in the Appendix. Elasticities record the proportional response of population growth rate (λ) to a proportional change in any of the other single model terms. For example, if we change adult survivorship (P), the percentage change recorded in λ is the elasticity of λ to P . A small percentage change in λ from altering P (low elasticity) indicates that adult survivorship has only a minimal effect on population growth rate. Elasticity calculations, especially with high quality data to parameterize a demographic model for a particular primate population with more detailed age-specific information on vital rates, can provide important information to assess the conservation consequences of changes in demographic parameters (Alberts and Altmann 2003). Elasticities are particularly useful for making comparisons among parameters that are measured on different scales (but see Caswell 2001 p. 243). In this model the elasticities of λ to l_{α} and b are equal (see Appendix).

Elasticities calculated for each of the New World primates in Table 5.1 show that changes in adult survival (P) consistently produce the largest demographic response. This is the highest ranking variable in our analyses of elasticities meaning that adult

survival has the greatest impact on the demographic health of populations, and has been shown in more detailed population viability analyses of particular primate species (e.g., Strier 2000a). As a very general rule, then, conservation strategies and tactics should seek to identify factors that impact the survival of adults. The other variables in the model do not impact population growth rate nearly as much as adult survival (Fig. 5.1). The second ranking variables are survivorship to maturity (l_α) and birth rate (b). Their elasticities are equal in this model. Finally, the lowest ranking variable is age of maturation (α). No species deviated from this ranking pattern of elasticities. If extremely high values of λ are allowed, the small-bodied, twin-bearing genera (*Callithrix*, *Cebuella*, *Saguinus*, and *Leontopithecus*) have low frequencies of other ranking patterns. Most of the alternate ranking patterns involved l_α and b ranked above P .

Our analyses show that birth rate and age of maturation are far less important than adult survival in affecting population growth rate. Reproductive output measures are generally unimportant in these models. Minor variations in age of maturation, for example, though often reported, are unlikely to have much effect on population growth rate. We find this result to be an important theoretical contribution, because

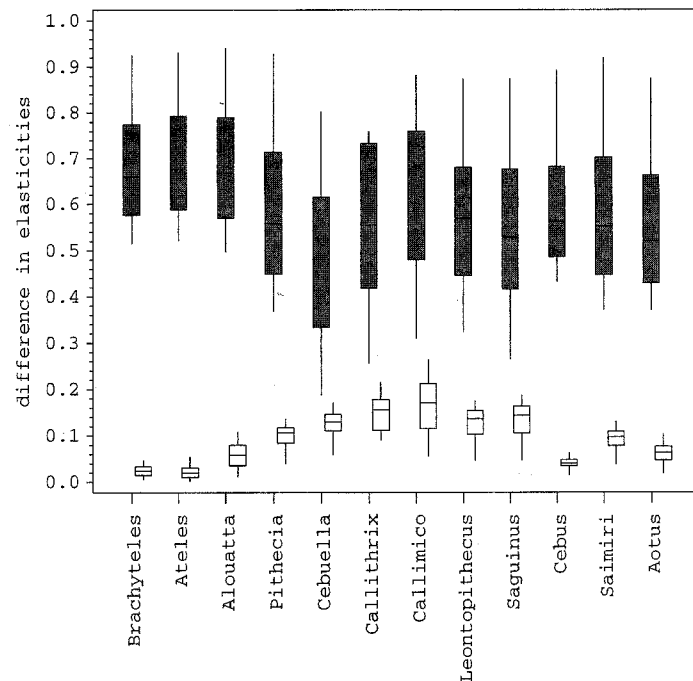


Fig. 5.1 Differences in elasticities of λ to P and l_α or b (grey), and between l_α or b and α (white). Species are ordered as in Table 5.1, which is roughly indicative of phylogenetic relationship

it suggests primate reproductive outputs can be viewed, in part, as simple consequences of negotiating the mortality risks of adulthood.

Changes in adult survival (P) clearly have a major impact on the demographic viability of primate populations. However, attempts to target P exclusively for management are misguided for several reasons. First, for all of the small-bodied species with high reproductive output the differences in elasticities of λ to P and l_α or b can be very small (<0.1) and are rarely larger than 0.6 (Fig. 5.1). This is not the case in larger species, where elasticity to P is typically between 0.5 and 0.9 units greater than that to l_α or b . In the small-bodied species, fairly modest changes in birth rates or survivorship to maturity can have a large effect on λ . Second, there may be no way of favorably influencing P due to economic costs or the population having reached a limiting value for P for internal physiological reasons (e.g., majority of deaths are due to senescent decay). Third, the elasticities for each parameter will change if any other parameter is changed, because λ will change. In this sense elasticities, or sensitivities, are “situational” (Stearns 1992 p. 34). This means that there are interactions among the model terms in determining the effects of each other on population growth rate. Fourth, the elasticity analysis will not identify responses in λ when there are correlated changes in the underlying life history traits. Elasticities are partial derivatives and identify the change in λ due to a single parameter when all other parameters are held constant. Documenting covariation among traits in response to habitat change is a more demanding, and interesting, empirical task for primatologists (Caswell 2000). Finally, because elasticities are derivatives, they only identify the effect of very small changes in a parameter on λ . Larger scale perturbations, such as a doubling of the inter-litter interval, can be made with a model explicitly targeting a certain population to explore how it might respond. Other limitations of elasticity analysis with limited data are discussed by Heppell et al. (2000).

5.4 Life History Modes and Ontogeny

At a broader theoretical level, the calculation of sensitivities or elasticities serves an important purpose aside from conservation applications. They are important because they identify the strength of selection on specific life phases for increases in fertility and survival thereby connecting life histories to evolutionary adaptations, particularly morphological and behavioral attributes. In this setting λ (normally a population growth rate) can be used to calibrate the *fitness* of the average life history, and sensitivities and elasticities document how much fitness changes with alterations in the life cycle.

The patterning of elasticities for primates shown here implies that adult survival will be particularly important in determining the overall pattern of selection. However, because primates take longer periods of time to reach adulthood than most other mammalian taxa, we expect to see diverse ways in which primates pass through development to reach adult sizes and shapes, and increased potential for

decoupling of adult and juvenile morphological and behavioral attributes. Patterns of growth and development, if molded by selection, should be tailored to avoid mortality while growing into an adult state that will maximize survival and fertility. At the most general level, this means either growing *quickly* out of small size to minimize the exposure to dangerous periods (Williams 1966) or growing *slowly*, to reduce caloric needs, through phases in which nutritional stress would be particularly detrimental (Janson and van Schaik 1993). On a finer scale, there may be many ways in which different metabolically expensive tissues can be grown, that minimize their competition for limited energy, either by initiating or terminating their growth at different times, or by growing them at different rates.

Recent research shows that growth patterns are intimately related to adaptation, and in complex ways (Altmann and Alberts 2005; Schillaci and Stallmann 2005; Bolter and Zihlman 2003; Pereira and Leigh 2003; Badyaev et al. 2001; Starck and Ricklefs 1998; Leigh 1994). Specifically, primates, unlike many other mammalian species, seem to exhibit patterns of morphological dissociation during ontogeny. In other words, organs, organ systems, and functional units can develop on differing time scales within the same species. Primate postnatal development often lacks the tight coordination seen in species with shorter ontogenetic periods. This dissociation of developing structures is a core concept for understanding how ontogeny can be molded into adaptive patterns, and contrasts remarkably with traditional “fast vs. slow” models for mammalian life history evolution in which development is entirely absent or is the vacant space between neonatal and adult endpoints. A *life history mode* is a distinctive pattern or arrangement of ontogeny with respect to the rate and scheduling of growth for various organs, organ systems, or developmental modules.

Several examples substantiate the importance of life history modes for underpinning demographic and life history variation in New World monkeys. Across primate species, age of first reproduction and body size are modestly correlated ignoring phylogenetic nonindependence among species values ($r = 0.881$; Leigh and Blomquist 2007). This, accords well with mammalian life history models that see adult size as a function of the span of the growth period, and a constant growth rate for all species (Charnov 1993). However, a phylogenetically corrected correlation between adult mass and age of first reproduction is not significant ($r = 0.059$; Leigh and Blomquist 2007). Among New World monkeys, the phylogenetically corrected correlation between adult mass and age of first reproduction is also not significant. One reason for this lack of association is that there is substantial variation in body mass growth rates among platyrrhine species. Specifically, comparative analyses of small-bodied species (e.g., *Saimiri*, *Saguinus*) show that major differences in body size can be produced in the same amount of growth time (Fig. 5.2). Species differences in size may be produced entirely by growth rate differences, not time differences as is assumed by most classic life history models. This implies that these species support the energetic costs of growth in a variety of ways, including different parenting tactics and patterns of maternal investment (Garber and Leigh 1997).

Comparisons of brain growth patterns further substantiate the view that the developmental patterns of New World monkeys are highly variable, ultimately contributing to variation in demographic parameters (Leigh 2004). For example, brain

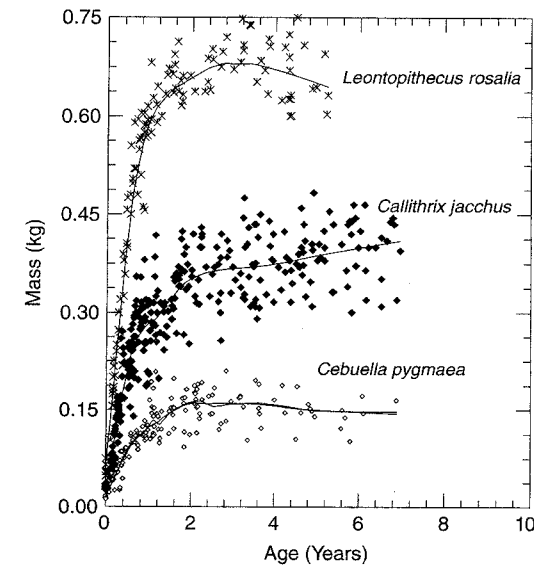


Fig. 5.2 Body mass growth trajectories in selected New World monkey species of differing body sizes (*Leontopithecus rosalia*, *Callithrix jacchus*, and *Cebuella pygmaea*). Different body size may be attained by over growth periods of similar duration. All data are from captive animals (see Garber and Leigh 1997)

growth curves in squirrel monkeys (*Saimiri sciureus*) and saddle-back tamarins (*Saguinus fuscicollis*) demonstrate one such difference (Fig. 5.3). Squirrel monkeys grow their brain quickly for a short period of time mostly during gestation, while tamarin brain growth occurs over a much longer interval at a much lower rate and extends through most of their post-partum somatic development. Goeldi’s monkey (*Callimico goeldi*) may reveal a pattern much like squirrel monkeys. Despite being larger bodied, larger-brained and reaching reproductive maturity later than tamarins, squirrel monkeys (and possibly Goeldi’s monkeys) have dissociated brain growth from body growth and sexual maturation. This means that patterns of brain growth do not necessarily determine the duration of life history stages in platyrrhines. Demographically, patterns of brain growth are important because they are correlated with a variety of patterns of maternal investment. For example, large brains that grow quickly are often associated with delayed female maturation (Leigh 2004), suggesting that the costs of brain growth have maturational, and thus demographic consequences.

In a larger sample of seven haplorhine species adult brain size and age of reproductive maturation are strongly correlated ($r = 0.93$) and age at brain growth cessation and age of reproductive maturation are moderately correlated ($r = 0.64$). Accounting for phylogenetic relatedness among the species using independent contrasts does not substantially diminish the adult brain size-age of reproductive

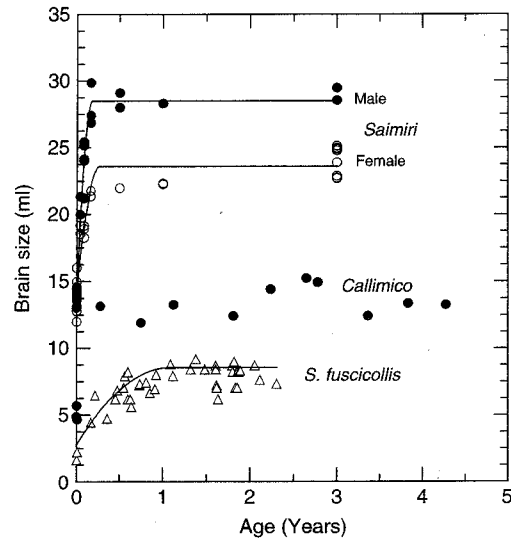


Fig. 5.3 Brain size (ml) plotted against age (years) for selected New World monkey species. Major differences in rates and timing of brain growth occur in these species. Piecewise regression lines are calculated for all species except *Callimico*, for which data are rare

maturation correlation ($r = 0.70$), but that between age of brain growth cessation and age of reproductive maturation evaporates ($r = 0.12$; Leigh and Blomquist 2007). Thus, age at brain growth cessation does not appear to determine directly and fully the age of reproductive maturation. Instead, once phylogenetic controls are applied, these variables are uncorrelated, suggesting that factors other than cessation of brain growth determine age at maturation.

While these patterns do suggest some association between adult brain size and life history, they do not fit models (e.g., Sacher and Staffeldt 1974) that identify the brain as a “pace-setter” of life histories. Instead, as we’ve shown, the length of the juvenile period and the time taken to grow the brain are unrelated. However, these relationships do emphasize the role of energetics and reducing mortality risk in primate life history evolution. The persistent correlation between adult brain size and age of reproductive maturation suggests indirect effects of brain ontogeny on both of these traits. Larger, faster-growing brains require larger, later-maturing mothers. Maternal energetics and mortality risk to both mother and offspring are crucial to understanding investment patterns (Martin 1983, 1996).

The contrast between *Saguinus* and other New World monkeys in terms of brain growth clearly relates to parental investment strategies in these species and the importance of social organization to these patterns. Mothers of the larger species in our comparison make heavy prenatal investments in their single offspring, while tamarin mothers invest little in their litter and deflect costs of growth to the offspring itself and other group members. These and previously mentioned patterns in these species suggests two distinctive life history modes. In squirrel monkeys maternal

costs are high, body mass development is slow, but there is an extended period of mass growth yielding larger adults, and brain growth is rapid and early in development. Facing lower maternal costs, tamarins grow their small bodies quickly over a short period to small adult size, but extend brain growth over a much longer period than squirrel monkeys. These interesting results mean that the earliest periods of ontogeny are likely the most energetically costly for squirrel monkeys. Perturbations of resource bases that differentially affect foraging success of mothers and infants might be expected to have disproportionately large impacts on mortality or morbidity. Tamarins may be less impacted by such changes. Moreover, the costs of brain growth, and thus the susceptibility to environmental perturbation, are very high early in *Callimico* and *Saimiri*, but these costs are minimized after this brief period.

The demographic models explored previously add further insights to these interspecific comparisons. We expect patterns of elasticities for these species to be quite different, despite the stability of their rankings (Fig. 5.1). For *Saimiri* (and all other larger-bodied taxa examined) to offset a small decrease in adult survival, an extremely large increase in survivorship to maturation or birth rate, or decrease in age of maturation would be required. This is not the case in *Saguinus* and the smaller-bodied taxa, where relatively minor changes in the other variables can compensate for or exceed decreases in adult survival. Tamarins achieve an early sexual and somatic maturity because the potential mortality risk for the mother is offset by gains in reproduction. Such compensation is surely outside of the bounds of squirrel monkey life histories, such that maternal survival is more critical. The decision to mature is consequently delayed to when she has the requisite size to carry larger infants to term and not place herself at risk. In effect, morphological considerations, rarely the province of traditional conservation efforts, may play a central role in understanding population dynamics and challenges that species under resource stress face. Furthermore, ontogenetic perspectives on morphology greatly enhance our understanding of the diversity of ways primate life histories can be adaptations to environmental circumstances, balancing the many selective forces that impinge on mothers and offspring as they grow to independence.

5.4.1 Life History Responses to Habitat Change

Anthropogenic habitat change is a common threat to primate populations (Strier 2007). Tropical deforestation often results in the conversion of once continuous forest into patches or fragments of remaining forest in a matrix of non-forest vegetation and alterations of both structure and composition of the forests (Johns and Skorupa 1987; Plumptre and Reynolds 1994; Turner 1996; Marsh 2003; Norconk and Grafton 2003; Rivera and Calme 2006). Habitat fragmentation presents primate populations with changes that may occur over very short time spans. This rate of change means that the concept of a reaction norm (Schlichting and Pigliucci 1998) can be applied, in a general fashion, to contrast the ways in which primate species

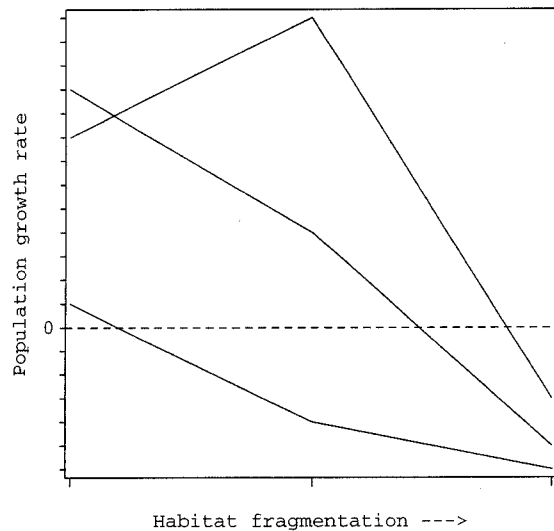


Fig. 5.4 Three imaginary reaction norms for species in three increasing levels of habitat fragmentation. Each solid line represents a population reaction norm. All populations are capable of positive growth in undisturbed habitat (*left*). One increases its growth rate in the mildly fragmented habitat (*middle*) while the growth rates of the others decline. In severely fragmented habitat (*right*) all have reduced growth rates such that they are experiencing population decline (growth rate below zero)

respond differently to changes in their habitats (Fig. 5.4). In a strict sense, a reaction norm is the set of phenotypes produced by a single genotype across a range of environments. In our loose application of the concept here, we will assume that primate populations experiencing rapid fragmentation are genetically unchanged, but simply expressing new phenotypes due to environmental changes. We hypothesize that the reaction norm view can be applied to suddenly fragmenting, essentially diversifying habitats, and has considerable power for assessing conservation risk. The reaction norm can interface directly with a demographic model. Specifically, greater accuracy and precision of models in projections of population change (growth or decline) can be obtained through models allowing for large-scale multi-trait perturbations. Such perturbations should only be performed with solid evidence on the variation and covariation in life history traits in response to environmental change. Unfortunately, little is known about life history responses to habitat fragmentation, and adult survival, the trait to which primate population growth rates are most responsive, is generally the most difficult to measure (Strier and Mendes this volume).

Feeding ecology and social organization often play important roles in predicting differing responses to disturbance. High quality habitats are likely to impact populations favorably both by increasing birth and survival rates, and reducing maturation ages. However, habitat quality is a subjective appraisal for species with differing habitat requirements. Species able to either meet or exceed their nutritional needs in a disturbed habitat are likely to persist (or even increase) in forest fragments,

while those that cannot diminish as a result of nutritional stress (Chapman et al. 2006). Behavioral changes induced by fragmentation can also be important. Infanticide, a particular male reproductive strategy, was shown to increase in habitats under intense human alteration in *Alouatta caraya* (M. Kowalewski pers comm.) and *Semnopithecus entellus* (Sterck 1999).

Examples of primates encountering changing environmental conditions illustrate the importance of life history considerations in assessing conservation problems. Our first example emphasizes feeding ecology and changes in nutrition among hanuman langurs (*S. entellus*). Borries et al. (2001) compared the variation of life history traits in two populations followed for at least 7 years. One population was provisioned and raided crops while the other did neither, leading to energy intakes 5 to 10 times higher in the provisioned crop-raiding population than in the non-provisioned population. Borries et al. recorded remarkable life history trait differences between the two populations. For example, provisioned females gave birth year-round, had younger ages of first reproduction (means: 42.5 mo. vs. 80.4 mo.). They also had shorter interbirth intervals (16.7 mo. vs. 28.8 mo.), mainly as a result of a shorter lactation period (12.8 mo. vs. 24.9 mo.). It should be emphasized that these life history traits vary by about a factor of about two—a level of variation often far exceeding differences recorded among species. It would be important to know how much life history traits vary within a group at the individual level and how genetically differentiated the populations are to understand if the comparisons between groups are microevolutionary differences or can legitimately be interpreted as evidence of a reaction norm. However, these data are unavailable. Other examples of life history changes in response to food abundance or within-group life history variation due to dominance hierarchies that predict priority of access to resources are well documented in catarrhines (e.g., Watanabe et al. 1992; van Noordwijk and van Schaik 1999 [*Macaca*], Packer et al. 1995; Altmann and Alberts 2003; Wasser et al. 2004; Cheney et al. 2006 [*Papio*]; Pusey et al. 1997 [*Pan*]).

A second example emphasizes social pressures and male maturation patterns in black and gold howler monkeys (*A. caraya*). Adult males in this species have black fur and are much larger than females, which are either blond or beige. Both males and females are born blond, but males turn black upon maturity (Neville et al. 1988; Rumiz 1990; Bicca-Marques and Calegario-Marques 1998). Explanations for dichromatism have been proposed (Zunino et al. 1986; Crockett and Eisenberg 1987; Bicca-Marques and Calegario-Marques 1998; Dixson 1998). However, little research has been devoted to understanding how coloration relates to patterns of male maturation among groups. In particular, males in multi-male groups seem to maintain remnants of their golden pelage, especially on their upper torso and shoulders, and remain in their natal groups longer than males maturing in unimale groups. These males turn black rapidly and are quickly evicted by resident males (M. Kowalewski pers. obs.). The little evidence available on somatic growth patterns in male black and gold howlers indicates they have a sub-adult growth spurt (Leigh 1994). Both the pattern of color change and the presence of a sub-adult growth spurt suggest it is important for *A. caraya* males to make a rapid transition to adulthood. We expect that the pattern of somatic growth is generally species-typical,

though nutritional changes will obviously impact the pace of mass gain. However, we hypothesize that the interesting differences in color change between males maturing in unimale and multi-male groups are decoupled from somatic growth and respond to social cues, possibly through some hormonal mechanism, perhaps similar to the hypothesized cause underlying bimaturism in male orangutans (Atmoko and van Hoof 2004). A more continuous habitat could increase the frequency of multi-male troops, causing delayed maturation for males. In a study of black and gold howlers in continuous forest, Kowalewski and Zunino (2004) reported only 3 of 27 groups (11%) were unimale. Zunino et al. (2007) present additional data on a population of black and gold howlers living in fragmented forests. Of these 34 groups, 27 (80%) groups were unimale. While males are “demographically disposable,” meaning that their numbers do not limit population growth as much as females, changes in their maturation patterns could have important influences on patterns of inter-group gene flow and inbreeding depression that affect the viability of local populations.

If the general pattern is for multi-male groups in more continuous forests and unimale groups in more fragmented habitats, the low ability of maturing males to successfully migrate among groups—limiting intergroup gene flow—and high concentration of paternity within groups—reducing effective population size—will raise the risk for loss of genetic diversity and severity of inbreeding depression in unimale groups. This is particularly true if forest patches are becoming more isolated from the destruction of natural corridors among them. Male maturation patterns contribute to the problems of unimale groups. Were maturing males in unimale groups able to retain portions of their golden pelage, they might be able to gain further mass and experience prior to eliciting the evictionary violence of the group male. With greater mass and experience the young male has a better chance of becoming the group male himself, and even if the newly mature male loses he might have a better chance of successfully finding and entering a new group. Neville et al. (1988) also suggested that the retention of juvenile color in maturing male *Alouatta caraya* may allow them to become sexually active while they remain in their natal groups. However, in a captive study of *A. caraya* it was found that counts of abnormal sperm were higher in subadult individuals ($n = 3$) than in adult individuals ($n = 3$) (Moreland et al. 2001). Although these data are extremely limited, it could explain why adult males are tolerant of interactions between subadult males from neighboring groups with resident subadult and adult females during intergroup encounters (Kowalewski 2007). When, these subadult males are fully black, resident males actively stop any contact with resident females. Kingdon (1980) also suggested this juvenile color retention for *Cercopithecus neglectus* subadult males. For several primate species a relationship between the expression of secondary sexual traits and social suppression as a consequence of intermale competition (Gerald 2003) has been reported (Fontaine 1981 [*Cacajao calvus*]; van Noordwijk and van Schaik 1985 [*Macaca fascicularis*]; Dixson et al. 1993 [*Mandrillus sphinx*]; Kummer 1990 [*Papio hamadryas*]; Knott and Kahlenberg 2007 [*Pongo pygmaeus*]).

Under either outcome of successful replacement of the resident male or successful migration to a new group, a situation more amenable to population persistence

would result. If the young male wins, we can imagine a long sequence of very short tenures of males in unimale groups. This will raise the effective population size. If he loses he may survive migration and increase inter-group gene flow. While both are results beneficial to the population such outcomes are usually of little importance for selection, which acts primarily on individuals and genes (Williams 1966). Instead males that mature rapidly under such situations must win eviction contests enough of the time that their mode of maturation is selectively favored. Males in multi-male groups must sire enough offspring while retaining their golden pelage, or they must survive at high enough rates to a fully adult state in which they perform well reproductively (Dixson 1998), that this mode of maturation is adaptive.

We would speculate that these differences are alternative tactics *A. caraya* males have evolved to deal with fringe habitats, where fragmentation may have been common in the past, though not on the present scale. These tactics are probably environmentally dependent—as opposed to microevolutionary differences among populations—and can be thought of as a norm of reaction. Males from either kind of group could follow either developmental mode but the social conditions, which may correlate very directly with habitat fragmentation, will induce which pattern is followed.

Some long-term studies have found relationships between human disturbance, habitat loss or fragmentation and a decrease in density of certain primate populations (e.g., *Gorilla gorilla* [Harcourt and Fossey 1981; Watts 1985]; *Cercopithecus mitis* [Lawes 1992]; *Cercocebus galerritus galerritus* [Medley 1993]). Despite inconsistencies in the responses of primates to different degrees of fragmentation across sites, some of this variation may relate to life history differences among species. Spider monkeys (*Ateles*) and muriquis (*Brachyteles*) have extremely long interbirth intervals compared to other platyrrhines and, aside from *Cebus*, much late ages of first reproduction. These traits normally imply that recovery from major environmental alterations will take many years (Strier 2000b). This may indicate a trade-off. Long interbirth intervals may afford these species a buffer during food shortfalls, if they forgo reproduction in such periods. However, such long interbirth intervals *centeris paribus* also depress population growth rates. How these responses relate to high levels of fragmentation is not yet known, though lowered adult survival rates would be expected to have a greater impact.

Primate populations respond in different ways to different environments (i.e., reaction norm differences) making generalization or extrapolation difficult (Marsh 2003). For example, howlers seem to cope easily with alteration of habitat, maintaining population numbers (Zunino et al. 2007) or increasing even when the fragments become smaller (Bicca-Marques 2003; Rodriguez-Luna et al. 2003). In contrast, spider monkeys simply cannot be found in certain fragments (Ferrari et al. 2003; Gilbert 2003; Marsh 2003). These responses vary across sites and populations, and seem to be related to both the characteristics of the fragments and the species under consideration. These differences are usually attributed to the variation in ecological specialization between these taxa. For example, howlers, being more folivorous than other atelines, are able to persist in seasonal environments and higher

latitudes because they can rely mostly on leaves when fruits and flowers decrease in availability. Howlers also have a shorter interbirth interval, shorter gestation length, and lower ages of weaning and first reproduction than other atelines (Di Fiore and Campbell 2007). These characteristics together possibly make howlers, a successful genus in habitats with lower diversity of plant species, and as such howlers are often considered colonizing species (Crockett and Eisenberg 1987). Morphological attributes, beyond those related solely to life history, clearly play roles in these kinds of contrasts.

5.5 Conclusions

A planned conservation effort should include concentrated study of life history schedules and their relationship with ontogeny, genetic patterns, and population dynamics (Hapke et al. 2001; Kappeler and Pereira 2003). Life-history strategies, which are not only constrained but interact with phylogeny, demography and ecology deeply affect the viability of endangered primate populations (Strier 2003).

We recommend abandoning “fast vs. slow” characterizations of life histories and focus on more general theoretical structures such as energetic trade-offs and the life history mode in addressing how life histories should be empirically researched and used in the planning of conservation efforts. Demographic modeling, even with limited data, can provide valuable information on which life history traits should be targeted to impact population growth rates most favorably from a strictly biological standpoint. Field study of the variation in and covariation among life history traits in response to habitat change further inform such efforts, and morphological investigations of development serve to highlight how primates negotiate demographically important mortality risks in the face of trade-offs.

We emphasize that the little available data on life history and genetic changes in response to habitat fragmentation indicate differing reaction norms among species. Some species, such as howlers, cope adequately with fragmentation while others simply cannot and some of these differences relate to feeding ecology and social organization (Kowalewski and Zunino 1999; Clarke et al. 2002; Bicca-Marques 2003; Estrada et al. 2006; Muñoz et al. 2006; van Belle and Estrada 2006; Pozo-Montuy and Serio-Silva 2006; Zunino et al. 2007). We recommend concentrating conservation studies on the understanding of the total life history strategy across species and the potentially differing responses of populations within species.

5.6 Summary

We explore the connections among demography, life histories, and growth and development in primate evolution assessing responses to habitat change, with an emphasis on New World monkeys. An appreciation of life history, and particularly the relations between life history, morphology, and demography can contribute

solutions to vexing conservation problems and illuminate underappreciated adaptive diversity in New World monkey life histories. We briefly discuss demographic modeling, and relate how even very basic data can provide insights into understanding threats to populations. Second, we consider how patterns of morphological development impact the course of life history. Morphological analyses have traditionally played little role in either demographic analyses or conservation efforts, but our studies reveal considerable potential for morphology in understanding how life histories, and thus the basic demographic properties of populations, evolve. Finally, these dual foundations permit us to bring the concept of reaction norms to bear on conservation questions for primates in disturbed habitats. Throughout, we emphasize the limited value of a “fast vs. slow” perspective on life histories for conservation planning and understanding adaptation.

Appendix

Partial derivatives of λ with respect to the life history parameters in Charlesworth’s model (l_α , b , α , and P) can be obtained through implicit differentiation. The partial derivatives are the sensitivities of λ to each of the parameters, symbolized as $s(x)$ where x is the parameter in question. These are given below.

$$s(l_\alpha) = \frac{\partial \lambda}{\partial l_\alpha} = \frac{\frac{b\lambda^{-\alpha}}{1 - P\lambda^{-1}}}{\frac{l_\alpha b \lambda^{-\alpha} \alpha}{\lambda(1 - P\lambda^{-1})} - \frac{l_\alpha b \lambda^{-\alpha} P}{\lambda^2(1 - P\lambda^{-1})^2}} \quad (5.2)$$

$$s(b) = \frac{\partial \lambda}{\partial b} = \frac{\frac{l_\alpha \lambda^{-\alpha}}{1 - P\lambda^{-1}}}{\frac{l_\alpha b \lambda^{-\alpha} \alpha}{\lambda(1 - P\lambda^{-1})} - \frac{l_\alpha b \lambda^{-\alpha} P}{\lambda^2(1 - P\lambda^{-1})^2}} \quad (5.3)$$

$$s(\alpha) = \frac{\partial \lambda}{\partial \alpha} = \frac{\frac{l_\alpha b \lambda^{-\alpha} \log_e \lambda}{1 - P\lambda^{-1}}}{\frac{l_\alpha b \lambda^{-\alpha} \alpha}{\lambda(1 - P\lambda^{-1})} - \frac{l_\alpha b \lambda^{-\alpha} P}{\lambda^2(1 - P\lambda^{-1})^2}} \quad (5.4)$$

$$s(P) = \frac{\partial \lambda}{\partial P} = \frac{\frac{l_\alpha b \lambda^{-\alpha}}{\lambda(1 - P\lambda^{-1})^2}}{\frac{l_\alpha b \lambda^{-\alpha} \alpha}{\lambda(1 - P\lambda^{-1})} - \frac{l_\alpha b \lambda^{-\alpha} P}{\lambda^2(1 - P\lambda^{-1})^2}} \quad (5.5)$$

Elasticities can be obtained from the sensitivities by multiplying the sensitivity by the ratio of the parameter to λ .

$$e(x) = \frac{\partial \lambda}{\partial x} \frac{x}{\lambda} \quad (5.6)$$

Note that this multiplication results in $e(l_a) = e(b)$. An identical life cycle model and derivation of sensitivities can be found in Skalski et al. (2005).

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Chapter 6

Long-Term Field Studies of South American Primates

Karen B. Strier and Sérgio L. Mendes

6.1 Introduction

Field studies on South American primates have historically lagged behind those of Central American and Old World taxa, but research efforts on a variety of different taxa (e.g., *Alouatta*, *Aotus*, *Brachyteles*, *Callithrix*, *Cebus*, *Lagothrix*, *Leontopithecus*, *Saguinus*) have intensified over the last 25 years (Strier 1994; see also Estrada, this volume). Today, field studies on some populations of South American primates are approaching the longest-running Old World primate field studies in their multi-generational durations and in their empirical scopes (Strier 2003a). As a result, long-term studies of South American primates are contributing valuable comparative perspectives on the diversity of primate behavioral responses to ecological and demographic fluctuations.

In this chapter we review some of the key contributions that longitudinal studies on South American primates have made. We begin by considering the different kinds of data that different types of long-term studies can provide. Ecological and demographic changes can occur over a range of temporal scales, and they can have both immediate and persistent effects on behavior. Long-term studies can provide unique perspectives on the ways in which primates adjust their behavior in response to ecological and demographic fluctuations, and they are the only sources of information on life histories, which may mediate behavioral responses. Accumulating individual-based life history data require intensive, continuous research effort, and we therefore consider some of the trade-offs between these and other less intensive sampling protocols that can include a greater number of individuals and multiple groups.

We then review some of the factors that shape population dynamics of South American primates based on insights that have emerged from long-term field studies. We focus on variation in South American primate dispersal regimes and life history patterns, and how these affect population dynamics. The size, composition,

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