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## Life History

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## INTRODUCTION

And then increasingly, it was screaming at me, "These are the most interesting individuals; this has the greatest evolutionary impact; this is where the ecological pressures are". (Jeanne Altmann, interview with D. Haraway on baboon mothers and infants [Haraway 1989:312])

The events, transitions, and phases that occur during the life course are fundamental to the diversity of life (Raff 1996). Primates are especially interesting in this regard, presenting a fascinating array of variation in terms of changes that occur during life. A special class of theory, termed *life history theory*, explains the evolution of changes during the life course by analyzing demography, genetics, behavior, and morphology in a developmental and, typically, quantitative context (Lande 1982; Roff 1992, 2002; Stearns 1992; Charnov 1993). Most broadly, life history theory includes "not only the age-specific fecundity and mortality rates, but the entire sequence of changes through which an organism passes in its development from conception to death" (Lande 1982:608).

## THEORETICAL CONTEXT OF PRIMATE LIFE HISTORY

Life history studies have a long tradition in both primatology and biological anthropology, manifested by several distinct research "lineages." The first theoretical focus owes much to Jeanne Altmann's interest in baboon infants and their mothers, with projects centering on long-term field studies such as the Amboseli Baboon Project (J. Altmann 1980, S. Altmann 1998, Altmann and Alberts 2002, Silk et al. 2003), the Cayo Santiago rhesus macaque colony (Sade et al. 1985), and Jane Goodall's (1986) chimpanzee research at Gombe. These studies couple information on vital population parameters (e.g., birth and death rates) with fine-grained behavioral observations on the day-to-day lives of study subjects. A second research area explores human life histories, concentrating on how an apparently distinctive set of human demographic and ontogenetic characteristics might have evolved (Bogin 1999, Hawkes et al. 2002, Hill and Hurtado 1996, Kaplan et al. 2000, Leigh 2001). Studies of human life histories also utilize both demographic and behavioral data, but many studies also consider patterns of somatic growth in relation to demography, behavior, and culture. In this chapter,

we emphasize a third research tradition that highlights interspecific comparisons of ontogenetic and *allometric* (size-related) variation in life history traits. Studies here focus on key events in life histories, such as birth, age at maturation, birth rates, and longevity, to understand how evolutionary forces shape the life courses of primates (Harvey et al. 1987; see also Godfrey et al. 2002, 2004; Harvey and Clutton-Brock 1985; Martin 1983, 1996; Martin and MacLarnon 1990; Ross 1988, 1991, 1992, 2002, 2004; Ross and Jones 1999; Shea 1987, 1990). This perspective departs somewhat from theoretical priorities on genetic and demographic data in traditional life history theory, which emphasize measures of heritability and rates of gene substitution in populations (Stearns 1992). However, these approaches are compatible, and their interrelations have received some theoretical treatment (e.g., Charnov 1993). We stress theoretical developments and current ideas that emerge from interspecific analyses but briefly incorporate advances from other research areas and explore ways in which genetic and demographic insights articulate with interspecific analyses.

## HISTORICAL CONSIDERATIONS

Research conducted in the late 1970s through the 1980s marked a transition in studies of primate life histories (Martin 1983, Harvey and Clutton-Brock 1985, Harvey et al. 1987). Prior to this period, such studies focused most on comparative analyses of human growth and development (Gavan and Swindler 1966, Schultz 1969, Watts and Gavan 1982). Adolph Schultz made major contributions to this tradition, encapsulated by his often-repeated line drawing that shows "progressively" extended life stages in primates (1969:Fig. 57). The figure shows unidimensional, evenly proportioned, and progressive increases in each life stage during primate evolution, conveying the erroneous impression that primate life histories follow an orderly, orthogenetic, and unilinear advance. Schultz's view was consistent with bioanthropology's focus on evolutionary trends prior to the 1960s. However, cladistic thinking showed flaws with this and other "trends" by revealing that several "trends" were, in fact, independently evolved similarities (*homoplasies*) (see Leigh 2001).

Unfortunately, advances in biogeography, particularly the concepts of *r* and *K* selection, seemed to reinforce Schultz's

schematic (MacArthur and Wilson 1967, Pianka 1970). These ideas found rapid deployment in bioanthropology, particularly in studies of human evolution. For example, the late Stephen Jay Gould (1977) promoted the idea that K selection produced a slowing of developmental change during the course of evolution. Similarly, Owen Lovejoy's (1981) influential model linked early hominin monogamy with life history, explicitly invoking r-K selection theory under Schultz's orthogenetic scheme. Regrettably, these theoretical turns came at the expense of more powerful genetic and demographic concepts, advanced mainly by George C. Williams, that emphasized the unequal force of selection throughout the life span (1957, 1966a; see also Lack 1954; Medawar 1946, 1952). Differences in the effects of selection could explain diversity in the attributes of life stages, especially how genes deleterious late in life, including those producing senescence, could become fixed in populations. Senescence and diminishing reproductive output might occur because genes with tiny advantages during phases of relatively high reproduction can be selectively favored during these phases and, thus, increase in frequency. However, such genes may have detrimental effects later in life, with little consequence from selection because of low reproductive output. This basic insight imbued life history theory with ideas of genetic trade-offs (antagonistic pleiotropy), juvenile phases, and risks of juvenility. The notion of trade-offs is fundamental to life history theory, particularly when formalized by the concepts of reproductive value (Fisher 1930) and residual reproductive value (Williams 1966b). A *trade-off* means that energy invested in one area impacts, and usually limits, expenses in other areas. For example, an investment in a current offspring, like delaying weaning, may limit investment in future offspring.

The ideas of Williams, Fisher, and Medawar seem to have gone unrecognized in early primate life history studies, probably owing both to priorities established by Schultz and to the general appeal of r and K selection. Primates are long-lived relative to other mammals (Austad and Fischer 1992, Flower 1931, Prothero and Jürgens 1987), a finding superficially consistent with r-K ideas. In addition, the suggestion that the brain served as a pace-setter of life histories was consistent with r and K selection. In this model, larger brains were associated with greater longevity by increased "precision of physiological regulation" (Sacher 1959:129, Sacher and Staffeldt 1974; see also Allman and Hasenstaub 1999, Deaner et al. 2002). This suggestion had obvious implications for an order classically defined in part by a trend toward large relative brain size (Le Gros Clark 1959, Martin 1983, Shea 1987), but it relied upon an ageing paradigm uninformed by Williams' ideas.

Influential analyses in the 1980s marked a change in primate life history perspectives, although these analyses worked within a general framework that derived mainly from the traditions of Schultz and biogeography (Harvey et al. 1987). These studies concentrated on questions relating primate life history to brain and body size, but they also

presented data enabling researchers to test novel hypotheses and raised awareness of statistical complications posed by phylogeny. Harvey et al. assembled large databases representing estimates of "life history variables" for many primate species. Variables included markers of time points or intervals (gestation length, weaning age, age at maturation, age at first breeding, interbirth interval, and maximum recorded life span) and morphological variables (adult brain size, neonatal brain size, adult body size, and neonatal body size). They interpreted significant statistical variation among species as an outcome of evolutionary changes in body size, given high correlations between mass and other variables. Analyses of these data suggested considerable complexity in the relations of brain size to life history. Specifically, brain size and maturation age seemed to be linked, but further analyses indicated that this correlation reflected prenatal factors to a greater degree than postnatal factors. Essentially, later-maturing species have larger-brained infants, but the majority of brain growth seem to occur prenatally in larger-brained species. The mechanistic bases and implications of these correlations for life history have been difficult to comprehend fully and unambiguously (see below).

## POPULATION DYNAMICS AND PRIMATE LIFE HISTORIES

Despite Harvey et al.'s (1987) major advances, several areas of theoretical concern went unaddressed. Perhaps most importantly, while the article drew inspiration from population biology, it neglected questions regarding demography, quantitative genetics, and developmental biology. Fortunately, an influential study, published by Caroline Ross (1988), made a major step in this direction by merging comparative approaches with ideas about population dynamics codified by Cole (1954). Specifically, Ross (following Hennemann 1983, 1984) solved for  $r$ , the intrinsic rate of natural population increase (Table 23.1), by measuring key variables (age at maturation, age at death, and birth rate) from published studies of many primate species. She suggested that values for each species provided a measure of maximum possible reproductive output ( $r_{\max}$ ). Ross discovered that species with low body mass tended to have high  $r_{\max}$  values, while large-bodied species had low values (Pearson product-moment correlation  $r = -0.869$ ). The details of this correlation implied to her that the general idea behind r and K selection may hold for primates. Specifically, given the pattern of high  $r_{\max}$  residuals from species designated as occupying "unpredictable" habitats, she suggested that such species tended to be r-selected. Covariation between  $r_{\max}$  values and environments thus seemed to fit basic predictions of r and K selection.

Despite these important findings, some results were tenuous. Our objective in pointing this out is not to diminish Ross' important research. Rather, we wish to recognize limitations of r and K selection for primates and follow Ross in

**Table 23.1** Important Life History Equations

Equation 1: Cole's equation, used by Ross (1988) for primates:

$$1 = e^{-r} + be^{-r\alpha} + be^{-r(n+\alpha)} \quad (1)$$

In this equation,  $e$  is the base of the natural logarithm,  $\alpha$  is age at first reproduction,  $b$  equals the birth rate of female offspring,  $n$  is estimated by calculating  $\omega - (\alpha + 1)$  (where  $\omega$  = age at last reproduction), and the value of  $r$  is estimated through iteration (Cole 1954:eq. 21).

Equation 2: Euler-Lotka or characteristic equation:

$$\int_0^{\infty} l(x)m(x)e^{-rx}dx = 1 \quad (2)$$

This equation summarizes population rates of age-specific survivorship,  $l(x)$  and production of female offspring,  $m(x)$ , for age  $x$  and measures the intrinsic rate of population increase ( $r$ ).

Equation 3: Algebraic expression of the Euler-Lotka equation:

$$\sum_{x=0}^{\omega} l(x)m(x)e^{-rx} = 1 \quad (3)$$

this regard (Ross and Jones 1999; see also Stearns 1992). First, the measure of habitat predictability employed was imprecise, being derived from a tertiary literature source (see Ross 1992 for improved habitat estimates). Second, the association between higher relative  $r_{\max}$  values and habitat predictability was modest at best, being represented by positive residual values that overlapped entirely with data points from species found in "predictable" habitats. In fact, a species occupying a predictable habitat seemed to present the highest positive residual  $r_{\max}$  value. Third, as with most studies at this time, phylogenetic adjustment methods could only roughly counter effects of phylogeny. More recent analyses that include phylogenetic adjustments show "no significant links" between habitat and measures of reproductive rate (Ross and Jones 1999:94).

Ross' original analysis, despite these difficulties, was extremely important because it incorporated Cole's research (1954) and that of demographically oriented theoreticians (Blomquist in press) into considerations of primate life histories. Unfortunately, it seems simultaneously to have reified  $r$  and  $K$  selection among primatologists. The role of  $r$ - $K$  selection is sometimes abstracted by the catchy phrase that primates experience "slow" life histories, with some occupying slower "lanes" than others, with variation among species described along a "fast-slow continuum" (Ross 1992:383, Kelley 2004, Promislow and Harvey 1990). In any case, the inclusion of ideas about population dynamics and life histories significantly advanced the field, sustaining many further theoretical developments and forcing a reconsideration of the brain's role in primate life history.

### EMERGENCE OF THEORETICAL DIVERSITY

Ross' studies were complemented by two influential life history theory texts published in 1992 (Roff 1992, Stearns

1992). Charnov's theoretical monograph (1993) and two major edited volumes devoted to primate life histories and juvenility (DeRosseau 1990, Pereira and Fairbanks 1993) supplemented these works, as did quantitative analyses at the population level (Sade 1990, Stucki et al. 1991). Moreover, phylogenetic adjustment techniques advanced tremendously (Felsenstein 1985, Garland and Adolph 1994).

Volumes by Roff (1992, 2002) and Stearns (1992) ground contemporary life history theory firmly in the ideas and methods of demography and quantitative genetics. This foundation derives directly from R. A. Fisher's (1930) interest in the demographic dimensions of the maintenance of genetic variation in populations. As Stearns notes, the main idea is that demographic methods facilitate a concern with "marginal effects of gene substitutions, not with numbers of organisms in a population" (1992:21). Stearns' six-point "rejection of  $r$  and  $K$  selection" is an exceptionally valuable contribution (1992:206–207). In showing the limitations of this idea beyond biogeographic studies, Stearns advocates a life history paradigm shift from the idea (latent in  $r$ - $K$  selection theory) of direct habitat effects on life history (habitat  $\rightarrow$  life history) to that of habitat  $\rightarrow$  mortality regime  $\rightarrow$  life history (1992:208). In a related advance, DeRousseau argued that a life history perspective differs considerably from traditional approaches to evolution, relaxing many of the simplifying assumptions of the evolutionary synthesis by introducing sex and, in particular, age structure to populations (1990; see also Shea 1990).

These advances set the stage for an especially active period of theory construction in life history studies that improve our understanding of primate life history variation. We review key theories and briefly consider the problem of trade-offs and the calibration of trade-offs in primate life histories. While not a theory per se, the problem of trade-offs requires more extensive theoretical and empirical investigation. Trade-offs may be especially important for long-lived organisms such as primates and have considerable relevance for understanding the evolution of human life histories (Hawkes et al. 2002). We use this review to point to new ways of exploring primate life histories.

### Charnov and Life History Invariants

Models formulated in the early 1990s are still debated, as are long-standing ideas about learning and the brain as a direct pace-setter of life history (Allman and Hasenstaub 1999, Leigh 2004, Ross and Jones 1999, Sacher 1959, Sacher and Staffeldt 1974). These models have generally undergone initial rounds of empirical testing with primate species (Ross and Jones 1999), but critical evaluation of alternative life history models shows that much research remains to be done. A major theoretical development was the integration of optimality theory and comparative data in Charnov's life history invariants model (Charnov 1991, 1993; Charnov and Berrigan 1993; Berrigan et al. 1993). Charnov argued that primate life histories are impacted by a single

trade-off between delaying reproduction to increase body size (an investment offset by higher fecundity) and the risk of mortality during the waiting period prior to reproduction. Primates could grow for a long time, to enjoy larger size and higher fecundity; but the risk of dying limits the degree to which they can delay reproduction. Mathematically, the model proposes that  $dM/dt = AM^{0.75}$ , where  $M$  is the mass of either a growing (female) individual or an adult,  $dM/dt$  is the growth rate or annual litter mass, and  $A$  describes the height of the production function. The *production function* describes the fraction of total energy put into either growth or reproduction. Growth, by definition, ceases at maturity, diverting energy from adding body mass (growth) into producing offspring. Externally imposed adult mortality rates set the optimal age of maturation, circumscribing an optimal body size. Optimal maturation age is also conditioned by the reproductive benefits of larger size, which translates to higher levels of energy available for production. Finally, juvenile mortality is assumed to be density-dependent and keeps populations stable ( $R_0 = 1$ ) (see Mylius and Diekmann 1995 for problems of this assumption).

Empirical analyses of Charnov's model indicate exceptionally low values of  $A$  for primates ( $A = 0.42$ ), with  $A = 1$  for other mammalian taxa (Charnov 1993). So, for primates, the amount of energy allocated to either growth or reproduction is small. This forces primate females to spend much time growing until they reach sizes large enough to produce offspring efficiently. Consequently, they grow for longer time frames and produce fewer offspring than other mammals. Comparatively low mortality should mean that primates have the opportunity to live longer, achieving sufficient fitness to compensate for lost reproduction during long preadult periods.

A powerful element of Charnov's (1993) model lies in its potential to fuse growth or ontogenetic phenomena to population dynamics. Charnov demonstrates the compatibility between these fields by deriving the value of  $A$  through several different means. For example, he shows that the value of  $A$  can be calculated directly from data that describe ontogeny, including size at weaning ( $\delta$ ), body mass at maturation, and age at maturation (Charnov 1993: eq. 5.3). However,  $A$  also emerges from population dynamics, such as his value of  $A_3$ , obtained by estimating the height of a

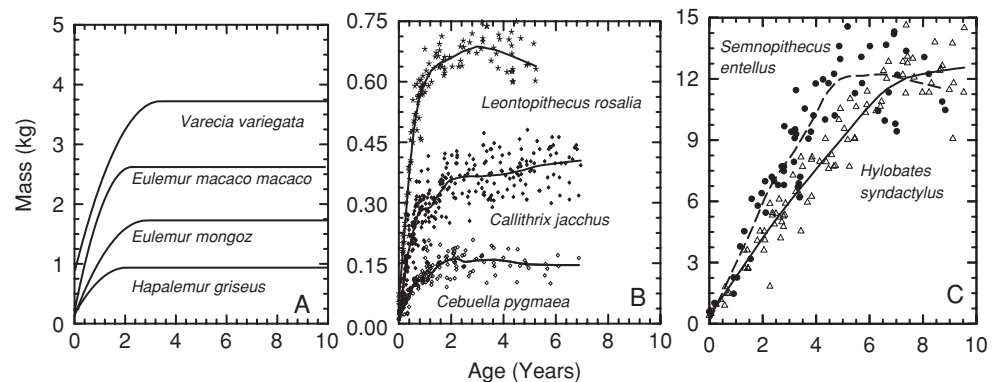
regression line of Ross' (1992)  $r_{\max}$  against body size (Charnov 1993: Fig. 6.4, Charnov and Berrigan 1993). Articulations between ontogenetic and population dynamic perspectives are significant because they tie ontogenetic patterns, particularly aspects of growth and developmental energetics, directly to population growth parameters. Consequently, the impact of life history variation on individual fitness can be assessed with respect to population dynamics. Finally, Charnov and Berrigan bluntly question life history models that involve the brain (1993; cf. Deaner et al. 2002, Ross 2002), contrasting with older models (Sacher 1959, Sacher and Staffeldt 1974; see also Allman and Hasenstaub 1999, Kelley 2004).

Empirical tests of Charnov's model among mammals (Purvis and Harvey 1995) and within primates (Ross and Jones 1999) support some of its predictions but reveal a number of deficiencies, at least given available comparative data sets. One particular prediction of Charnov's model lacking empirical support is the invariance of mass at independence (weaning,  $\delta$ ) with adult mass (but see Hawkes et al. 2002). In addition, many of the simplifying assumptions of the original Charnov model have been criticized and reevaluated. The production constant  $A$  and constant exponent of about 0.75 permit evolutionary change in body size only through differences in duration of growth and do not allow for change in growth rates. However, primate growth rates vary substantially: some species reach different adult sizes in the same amount of time (Fig. 23.1A,B), but others reach the same size in different amounts of time (Fig. 23.1C) (Pereira and Leigh 2002). Charnov (2001) noted how changes in the exponent affect the scaling of body size and annual fecundity. Jones and MacLarnon (2001), applying Charnov's logic to analyses of bat life histories, found a higher exponent ( $\sim 1$ ) which still seemed to follow a power function relation with fecundity. Finally, a loose interpretation of Charnov's (1993) model could be construed as a restatement of r-K selection, possibly promoted by the subtitle of Charnov and Berrigan's article "Life in the Slow Lane."

### Juvenile Risks

The juvenile risk aversion model, proposed by Janson and van Schaik (1993), answers some questions unaddressed by

Figure 23.1 Comparative body mass growth curves for strepsirrhines (A), platyrrhines (B), and catarrhines (C). Primates can reach the same size through differences in rates of growth, either with no difference in total growth time (A, B) or with a difference in growth duration (C). Data on females are shown for *Semnopithecus entellus*, but sexes are combined in these plots, given the absence of dimorphism in these taxa. In A, lines represent piecewise regressions (Leigh and Terranova 1998), but other lines represent lowest regressions (Leigh 1992).





Charnov's model, particularly growth rate variation among species. Their model also accommodates Williams' (1966a) notions about life stage duration and risk. Janson and van Schaik attribute the long period of primate juvenility to a low growth rate that serves as metabolic risk adaptation during ontogeny. Juvenile primates face a simultaneous trade-off between predation risks and the metabolic costs of feeding competition from conspecifics: they can forage at the center of groups, encountering competition from adult group members, or they can forage at the periphery, increasing their susceptibility to predators. Predators (and infanticide) should select against a low growth rate, favoring juveniles that grow out of harm's way (a constant growth rate is assumed for each species). On the other hand, growing rapidly raises metabolic risks because growth is metabolically costly as a result of protein turnover (Tanner 1978). Thus, feeding competition should favor a slow growth rate, especially if the metabolic expenses of growth mean that juveniles face disproportionately high costs of intra-group feeding competition. Juveniles face extra burdens if they forage less efficiently than adults. In this model, trade-offs involving predation pressure and possibly infanticide, contrasted with metabolic risks of feeding competition, select on growth rate. For primates, low growth rates seem to predominate, resulting in deferred maturation by forcing extended juvenile phases.

This model provides a compelling way to account for growth rate variation among primate species and follows from Williams' recognition that mortality risk conditions the pace of development, affecting either rates of morphological change, duration of high-risk developmental phases, or both. However, the model does not explain growth spurts or growth rate variability within a species (Leigh 1996). Analyses of restricted data sets show mixed support for the model, and field-based evaluations have been slow in coming. For example, growth patterns in leaf-eating anthropoids are consistent with the model (Leigh 1994), and variation among ape species aligns with its predictions (Leigh and Shea 1996). In contrast, neither small-bodied New World monkey growth (Garber and Leigh 1997) nor Malagasy lemur growth (Godfrey et al. 2004) seems to fit the model. A recent field study of *Saimiri sciureus* (squirrel monkeys) shows mixed support for components of the model. Juvenile squirrel monkeys experience negligible intraspecific feeding competition, and few differences in foraging proficiency occur across age classes. In squirrel monkeys, predation pressure seems to influence group dynamics, so elements of the model seem to fit (Stone 2004). Interspecific comparative analyses also show modest support for this model (Ross and Jones 1999).

### Body Mass Optimization

Kozłowski and Wiener (1997) modified Charnov's model, interpreting it as a special case of their own. Kozłowski and Wiener's computer simulations indicate that adult body mass is optimized within a species in response to ecological

parameters that affect the growth function. These ecological parameters can generate interspecific correlations between life history and morphological and physiological variables of body mass. These interspecific allometries are, however, epiphenomena of selection that act only within species to optimize body size. The model also predicts some recognized empirical patterns of growth rate scaling and species body mass distributions (Kozłowski and Galwelczyk 2002, Kindlerman et al. 1999). Most importantly, their research generally supports the idea, following Charnov, that age and size at maturity are strongly influenced by optimal resource allocations to either growth or reproduction. We expect difficulties in formulating critical tests between the Kozłowski-Wiener and Charnov models and note that applications to primates have yet to be undertaken.

### Charnov and Sigmoidal Growth

Charnov's (2001) recent model of mammalian life history evolution incorporates a sigmoidal growth law developed by West et al. (2001; but see Ricklefs 2003). In sigmoidal growth, rates of change follow a curvilinear pattern, much like an italicized letter *S*. Along with this somewhat more realistic assumption about growth, the model does not reflect reproductive output as merely diverted self-growth but as some proportion of it. Charnov proposes several new invariant relationships based on adult size and mortality, cellular maintenance costs, offspring production, and growth rate and age at adulthood. This model has not been subjected to empirical tests, and many of its predictions may be untestable until both accurate life tables and growth data are available on a large number of species.

### Life History Trade-Offs

The idea of a trade-off is fundamental to life history thinking. This concept requires treatment in the context of the present theoretical review because trade-offs are evident in these models and complicate attempts to test them. The basic problem is that fitness components (variables directly related to fitness like maturation age, interbirth interval, and litter size) cannot be individually maximized, which may lead to negative correlations among them. In other words, organisms face "decisions" of how, when, and in what proportions energy should be allocated to various fitness components and the physiological processes that impact these components. This produces classic patterns like the trade-off of current versus future reproduction or current reproduction versus survival (Fisher 1930, Williams 1966a). Furthermore, trade-offs may not act directly on reproduction and survival but can be mediated through other variables, such as body size (Roff 2002).

Perhaps the most significant problem in explaining primate life histories, especially human life histories, is that researchers have had difficulty in actually finding predicted trade-offs (Hill and Hurtado 1996). For example, humans,

and possibly other primates, do not show expected trade-offs between current and future reproduction, so it appears that the cost of current reproduction does not seem to reduce resources for future reproduction. New models are beginning to provide an answer to this paradox, by suggesting that variation in resource allocation and acquisition must be analyzed. Specifically, two conditions may obscure trade-offs. First, resource acquisition may be high enough to obviate trade-offs. Second, and more subtly, trade-offs may not be evident when variation in resource acquisition exceeds variation in allocation (van Noordwijk and de Jong 1986). *Variation in allocation* refers to differences in how organisms devote energy to either survival (e.g., body maintenance, size, condition) or reproduction. If there are huge differences in populations in terms of energy acquired but few differences in how it is allocated, then trade-offs may not be apparent at the population level.

Quantitative genetic models help resolve this, showing that trade-offs among fitness components may be obscured under two conditions. First, more genes may contribute to variation in acquisition than to resource allocation. Second, there could be greater variation at higher levels in an allocation hierarchy (Houle 1991, de Jong and van Noordwijk 1992, de Jong 1993, de Laguerie et al. 1993, Worley et al. 2003). For example, an organism may allocate a certain fraction of resources to reproduction with the remainder going to somatic maintenance, but the fraction allotted to reproduction may then be subdivided among traits that are traded off against one another, such as offspring size and number. Establishing whether or not primates face such trade-offs is a crucial area of future research, requiring ecological, demographic, and quantitative genetic information.

## PATTERNS OF LIFE HISTORY VARIATION

This brief theoretical review establishes a context in which we can present summary analyses of life history correlations. Our objective is not to test various models. Instead, these

correlations offer empirical experience with the relevant data and show limitations of data used to analyze life histories. These deficiencies reveal a need for new kinds of data for testing and extending life history theories. They also raise questions about precisely how life history analyses should be conducted and interpreted.

Space limitations preclude detailed descriptions of data and methods. However, we use the most up-to-date source for interspecific data known to us (Kappeler and Pereira 2002:Appendix). This compendium includes carefully vetted sources for both adult and neonatal body mass data (Smith and Jungers 1997, Smith and Leigh 1998, respectively). We conduct analyses of both raw and phylogenetically adjusted estimates, with adjustments undertaken with independent contrasts computed through the PDAP module of Mesquite phylogenetic software (Maddison and Maddison 2004). Phylogenies utilized are modified from Smith and Cheverud's (2002) rendition of primate phylogeny. Statistically, species values are not independent data points, but standard statistical techniques can be used if we can measure of the degree to which data points are independent. In essence, phylogenetic adjustments account for the fact that we expect closely related species to share greater similarity than distantly related species. Controlling for phylogenies is essential in order to account for differences in the degree to which species are related. Throughout, we use Pearson product-moment correlations to measure associations on both kinds of data.

Correlation estimates are consistent with numerous previous studies of primate life history variation (Table 23.2). However, phylogenetically adjusted correlations document surprisingly weak associations among certain variables traditionally regarded as fundamentally important (Table 23.2). For example, the correlation between age at reproductive maturation and body size, measured in Harvey et al.'s (1987) study at  $r = 0.92$ , diminishes to  $r = 0.059$  given our phylogenetic adjustment. Ross and Jones (1999) report a higher adjusted value ( $r = 0.42$ ), estimated after a special statistical procedure (trimming contrasts among terminal nodes, which may be problematic).

**Table 23.2 A: Correlations Estimated by the Current Study with Values Published by Kappeler and Pereira (2002:Appendix)**

	ADULT BODY MASS (G)	ADULT BRAIN MASS (G)	AGE AT FIRST REPRODUCTION (YEARS)	GESTATION LENGTH (DAYS)	INTERBIRTH INTERVAL (MONTHS)	LITTER SIZE	NEONATAL MASS (G)	WEANING AGE (DAYS)	NEONATAL BRAIN MASS (G)
Adult body mass (g)	–	0.961	0.881	0.683	0.821	–0.579	0.960	0.860	0.973
Adult brain mass (g)	0.846	–	0.898	0.707	0.745	–0.465	0.968	0.865	0.989
Age at first reproduction (years)	0.059	0.202	–	0.727	0.829	–0.571	0.914	0.861	0.948
Gestation length (days)	0.484	0.429	0.074	–	0.604	–0.537	0.735	0.733	0.760
Interbirth interval (months)	0.389	0.342	0.345	0.394	–	–0.400	0.779	0.813	0.837
Litter size	–0.149	–0.191	–0.023	–0.198	0.040	–	–0.647	–0.560	–0.633
Neonatal mass (g)	0.798	0.867	0.255	0.386	0.277	–0.280	–	0.879	0.987
Weaning age (days)	0.366	0.207	0.055	0.328	0.436	–0.118	0.404	–	0.872
Neonatal brain mass (g)	0.891	0.972	0.714	0.454	0.402	–0.488	0.853	0.574	–

Estimates above the diagonal represent unadjusted or “species” values, and estimates below the diagonal are adjusted using independent contrasts; raw data concern values for females unless otherwise noted.

**Table 23.2 B: Correlations Published by Harvey et al. (1987) (Based on Subfamily Data)**

	MALE ADULT BODY MASS (G)	GESTATION LENGTH (DAYS)	INDIVIDUAL NEONATAL MASS (G)	NUMBER OF OFFSPRING PER LITTER	WEANING AGE (DAYS)	AGE AT FIRST BREEDING (YEARS)	AGE AT SEXUAL MATURITY (YEARS)	MAXIMUM RECORDED LIFE SPAN (YEARS)	INTERBIRTH INTERVAL (MONTHS)	AGE AT SEXUAL MATURITY (MALE, YEARS)	NEONATAL BRAIN WEIGHT (G)	ADULT BRAIN WEIGHT (G)
Adult body mass (g)	0.996	0.74	0.97	-0.52	0.91	0.92	0.89	0.78	0.86	0.89	0.95	0.96
Male adult body mass (g)		0.73	0.97	-0.51	0.92	0.92	0.89	0.78	0.85	0.91	0.95	0.96
Gestation length (days)			0.82	-0.61	0.84	0.81	0.81	0.62	0.63	0.84	0.84	0.8
Individual neonatal mass (g)				-0.56	0.94	0.95	0.94	0.8	0.87	0.95	0.99	0.98
Number of offspring per litter					-0.56	-0.49	-0.47	-0.3	-0.41	-0.44	-0.51	-0.5
Weaning age (days)						0.9	0.92	0.7	0.89	0.93	0.89	0.91
Age at first breeding (years)							0.97	0.87	0.88	0.94	0.93	0.96
Age at sexual maturity (years)								0.83	0.85	0.96	0.95	0.94
Maximum recorded life span (years)									0.72	0.78	0.82	0.85
Interbirth interval (months)										0.83	0.86	0.86
Age at sexual maturity (male, years)											0.97	0.96
Neonatal brain weight (g)												0.99

**Table 23.2 C: Correlations Published by Ross and Jones (1999) Comparing Body Mass to Other Variables**

	Body Mass	
	SPECIES VALUES	INDEPENDENT CONTRASTS
Length of Juvenile Period (years)	0.71	0.60
Birth rate	0.81	0.60
$R_{max}$	0.89	0.65
Age at first reproduction (years)	0.87	0.42
Average instantaneous adult mortality rate	0.22	0.32
Prereproductive mortality rate	0.41	0.20
Average infant mortality rate	0.37	0.46
Survival to reproductive age	0.16	0.35

### RETHINKING PRIMATE LIFE HISTORIES

Our review points to problems with theories, models, and empirical analyses that can be solved by new approaches to life history problems. Both the ontogenetic and population dynamic sides of the field require critical theoretical examination, but we prioritize ontogenetic studies. Recent theoretical advances in developmental biology (Raff 1996) have yet to be considered by life historians but provide important insights into life history problems. More specifically, developmental biology sees animal development as modular,

with dissociation among developing parts playing a major role (Raff 1996, Raff and Raff 2000). *Modularity* means that morphological structures or organ systems may vary in the degree to which they are interrelated during development. Therefore, different levels of correlation, integration, and interaction among tissues should be expected during ontogeny. This means that different organs or organ systems may grow over separate age spans and at very different rates (i.e., they may be dissociated during ontogeny).

Dissociation of morphological structures causes the emergence of particular patterns or modes of ontogeny during development. These modes are mediated by adjustments in the growth of metabolically expensive tissues (e.g., the brain) so that there may be various ways of being a juvenile. The “fast versus slow” continuum that has dominated discussion of primate life histories does not account for these different modes and, thus, appears to be inaccurate. The emerging view of primate life history is much more complicated than is revealed by the “fast versus slow” perspective so that understanding life histories requires high-quality developmental data.

In this view, dissociation of developing structures is especially important for primates because of their extended life spans. Primate longevity may be a benefit conferred by life in the trees (or at least, typically, not on the ground [Austad and Fischer 1992]). Bats and birds also have relatively long life spans (Williams 1957), but developing anatomy for flight may actually favor reduced juvenile periods. In terrestrial taxa, selection probably favors a short

developmental period coupled with a very rapid shift of energetic resources from growth to reproduction, especially if juvenile mortality is high (Williams 1966a,b). We further expect few opportunities for dissociation and the emergence of life history modes in these taxa, so these species should meet the assumptions of Charnov's model well. In primates, life history modes minimize risks from energetic competition between still-growing structures and offspring production, offering flexibility as to when to grow different structures and when to complete the juvenile period. Reduced primate mortality provides opportunities for the evolution of diverse patterns of development, depending on energetic risks and mortality profiles at different stages. Therefore, instead of a "fast-slow continuum," "modes" and phases characterize primate life histories (see Pereira and Leigh 2002, Leigh and Bernstein in press). We define a *life history mode* as a distinctive pattern or arrangement of ontogeny with respect to the rate and scheduling of growth for various organs, organ systems, or modules.

Unfortunately, the theoretical infrastructure devoted to modularity in life history remains underdeveloped, as lamented by Stearns over a decade ago (1992, see also Watkinson and White 1985). Despite these difficulties, it is important to note that previous primate life history theory tends to assume, either implicitly or explicitly, that primate life histories are tightly integrated, with low dissociation and minimal modularity (e.g., Kelley 2004). High interspecific correlations reported by previous studies but shown to be problematic by the current study are at the heart of this interpretation. In addition, correlation studies virtually always lack true ontogenetic dimensions, blinding them to modularity. Correlation studies assume that all structures cease growth synchronously at the age of reproductive maturation. In contrast, ontogenetic studies accommodate variation in pathways through the juvenile period that arise from modularity. Moreover, an ontogenetic view incorporates ideas about metabolic risks and extrinsic mortality (Janson and van Schaik 1993, Williams 1966a).

We expect that alternative life history modes among primates have evolved in response to combinations of metabolic risks and differences in mortality at various phases of life histories. This idea relies on classic trade-off theory, anticipating that organisms face "decisions" as to how and when to allocate effort to growth and reproduction. We suggest that the situation for primates is more complicated than this, involving hierarchies of trade-offs. Specifically, a relatively lengthy period of primate ontogeny means that primates (including humans) have options (unavailable to other species) regarding energy allocation among modules. Three factors in primate energy allocation may be important. First, energy allocation may follow temporal patterns, involving a simple energetic shift from growth to reproduction, as predicted by classic theory. Second, dissociation may enable trade-offs among modules, with expensive tissues growing during ages of relatively low risk. Third, variation in total body mass growth rates may mediate energy allocation.

Obviously, different combinations of these factors may play roles, but the important point is that the idea of a life history mode captures these different ways of arranging ontogeny and, thus, of "assembling" adults.

## THE BRAIN AND MODULAR LIFE HISTORY

A cursory empirical example focusing on the brain illustrates advantages of the life history mode concept (see Leigh 2004, Leigh and Bernstein in press, Pereira and Leigh 2002 for additional examples). Full documentation of modular ontogenies mandates analyses of many species and several organ systems, or structures (modules). However, consideration of body and brain size growth can provide preliminary insights into this idea. First, body mass growth rates vary substantially among species to produce comparably sized organisms (Fig. 23.1). Growth rates also fluctuate (Leigh 1996) so that, when measured by the progression of size, life histories can consist of both "fast" and "slow" phases. Different combinations of these phases imply alternative pathways through the juvenile period. Second, turning to the brain (and mindful of editorial space limitations), we assume the brain is an energetically costly module that is responsive to selection partly on metabolic performance (Aiello and Wheeler 1995).

Brain modularity can be illustrated by summarizing analyses of brain growth in relation to key life history variables. Our example tests the hypothesis that the age at brain growth cessation, adult brain size, and age at reproductive maturation are tightly intercorrelated. Rejection of this hypothesis implies that modularity plays a role in primate life history evolution, while failure to reject it supports models that see the brain as a pace-setter of life histories (see also studies by Deaner et al. 2002; Ross 2002, 2004; Ross and Jones 1999; Sacher 1959; Sacher and Staffeldt 1974). Moreover, this test has significant implications for refining ideas proposed by Martin (1983, 1996; Harvey et al. 1987) that reveal ties between gestation, maternal reproductive or energetic effort, brain size, and life history.

Ontogenetic data for brain size can be gathered for only a handful of species. We follow procedures outlined previously (Leigh 2004), which involve estimating age at brain growth cessation, then compare these estimates against adult brain size and literature-reported estimates of age at reproductive maturation. We present both raw and phylogenetically adjusted correlations. The latter correlations take into account differences in degrees of relatedness among species.

Evaluations of brain growth curves reveal variation independent of reproductive maturation age. An especially obvious case concerns comparisons between squirrel monkeys (*S. sciureus*) and tamarins (*Saguinus fuscicollis*). Brain growth curves show that the former grow brains at higher rates than the latter but over a much shorter age interval (Fig. 23.2). Moreover, squirrel monkey brains and bodies are larger as adults than those of tamarins, with squirrel monkeys reaching reproductive maturation later than tamarins (Garber



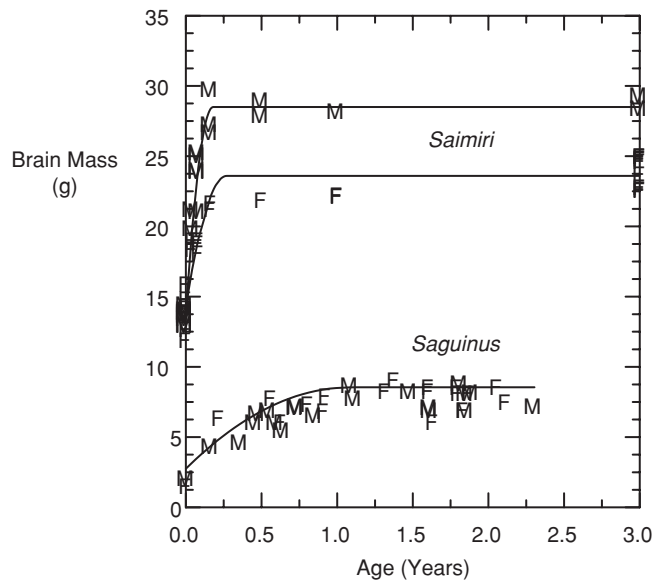


Figure 23.2 New World monkey brain growth trajectories. Squirrel monkeys (*Saimiri sciureus*) cease brain growth earlier than saddle-back tamarins (*Saguinus fuscicollis*). Lines represent best-fit piecewise regressions. M, males; F, females. Sexes are combined in the tamarin sample. See Leigh (2004) for details on data utilized.

and Leigh 1997). Chimpanzees and humans provide another clear example, showing major differences in brain size produced by different growth rates (Fig. 23.3). Major distinctions in total time of brain growth are difficult to discern between these species, despite differences in brain size, age at reproductive maturation, age at body mass growth cessation, and adult body size. Both comparisons indicate some level of independence of brain and somatic growth.

Statistical analyses for a larger sample show that adult brain size and age at reproductive maturation are strongly correlated (Fig. 23.4A,  $r = 0.93$ ) and that age at brain growth cessation and age at reproductive maturation are correlated (Fig. 23.4B,  $r = 0.64$ ). Phylogenetic adjustment does not greatly alter the first correlation (brain size and reproductive maturation age,  $r_{\text{adj}} = 0.70$ ), but the latter correlation evaporates ( $r_{\text{adj}} = 0.12$ ).

Our small sample size presents obvious limitations. Nevertheless, these results refute models that designate the

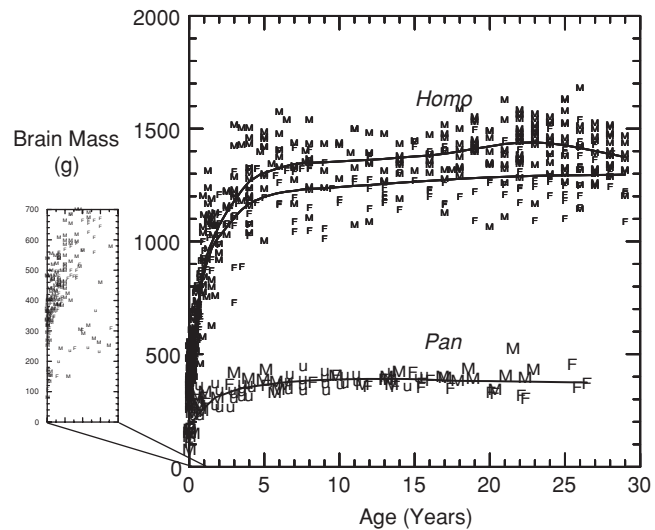


Figure 23.3 Brain mass growth data for humans (*Homo sapiens*) and chimpanzees (*Pan troglodytes*). Lines represent best-fit loess regressions through data. Symbols represent females (F), males (M), or unrecorded (u). The inset shows brain mass growth for each species during the first postnatal year. See Leigh (2004) for details on data utilized.

brain as a direct pace-setter of life histories. The time it takes to grow a brain and the length of the juvenile period are unrelated. However, these results point toward models that see roles for energetics and risk aversion in driving life history variation. Specifically, adult brain size and reproductive maturation age are correlated, no matter how we measure the association. This suggests indirect effects of brain ontogeny on both body size and reproductive maturation age. So, larger, faster-growing brains seem to require larger, later-maturing mothers (Leigh 2004). Species in which mothers invest relatively little in prenatal brain growth seem to produce offspring that grow brains slowly but through much of the postnatal period. In these cases, costs of brain growth are borne by the offspring itself; and in the specific case of tamarins, males and other group members subsidize offspring (Garber and Leigh 1997).

These results suggest a significant role for the brain in primate life history. Species that produce large-brained offspring during the prenatal period invest heavily and

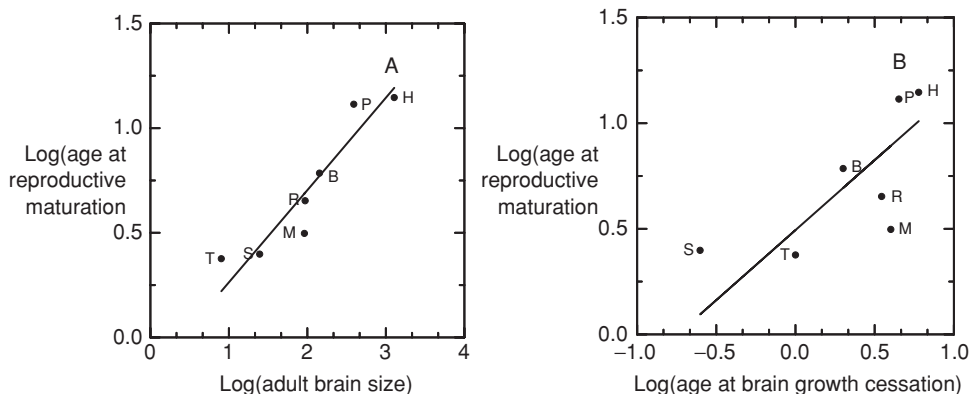


Figure 23.4 Regression analyses of brain attributes and age at reproductive maturation. A: Age at reproduction is highly correlated with adult brain size. B: Age at reproduction is also correlated with age at brain growth cessation, but the relationship is not as strong. Plot abbreviations are as follows: T, *Saguinus fuscicollis*; S, *Saimiri sciureus*; R, *Macaca mulatta*; M, *Lophocebus/Cercocebus* (mangabeys); B, *Papio*; P, *Pan troglodytes*; H, *Homo sapiens*. All values are measured on females.

“single-handedly” in brain size, a situation ameliorated by late maturation and large maternal size (see also Leigh 2004, Leigh and Bernstein in press), while other species mature early in part because of limited investment in prenatal brain growth. These inferences rely on Martin’s (1983, 1996) ideas tying brain size to life histories through maternal energetics (see Leigh 2004). Perhaps most importantly, these results suggest the potential for relating ontogeny to demographic views of life histories.

## PROSPECTUS

This chapter illustrates several key issues for the future of life history studies. First, we advocate a shift in life history studies toward ontogenetic data. Such data are absolutely essential to furthering our knowledge. We recommend a shift from the kinds of life history data analyzed by traditional studies to data that speak directly to ontogeny and development (see Shea 1990). A longitudinal perspective is likely to be especially valuable in this context (DeRousseau 1990) because it provides an opportunity to measure fitness consequences of events occurring prior to adulthood (see S. Altmann 1998). This perspective readily accommodates ideas about genetic trade-offs. Second, traditional interspecific comparative studies are not likely to add to what we currently know about life history evolution in primates. However, it is clear that such analyses serve as a valuable foundation for large-scale life history theories (e.g., Charnov 1993). These kinds of analysis also provide insights into historical processes (Shea 1987). Third, theoreticians should follow Charnov’s lead by investigating ontogenetic dimensions of maternal energetics, metabolic risk aversion, and differences in extrinsic mortality among phases of life history (including infanticide and predation) and the relation of these to population dynamics. This will require approaches that rely on quantitative genetics and demography. Fourth, we are sorely lacking in ontogenetic data from noncaptive populations. Recent analyses are beginning to solve this problem (S. Altmann 1998, Johnson 2003, Stone 2004). Future researchers must be well versed in both ontogeny and population dynamics to productively extend these theories. We can note that ontogenetic studies of captive samples are also necessary, particularly given new imaging technologies that will revolutionize studies of ontogeny. Taken together, these advances present significant opportunities to develop life history theories that accommodate both ontogenetic and population phenomena.

## CONCLUSIONS

Applications of life history theory to primates have generated significant insights at many levels. These theories prioritize understanding of how energetic resources are allocated either to growth or to reproduction and seek a general understand-

ing of the mechanisms responsible for patterns of allocation and resulting life histories. Theories reviewed here, including Charnov’s ideas, Janson and van Schaik’s risk aversion hypothesis, and Kozłowski and Weiner’s optimization model, all contribute to our understanding of primate life history evolution. However, this theoretical plurality implies possibilities for a more robust life history theory.

Improvements in life history theory rely on a better understanding of trade-offs and development of models that establish stronger links between ontogenetic processes, quantitative genetics, and demography. Moreover, explicit recognition of the paradigm established by Williams can aid in advancing contemporary primate life history theory. Specifically, greater attention to selection during all phases of life history (e.g., S. Altmann 1998, Johnson 2003) will improve our understanding of how changes during life evolve. Reconceptualizing primate life histories in terms of modes and phases offers new insight into patterns of variation across the primate order by fitting this priority more adequately than traditional approaches. Theories that address modularity of development may be especially valuable in promoting theoretical advances. Of course, the goal of better theory also relies upon generation and analysis of high-quality data from primate species and populations.

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