

University of New Mexico

## UNM Digital Repository

---

Biology Faculty & Staff Publications

Academic Department Resources

---

1-1-1993

### Why do primates have such long lifespans and so few babies

Eric Charnov

David Berrigan

Follow this and additional works at: [https://digitalrepository.unm.edu/biol\\_fsp](https://digitalrepository.unm.edu/biol_fsp)



Part of the [Biology Commons](#)

---

#### Recommended Citation

Evolutionary Anthropology 1:191-194

This Article is brought to you for free and open access by the Academic Department Resources at UNM Digital Repository. It has been accepted for inclusion in Biology Faculty & Staff Publications by an authorized administrator of UNM Digital Repository. For more information, please contact [disc@unm.edu](mailto:disc@unm.edu).

# Why Do Female Primates Have Such Long Lifespans and So Few Babies? or Life in the Slow Lane

ERIC L. CHARNOV AND DAVID BERRIGAN

A major goal of life history studies is to identify and explain features of the life history of individual species that follow broad rules across many groups of organisms, features that are characteristic of particular phylogenetic lineages, and features that are specific adaptations to local ecological situations. In recent years we have developed a general theory of life history that interrelates many aspects of ontogeny and reproduction across a wide range of organisms. Contrasted to most other mammals, primates have long average adult lifespans and few babies per year for their adult body size. This new theory suggests that these aspects of life history follow directly from the fact that primates have slow individual growth rates. This slow growth rate is thus the basic phenomenon that needs explanation to understand primate slowness.

As mammal life histories go, primates are slow. We grow up, reproduce, and die at a much slower rate than other mammals. Stated another way, our birth rates, death rates, and individual growth rates are roughly one-fourth to one-half those of other mammals with similar body sizes.<sup>1-9</sup> Figure 1 compares average adult lifespan and age of maturity (represented by age at first reproduction) for a wide range of primates and other mammals. The primate lines are well above those of other mammals and also seem to have steeper slopes, between .3 and .4, compared with slopes of between .2 and .3 for other mammals. This indicates that primates take

longer to reach maturity and have longer average lifespans for their body mass in comparison to other mammals. In this discussion we will ignore the differences in slope by assuming a central value of .3 for all mammals and concentrate on the differences between the height of the primate lines and those of the other mammals. Figure 2 compares the average number of daughters produced each year for primates compared to other mammals. Here the primate line is significantly lower. For our body size, we primates also produce fewer offspring per year than other mammals. Are these unusual life history characteristics of primates interrelated? If so, what is driving us to be so slow in growing, reproducing, and dying?

In terms of the energetics of growth and reproduction, the life history of any mammal can be divided into several distinct periods, as diagrammed in Figure 3. From birth (actually from conception) until weaning, the growth of a young mammal is dependent upon energy derived from its mother. The growth of an individual from weaning until adulthood (taken as the time of first reproduction) is part of the individual's own metabolic energy expenditure and can be modelled by the simple growth equation discussed

below. In general, the end of growth coincides with first reproduction and at this point in its life, an individual channels all of the energy it previously used for growth into producing offspring. Each of these periods has a characteristic mortality rate.

If the causal model described in Figure 3 is correct, the key to the slow primate life histories lies in the slow growth of juveniles, as demonstrated by the  $\alpha$  lines in Figure 1, because the energy allocated to growth also determines how much energy is allocated to reproduction later. Since  $\alpha$  has an allometric scaling of approximately .3 with body weight, we can model individual growth after weaning as a production allometry of .7:

$$\frac{dW}{dt} = A \times W^{.7}$$

where  $W$  is weight prior to and at maturation,  $A$  is the height of the production rate function, and  $dW/dt$  is the production energy (Fig. 3). Because mammalian total metabolic rates are roughly proportional to  $W^{.7}$ , this is analogous to saying that the energy used for growth is a fixed fraction of an animal's total metabolic budget at any given size. This equation can be solved for  $W$  at any age, generating the  $\alpha$  (age at maturity) versus  $W$  (adult body mass) of Figure 1. The allometric relationship between  $\alpha$  and  $W$  in Figure 1 allows us to estimate  $A$ , the height of the postweaning production function. Since primates take longer to reach a given size than do other mammals, the height of their production function must be less. Using the  $\alpha$  lines in Figure 1 to estimate  $A$ , we find that  $A$  is .42 for primates, whereas it is approximately 1 for other mammals.<sup>6</sup> The estimates are derived only from

Ric Charnov is Professor of Biology and Adjunct Professor of Anthropology at the University of Utah, Salt Lake City, Utah. His interests include foraging decision theory, life history theory, and the theory of sex allocation. These topics are explored further in his upcoming book, *Life History Invariants* (1993, Oxford). David Berrigan is a graduate student in biology at the University of Utah. His interests include life history evolution, particularly its interaction with production/metabolic physiology, and the comparative method.

Key Words: Life history theory, growth, reproduction, metabolism

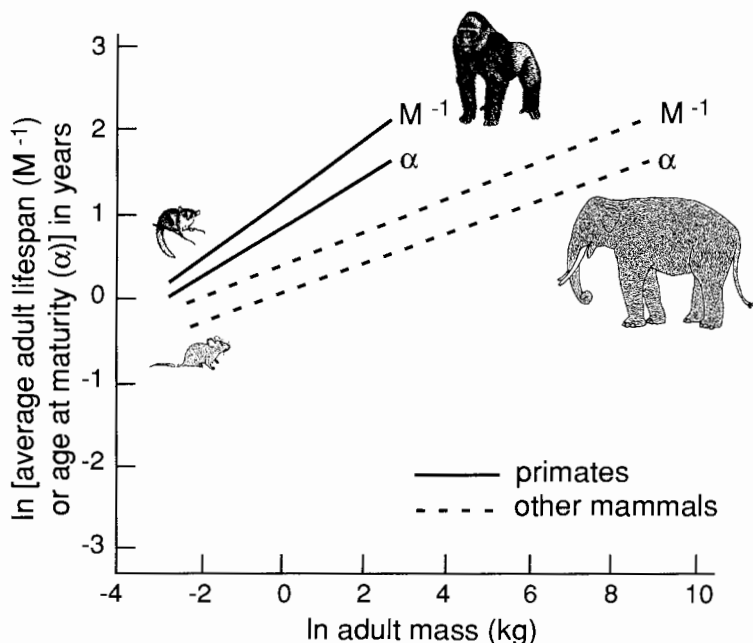


Figure 1. Allometries for age at first reproduction ( $\alpha$  measured from weaning to age at first birth) and average adult lifespan (the inverse of the average adult instantaneous mortality rate,  $M$ ) for primates versus other mammals.  $\alpha$  data from refs. 1 and 9; life table data from ref. 9, with  $M$  estimates in refs. 5, 6 for typical mammals.  $M$  estimated for primates from zoo maximum lifespan ( $T_{max}$ ) data in ref. 4 combined with a calibration equation linking  $M$  to  $T_{max}$ , as developed in Figure 5.6 of ref. 6.

data for growth after weaning since, prior to weaning, growth is assumed to be supported by the mother's metabolism.

According to our model, growth ceases at adulthood and the produc-

tion energy ( $dW/dt$ ) is then channelled into offspring. From conception to independence (weaning), the rate of growth is limited by the mother's ability to deliver energy to her offspring; in this model she is allowed to deliver

energy to offspring at the same rate she utilized energy when she herself was growing ( $A \times W^7$ , where  $W$  is her adult weight). At any adult body size, a female primate has much less production to give to her offspring since  $A$  for primates is about 40% that of other mammals. On average, primates are like other mammals in weaning each offspring when they reach about one-third their adult weight.<sup>5,6,10</sup> The low production rate ( $A$ ) means that young primates spend longer reaching that weight and thus the number of daughters reared each year ( $b$ ) must be smaller. How small the number of offspring produced turn out to be depends on details such as how efficiently infants can use the resources provided by their mother for growth, and so forth. Rough calculations indicate that the yearly offspring numbers ( $b$ ) in Figure 2 for primates and other mammals are displaced by approximately the amount predicted by the differences in the value for  $A$  in the production rate equation.<sup>6</sup> Thus, according to our life history theory<sup>5,6</sup> offspring number ( $b$ ) in primates is lower relative to body size because the coefficient of the general rate of "growth production" ( $A$ ) is smaller.

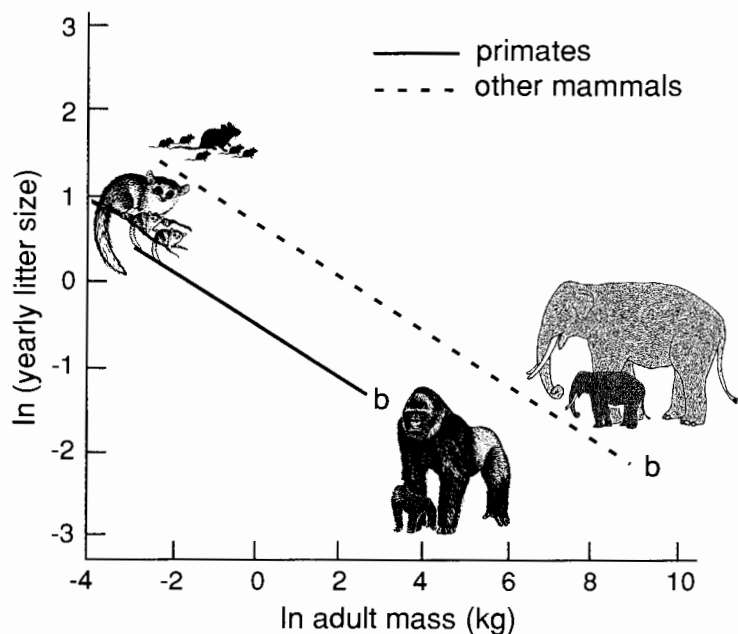
Our life history theory allows the age at maturity to evolve in response to externally imposed mortality. Since offspring production is a function of the growth allometry and is an allometric function of adult body size ( $W^7$ ), large size means greater production. But to grow to a greater size entails greater total prereproductive mortality, since the prereproductive period will necessarily be longer. The optimal adult body size ( $W$ ) maximizes lifetime production of offspring by balancing this mortality cost against the increased production benefits. In our evolutionary theory,<sup>5,6</sup> the mathematical relationship between these variables becomes:

$$\text{Average adult lifespan} = M^{-1} = \frac{1.4}{A} W^{.30}$$

where  $M$  is the instantaneous mortality rate; i.e., survival for one year =  $e^{-M(\text{one year})}$ .

But since  $A$  for primates is only .42 contrasted with 1 for other mammals, primates should have average adult

Figure 2. Allometries for yearly offspring production (daughters per year) for primates versus other mammals. Primate data from ref. 1, other mammal data from ref. 2. All correlations in the range 0.7-0.9. Primate slopes in the range 0.31-0.4. Other mammal slopes in the range 0.2-0.31.



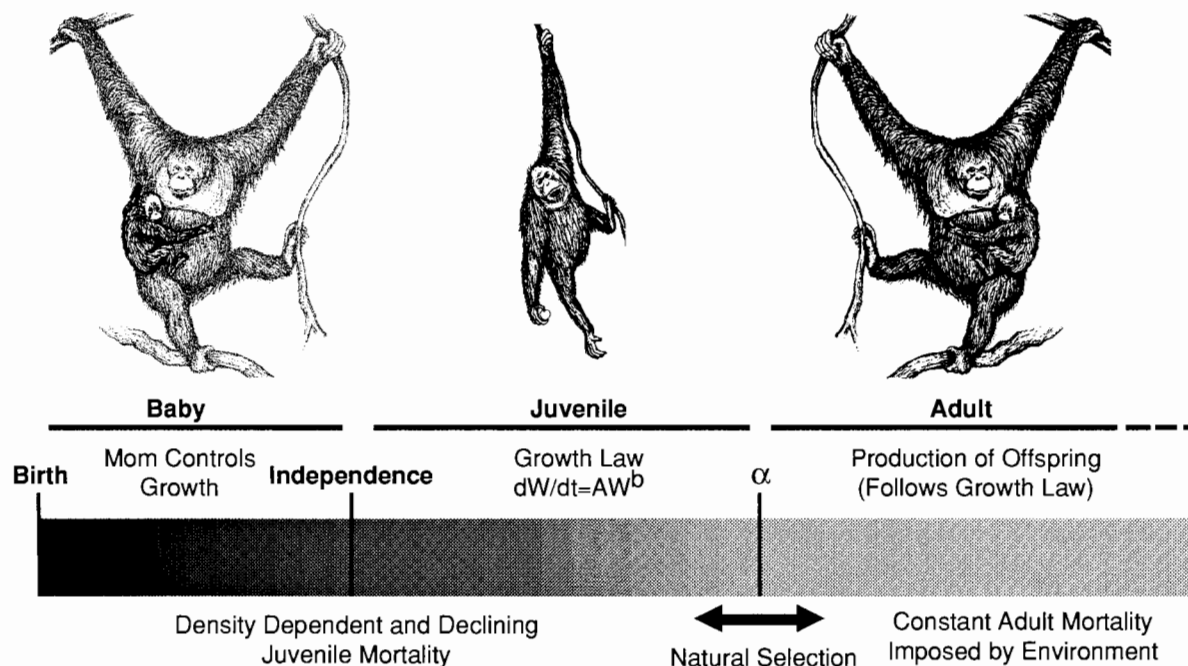


Figure 3. Schematic diagram of the life history model used to generate predictions about the role of production in life history evolution.<sup>5,6</sup> Selection acts on the age at maturity to maximize lifetime reproductive success in the face of adult mortality rates imposed by the environment. Growth in babies is controlled by the parent; that is, the rate of energy delivery to the offspring is determined by the mother's body size,  $W$  (through the growth law applied to *their* body weight). At maturity, adults cease growing and the resources available for reproduction are determined by the growth law as a function of adult size. Juvenile mortality is density dependent and declines until some point before the age at maturity. The density dependence of juvenile mortality ensures that, in the long term, birth and death rates are equal. This must be true in persistent natural populations.

lifespans that are about 1/42 or 2.5 times as long as those of other mammals of the same body weight. The data of lifespans plotted in Figure 1 show that the primate and mammalian curves have heights of approximately 3.0 and 1.5, respectively, which are very close to the values of 3.4 and 1.4 predicted by the theory on the basis of growth allometries.

Using the information on average adult lifespan and average age at maturity in Figure 1, we can rephrase these results in more general terms. The relationships underlying these results are that mortality rates determine adult body size (specifically the time when growth stops and production energy is diverted to offspring) and that slow growth rates (low value for  $A$ ) favor smaller adult body size at any specified mortality rate. Simply stated, it takes primates so much longer to grow to a size of, for example, 10 kg, with their low production rates, that only with very low mortality (and very long lifespans) will natural selection favor the delay in first breeding to enable a species to grow as large as 10 kg. Thus our theory predicts a relationship between  $\alpha$  and  $M^{-1}$ ; it predicts that the difference in height be-

tween  $\log \alpha$  and  $M^{-1}$  should be the same for primate and other mammals—a prediction that is borne out in Figure 1.

The life history theory makes several other successful predictions for

---

**According to our model, growth ceases at adulthood and the production energy ( $dW/dt$ ) is then channelled into offspring.**

---

mammalian life histories.<sup>5-7</sup> Perhaps its greatest utility in the present context is that it focuses attention on what emerges as a keystone difference between primates and other mammals: Why is  $A$  so low for primates? Answer that (says the theory) and many other features of primate life histories will also be explained.<sup>6</sup>

One possible explanation for the low values of  $A$  in primates is the greater (?) energy demands for grow-

ing and supporting big brains; there is a fair bit of irony in this suggestion because it implies that the long primate lifespan follows from the cost, rather than some cognitive benefit, of having a big brain. Primate biologists often seem (to us) to be obsessed with the benefits of large brains. It is worthwhile to note that snakes and lizards have relatively small brains but have relatively low values of  $A$ ;<sup>11,12</sup> they also have average adult lifespans (adjusted for body size) that are equal to or greater than those of primates.<sup>6,11</sup> We suspect that primate biologists can easily propose alternative explanations for the cause of low values of  $A$ .

Of course, the theory assumes that the evolution of mammalian histories is mostly governed by some very specific (and nearly universal) tradeoffs (Fig. 3); for example, the allometric production function ( $dW/dT = AW^{.7}$ ) for postweaning growth and offspring production. While these (and other) specifics are each testable in a piecemeal fashion, the entire theoretical package (Fig. 3) presents a useful target for alternative hypotheses about other potential tradeoffs (many possibilities are discussed in the books by Stearns<sup>12</sup> and Roff<sup>13</sup>). At the minimum, alterna-

tive life history theories for mammals should be asked to produce the allometric structure illustrated by the data of Figures 1 and 2, both the slopes and intercepts. After all, the theory discussed here does just that (and more<sup>5,6</sup>).

### ACKNOWLEDGMENTS

The paper was improved by J. Fleagle, K. Hawkes, A. Rogers, and C. Janson.

### REFERENCES

- 1 Ross C (1992) Environmental correlates of the intrinsic rate of natural increase in primates. *Oecologia* 90:383-390.
- 2 Hennemann WW (1983) Relationship among body mass, metabolic rate and the intrinsic rate of natural increase in mammals. *Oecologia* 56:104-108.
- 3 Prothero J, Jurgens KD (1987) Scaling of maximum lifespan in mammals: A review. *Basic Life Sci* 42:49-74.
- 4 Harvey PH, Clutton-Brock TH (1985) Life history variation in primates. *Evolution* 39:559-581.
- 5 Charnov EL (1991) Evolution of life history variation among female mammals. *Proc Natl Acad Sci USA* 88:1134-1137.
- 6 Charnov EL (1993) *Life History Invariants*. Oxford: Oxford University Press.
- 7 Harvey PH, Nee S (1991) How to live like a mammal. *Nature* 350:23-24.
- 8 Wooten JT (1987) The effects of body mass, phylogeny, habitat and trophic level on mammalian age at first reproduction. *Evolution* 41:732-749.
- 9 Millar JS, Zammuto RM (1983) Life histories of mammals: an analysis of life tables. *Ecology* 64:631-635.
- 10 Lee PC, Majluf P, Gordon IJ (1991) Growth, weaning and maternal investment from a comparative perspective. *J Zool* 225:99-114.
- 11 Shine E, Charnov EL (1992) Patterns of survivorship, growth, and maturation in snakes and lizards. *Am Nat* 139:1257-1269.
- 12 Stearns SC (1992) *The Evolution of Life Histories*. Oxford: Oxford University Press.
- 13 Roff DA (1992) *The Evolution of Life Histories*. London: Chapman and Hall.

© 1993 Wiley-Liss, Inc.

## Neandertals: Images of Ourselves

ERIK TRINKAUS AND PAT SHIPMAN

During the last two decades, paleoanthropology has focused increasingly on the global issue of modern human origins, and a preeminent part of that process has concerned the fate of the Neandertals of the northwestern Old World. Not so long ago, working on the origins of modern humans was a niche cloaked in convenient obscurity. Many human paleontologists were content to largely ignore, and thus remained ignorant of, the hominid fossils of the later Pleistocene, an attitude parallel to that of Bordes regarding the Neolithic in comparison to the more glamorous Paleolithic; he referred to the former simply as, "C'est de la merde!" However, the Neandertals have become a topic guaranteed to attract attention, thus drawing in scholars who until recently disdained interest in such basically human fossil hominids. They are now willing to direct their students' and even their own research toward late archaic humans (such as Neandertals) and early modern humans in whatever portion of the Old World is most readily available.

This trend is a mixed blessing to the small number of scientists who cut their paleontological teeth on the late Middle and Late Pleistocene hominid fossil record when it was an unpopular topic. These scholars saw in those re-

mains the potential to test interesting phylogenetic and evolutionary biology questions in an atmosphere in which the lack of intense competition and general interest made it possible to discuss disagreements cheerfully and even to collaborate with those holding opposing views. The recent renewed interest in the evolution of later Pleistocene humans has indeed generated more input of ideas and resources into long-standing and relatively intractable questions. The shift of attention has also generated so many international symposia and edited volumes<sup>1-13</sup> as to inhibit the primary research productivity of those who attend and contribute.

Most of all, it has brought into focus an issue that has been with us since the

19th century, an issue that dominates much of human paleontology and on which all of us have preconceptions. It is an issue that addresses a more general and more important point that, *au fond*, motivates most of the research into human origins: How do we define what it means to be human, and the inevitable corollary, to what extent are we willing to admit into our recent ancestry creatures who were less human than ourselves? The problem goes beyond simple phylogenetic problems such as whether early modern humans originated in Africa, whether the Neandertals evolved directly into early modern Europeans, or whether there were major biological and behavioral differences between the Neandertals and early modern humans in the Near East.

If we are to emerge successfully (in a scientific sense) from the current controversies regarding modern human origins, we must gain some perspective on the ways in which we approach this fundamental question. This is not the appropriate forum for the nearly impossible task of conducting a thorough analysis of the collective social psychology of the paleoanthropological community and its diverse cultural and intellectual milieus. We can only hope that the review offered here of the history of discoveries and interpre-

Erik Trinkaus is a Professor of Anthropology at the University of New Mexico, Albuquerque, New Mexico, and an Associate of the Laboratoire d'Anthropologie, Université de Bordeaux I, Talence, France. His research focuses on biological and behavioral interpretations of later Pleistocene human fossils. Pat Shipman is an Associate Professor of Cell Biology and Anatomy, Johns Hopkins University School of Medicine, Baltimore, Maryland. She spends most of her time writing on anthropological subjects for the public.

Key words: Paleoanthropology, Neandertals, history of science