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this knowledge on hundreds of daily decisions may be quite important, for families of older matriarchs have more calves per female than families of younger matriarchs.

Payne emphasizes the importance of acoustic communication in mediating social interactions among different groups of elephants, whose home ranges may encompass hundreds to thousands of square kilometers. Elephants produce low frequency calls that can carry for many kilometers. Roving adult males can find receptive females using these calls, and individuals appear to coordinate movements both within and between families with these calls.

Payne observes that different individual elephants often have very different behavioral reactions to the same event. She notes that this behavioral variability may increase the complexity of individualized societies. Some individual elephants can be suddenly dangerous to others nearby when they become aggressive. This suggests another reason why it may be so important for animals in individualized societies to be able to recognize individuals and remember their history of interaction—not just to maintain contact with partners, but also to avoid untrustworthy individuals.

Van Schaik and Deaner caution that each taxon that independently evolved large brains and intelligence may have arrived via a different evolutionary path, each involving an idiosyncratic constellation of selection pressures. In their view, it may be naïve to seek a single evolutionary cause for the evolution of intelligence in all animal groups. This is a useful cautionary tale, but one that runs contrary to the striking commonality of results from the participants of this conference, who have used a diverse array of methods to study such an assortment of mammals and birds. We hope that this section will encourage readers to evaluate the current status of the evolution of intelligence and of complex social behavior and seek new directions for future research.

I

Life History and Cognitive Evolution in Primates

CAREL P. VAN SCHAİK AND ROBERT O. DEANER

The study of animal cognition has become a highly active area (Dukas 1998; Balda et al. 1998; Shettleworth 1998), and primatologists have made some seminal contributions. Perhaps most important, primate researchers have put forth a variety of stimulating hypotheses to account for the apparently exceptional cognitive capacities of primates as a whole and for cognitive variation among primates in particular. These hypotheses focus on selective demands ranging from foraging and arboreal locomotion to sociality, but the common thread is that all are claimed to have selected for some type of fairly generalized ability (see Table 1.1).

In the past decade, several comparative tests of these contending hypotheses have been conducted. These tests were aimed at identifying the hypothesis that best explains variation in the size of the brain or brain structures (Dunbar 1992; Barton & Purvis 1994). Many of these tests have favored the social strategizing or Machiavellian intelligence hypothesis (Byrne & Whiten 1988), which claims that the need for effective competition and cooperation with conspecifics has provided the main selective advantage (i.e., served as the "pacemaker") for evolutionary increases in cognitive abilities. These tests have led workers to reject the other hypotheses or at least suggest that the social strategizing hypothesis holds most generally (Byrne 1995; Barton & Dunbar 1997; Dunbar 1998; Cummins 1998; Whiten 2000).

Table 1.1. Overview of hypotheses for the evolution of cognitive abilities, especially among primates

Hypothesis	Selective demand	Applicability	References
Social strategizing	Predicting and manipulating the behavior of conspecifics	All	Cheney et al. 1986; Byrne & Whiten 1988; Whiten 2000
Spatiotemporal mapping	Monitoring food availability in space and time	All	Clutton-Brock & Harvey 1980; Milton 1988
Extractive foraging	Extracting hidden food items from matrix	All	Parker & Gibson 1977, 1979
Food processing	Manual dexterity and bipedal coordination to process foods	All? (great apes?)	Byrne 1997
Arboreal clambering	Moving nonquadrupedally in a three-dimensional habitat	Great apes	Povinelli & Cant 1995

The widespread acceptance of one hypothesis may be premature, however, in part because of the nature of the tests used to reach this conclusion. We therefore begin this chapter with a discussion of the key features of the comparative neuroanatomical approach used to test hypotheses for cognitive evolution, and then examine the social strategizing hypothesis in some more detail. This analysis suggests that we should keep an open mind on the pace-makers of cognitive evolution in primates, and mammals in general.

Next we argue that consideration of the costs of cognitive adaptations may be useful. First, we demonstrate that life history and measures of brain size have undergone correlated evolution, indicating that animals with fast life histories are generally unlikely to evolve greater cognitive abilities. Second, we argue that the life history perspective explains why some species show more cognitive adaptations than others despite being subject to the same demands, that domain-general cognitive abilities may arise as a byproduct of slow life history, and that there are many likely, nonexclusive cognitive benefits. Accordingly, a single selective demand (e.g., social strategizing) is unlikely to have universal influence, and natural history characteristics should be expected to produce diverse pressures in different lineages.

Testing Hypotheses of Cognitive Evolution

Although there are several approaches to testing adaptive hypotheses, from a historical perspective (as defined by Coddington 1988) the most rigorous way is to employ the comparative method, asking whether traits have repeatedly evolved in a hypothesized adaptive context (Harvey & Pagel 1991;

Brooks & McLennan 1991; Shettleworth 1998). In the case of cognition, we would like to know whether lineages that faced a particular demand (e.g., spatial mapping, social strategizing) were especially likely to have evolved enhanced abilities. Although there has been some success in applying the comparative approach to the evolution of cognitive abilities (Balda et al. 1996; Lefebvre & Giraldeau 1996), primatologists have generally lacked the relevant data on the socioecological demands and the cognitive abilities. With respect to cognitive abilities, the issue is that the ever-formidable challenge of showing taxonomic differences in ability (compare Macphail 1982; Kamil 1988) becomes yet more difficult when the claim is that the abilities are domain-general (but see Johnson et al. in press). Given these issues, primate workers have used what we call the comparative neuroanatomical approach: rather than assessing cognition through behavioral performance, cognitive ability is assumed to correspond with the size of the whole brain or of brain structures implicated in cognitive tasks; and instead of appraising the socioecological demands empirically, they are assumed to correspond with other, proxy variables (for reviews, see Harvey & Krebs 1990; Barton & Dunbar 1997).

Although there are many difficulties with employing the comparative neuroanatomical approach, they are rarely discussed. With respect to socioecological demands, there is scant information regarding the degree to which the proxy variables used in the tests actually provide valid and reliable estimates of the supposed demands. For instance, tests of the spatio-temporal mapping hypothesis have employed home range size or percentage fruit in the diet on the assumption that the former assays spatial demands and the latter assays temporal demands. It is possible, though, that animals with larger ranges perceive them in a less "fine-grained" manner and so do not face exceptional spatial navigational problems; likewise, despite the impressions of several field-workers (e.g., Eisenberg & Wilson 1981; Clutton-Brock & Harvey 1980; Milton 1988), nonfruit items may also be highly ephemeral (Glander 1981). Similarly, the popular Machiavellian intelligence hypothesis has been tested mainly by using group size to assay social strategizing demands. Although group size is probably related to such things as the need to maintain dominance relationships and establish strategic alliances, the relationships are indirect and there are many exceptions, including gregarious groups that have little apparent complexity or even temporal stability (see Bradbury 1986; Strum et al. 1997).

The validity of brain structures as cognitive assays is also unclear. The un-

derlying assumption—that size matters—is reasonable because the size of brain structure predicts several neurophysiological characteristics, including the number of neurons at the cortical surface and the number of cortical columns (reviewed by Jerison 1991). Likewise, in several contexts, brain structure size corresponds with behavior. For instance, cerebellar size correlates with measures of visual memory and motor dexterity in humans (Paradiso et al. 1997), and avian taxa with superior spatial memory abilities tend to have larger hippocampi (e.g., Basil et al. 1996). Nevertheless, the fact remains that there is little direct indication that the size of brain structures corresponds with domain-general cognition in a comparative context (but see Rumbaugh 1997; Johnson et al. in press).

Furthermore, even if one accepts that the sizes of brain structures provide reasonable proxies for cognition, there are two additional problems. One is that it is unclear which brain structure should be employed. Earlier studies generally used whole brain size (e.g., Clutton-Brock & Harvey 1980; Gittleman 1986), a measure that has several advantages, including easy estimation, even for fossil specimens. More recent studies have generally employed the neocortex or the neocortex minus area V1, chiefly on the grounds that many structures involved in higher-order cognition (e.g., planning, working memory) are located therein (e.g., Sawaguchi & Kudo 1990; Dunbar 1992; Joffe & Dunbar 1997; see Barton 1998). However, many noncortical structures (e.g., cerebellum) are also implicated in higher-order cognitive processes (e.g., Middleton & Strick 1994). Because it is unclear what structure should be used, and because most data are available for whole brain size, we use whole brain size for the analyses in this paper.

A second problem with comparing brain structures across taxa is that species differ dramatically in body size, and it is unclear if and how this fact should be accounted for. Body size and whole brain size, for instance, are highly correlated, and hence most workers advocate scaling techniques (e.g., Jerison's [1973] Encephalization Quotient) to compare brain sizes after all effects of body size have been statistically removed. This approach has several drawbacks, though, including the possibility that cognitive ability and body size truly coevolved, making the control of body size undesirable (Deacon 1997). Several other methods of scaling the brain or brain structures have also been introduced, including the use of ratios (Passingham 1975; Dunbar 1992) that only partially control for body size. Deaner and colleagues (2000) have recently reviewed the various kinds of scaling methods and shown that all are of unproven validity and have potential drawbacks. In the analyses

presented below, we use residuals from the regression of whole brain on body mass. Although this may not turn out to be the best cognitive proxy, it is at least conservative because it strictly controls for body size and thus may prevent spurious correlations.

A final issue in comparative neuroanatomical studies is that once the decision has been made to employ specific socioecological variables and brain structures, species values for these measures cannot be treated as independent data points in a statistical analysis. The reason is that most biological traits are at least partially the product of phylogenetic history, meaning that closely related taxa will often share traits simply due to common descent (Felsenstein 1985). There is ongoing debate regarding how comparative analyses should address this issue, but the most widely adopted approach is to estimate evolutionary changes throughout a phylogenetic reconstruction of a trait's evolution (Harvey & Pagel 1991; Purvis & Webster 1999). In the case of hypotheses about cognitive evolution in primates, the question would be whether evolutionary changes in a socioecological demand consistently co-occur with evolutionary changes in the (scaled) size of a brain structure. Although comparative methods that account for phylogenetic nonindependence can be sensitive to the evolutionary models assumed and the accuracy of phylogenetic information, they are far more likely to provide correct answers than are analyses that do not account for phylogenetic relationships (Harvey & Pagel 1991; Martins & Hansen 1996; Purvis & Webster 1999; Nunn & Barton 2001). In the analyses below, we use the CAIC program (Purvis & Rambaut 1995) to implement the comparative method of independent contrasts (Felsenstein 1985). Nunn and Barton (2001) furnish a clear introduction to the rationale and use of this method.

To summarize, then, although the comparative neuroanatomical approach makes reasonable assumptions, the proxies employed measure the variables of interest with unknown (but possibly sizable) error. Furthermore, the techniques that estimate correlated evolution also include unknown error. For these reasons, the conclusions of all comparative neuroanatomical studies must be viewed cautiously.

Social Strategizing Revisited

As a result of several comparative neuroanatomical studies over the last decade, primatologists seem to be converging on the simple generalization that cognitive evolution, at least in primates, is best explained by responses to

social challenges (Byrne 1995; Barton & Dunbar 1997; Dunbar 1998; Cummins 1998). For several reasons we believe that this conclusion is premature.

The studies on which this conclusion is based (Dunbar 1992, 1995; Barton & Purvis 1994; Barton 1996) have several weaknesses. First, as noted above, group size may not be a good proxy for social demands. Second, the tests that have supposedly differentiated among the hypotheses have each only explored one neuroanatomical scaling method. Recent work has shown, however, that the outcomes of these tests are sensitive to the scaling method employed, so that under several conditions, home range is a better neocortex predictor than is group size (Deaner et al. 2000). Third, group size, home range size, and other socioecological proxies for the hypotheses are intercorrelated (Deaner et al. 2000), making it difficult to differentiate among the hypotheses with these (error-prone) proxies.

Besides these problems with the comparative tests, there are other empirical problems with the social strategizing hypothesis. One is that some major phylogenetic contrasts in primates cannot be accounted for in this way (Byrne 1997). Most obviously, great apes outperform monkeys on cognitive tasks (Byrne 1995; Johnson et al. in press), yet do not show greater social complexity, at least in most species (Tomasello & Call 1994). Similarly, the largest-brained of all the living prosimians—the aye-aye (*Daubentonia madagascariensis*)—is almost entirely solitary. Another problem is that the demands of social strategizing—at least as assayed by demographic variables—appear to have limited explanatory value in nonprimates. Relative brain size in sciurids or birds is not affected by degree of sociality (solitary versus gregarious lifestyle; Meier 1983; Bennett & Harvey 1985). In carnivores, Gittleman (1986) found that relative brain size was larger in multimale than in unimale breeding groups but also noted that other measures of social complexity do not correlate with relative brain size (see also Dunbar & Bever 1998). Marino (1998) reports that brain size and group size are related in odontocetes, but a similar analysis controlling for phylogeny could not confirm this result (R. Deaner, unpublished data).

In conclusion, it is at this stage premature to decide that social strategizing was the only, or even the major, selective pressure on cognitive evolution in primates or other mammals. We would like to stress that we do not claim that social strategizing is not a major force in primate cognitive evolution. It may well be, but we think it is too early to consider the issue settled and to

ascribe all cognitive evolution, at least in primates, to the need for social strategizing.

Life History and Cognition

Would not all animals benefit from being smart? For instance, if the common perception that social primates are smarter than social ungulates is true, then we must ask why ungulates did not undergo selection for similar abilities. Considering this issue underscores a fundamental point of evolutionary biology (and one not incorporated into the hypotheses proposed to date), namely that virtually all benefits entail costs of some kind. Among the many costs of cognitive adaptations, perhaps the most prominent one is that the neural tissue underlying the abilities is energetically expensive to grow and maintain (Aiello & Wheeler 1995; Deaner et al. in press). Thus, the key to understanding when improved cognition will be selected for is gaining insight into the relative costs and benefits of the ability for the lineage in question.

It is our contention that a crucial influence on the relative costs and benefits is life history. Life history summarizes the species-specific statistics of major life events: duration of gestation, age at weaning, age at first reproduction (AFR), interbirth intervals, litter or clutch size, and maximum life span (MLS). It has been well established that life histories, at least among mammals and birds, come in syndromes, i.e., many of the features covary predictably. Most important, we can recognize variation along a slow-fast continuum (Harvey et al. 1987; Read & Harvey 1989; Charnov 1993).

A connection between life history, especially MLS, and brain size has long been suggested (Sacher 1959; Sacher & Staffeldt 1974; see also Allman 1999). However, critics have pointed out that there is no evidence for the direct physiological connections between brain size and life history hypothesized by Sacher (Harvey et al. 1989; Read & Harvey 1989; Harvey & Pagel 1991). Recent life history studies, instead, emphasized the role of demography, especially the rate of ecologically imposed unavoidable mortality, as the main selective pressure on life history (Stearns 2000), and strongly contributed to the acceptance of this theoretical perspective (e.g., Promislow & Harvey 1990).

These recent studies have therefore downplayed the possibility of correlated evolution of life history and brain size. In fact, they suggested that

the apparent interspecific correlation between brain size and life history is a statistical byproduct of the correlation between body size and life history (Economos 1980): a stronger correlation between MLS and brain size than with body size could arise because body weight is subject to much more error (= phenotypic variation) than brain weight. With the analyses presented here, we would like to reconsider the old correlation, although we are obviously not arguing in favor of the original proximate constraint hypotheses or against the modern interpretation of life history evolution.

One solution to the problem of correlated errors is to remove the effects of body size on both variables by taking residuals from the regression of log AFR or MLS and of log brain size on log body mass. But then a new problem arises (see Harvey & Krebs 1990; Barton 1999). Because of the large error in body mass estimates, residuals against body size for life history measures and for brain size will share error in the same direction, potentially producing artificially high correlations (see Deaner and colleagues [in press] for a visual illustration). The simplest way to avoid this problem is to calculate the two residuals from independent estimates of body mass.

Recently, Deaner and colleagues (in press) have re-examined the relationship between life history and brain size. We tried to correct for the effects of body size by taking separate body size estimates to calculate residuals of brain and life history variables, and for the effects of phylogenetic nonindependence by using independent contrasts (Harvey & Pagel 1991; Purvis & Rambaut 1995; Nunn & Barton 2001).

We found that the correlation between life history, proxied by log relative MLS, and log relative brain size is real, in primates at least. The correlation between them is highly significant ($r = 0.46$; $n = 56$; $P = 0.0002$; details in Deaner et al. in press), and is maintained if we correct for the body size problem by taking independent sets of body mass estimates ($r = 0.43$; $n = 56$; $P = 0.0005$), and for possible effects of phylogenetic nonindependence and for the body size problem at the same time ($r = 0.31$; $n = 52$; $P = 0.03$; see Figure 1.1). We also found that it was not a byproduct of some obvious socio-ecological factors such as frugivory, home range size, or group size (Deaner et al. in press).

We also looked at the highest taxonomic level in eutherian mammals, i.e., the order. This analysis uses means of all species values within an order, which reduces the impact of error in the estimates of species values. It does not calculate independent contrasts because the phylogenetic relationships among higher taxa are still widely debated. However, since the orders sepa-

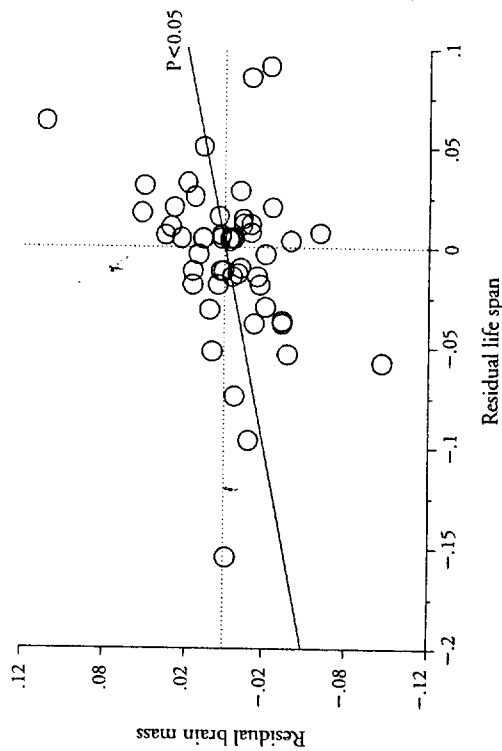


Figure 1.1. The relationship between life history (residual log AFR) and cognitive abilities (residual brain size) in primates, using independent contrasts. Based on Deaner et al. in press.

rated tens of millions of years ago, the problem of nonindependence should be much reduced. At first sight, the relationship between encephalization quotient and longevity quotient (observed maximum life span / expected maximum life span based on the body weight effect; from the database of Austad & Fischer 1992) is weak (see Figure 1.2): $r = +.39$ ($n = 13$, $P = 0.19$). However, there is one strong outlier: the bats (Chiroptera). If the bats are removed, the correlation becomes highly significant ($r = +0.859$, $P < 0.001$) (which is not because of the inclusion of primates: without bats and primates, $r = +0.751$, $P = 0.01$). Thus, after bats are removed, the relationship between life history and cognition is surprisingly strong at this highest taxonomic level.

The conclusion from these comparisons is that there has indeed been correlated evolution between life history and brain, although there is an important outlier, i.e., a clear exception to the rule, which a complete theory needs to explain. Independent support for this conclusion is provided by Promislow's (1991) analysis of senescence in natural populations of 49 different mammal species, which showed that "at least among longer-lived taxa,

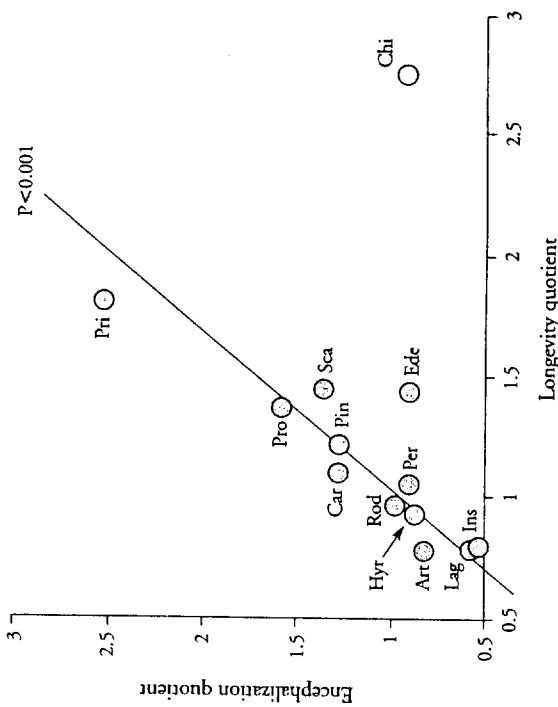


Figure 1.2. Size-controlled life history (longevity quotient) and cognitive abilities (encephalization quotient) at the level of orders of eutherian mammals. Source: Austad & Fischer 1992. Abbreviations: *Art* = Artiodactyla; *Car* = Carnivora (Fissipedia); *Chi* = Chiroptera; *Ede* = Edentata; *Hyr* = Hyracoidea; *Ins* = Insectivora; *Lag* = Lagomorpha; *Per* = Perissodactyla; *Pin* = Pinnipedia; *Pri* = Primates; *Pro* = Proboscidea; *Rod* = Rodentia; *Sca* = Scandentia.

large brains are correlated with low senescence." Additional support comes from earlier studies that found correlations between relative brain size and other aspects of life history, e.g., litter size, in several mammalian lineages (Eisenberg 1981; Mace & Eisenberg 1982).

This perspective answers at least partly the question of why primates are so smart: they have very slow life history, especially in light of their rather moderate body size (Charnov 1993). It also raises two major new questions: Why do primates have such slow life histories, and more fundamentally, Why did life history and cognition undergo correlated evolution?

Causes of Variation in Mammalian Life Histories

Slow life history can only evolve in animals that have both low unavoidable mortality and distinct advantages to delaying reproduction in terms of more

or better offspring (Stearns 1992, 2000). Low mortality is therefore a critical precondition of slow life history.

One of the major sources of reduced mortality is the evolution of larger body size (e.g., Read & Harvey 1989), but another source that does not require increased body size may be an arboreal lifestyle. It can be argued that arboreal animals face fewer predators than a terrestrial animal of the same size, and have more refuges and escape routes. In fact, an effect of arboreality on life history variables such as litter size and gestation length has been suggested before (Eisenberg 1981; Martin 1990; Shea 1987). To investigate this potential relationship systematically, we conducted an ordinal-level analysis of nonaquatic taxa. We considered primates, dermopterans, and bats to be arboreal, although obviously with bats flight adds a confounding effect. We considered the rodents, tree shrews, fissiped carnivores, edentates, and hyraxes to be mixed arboreal-terrestrial, and the other orders terrestrial. At the ordinal level, arboreality has a strong effect on relative longevity ($F_{[2, 13]} = 12.61, P < 0.001$), and also a significant effect on relative age at maturity ($F_{[2, 9]} = 8.01, P < 0.01$). These patterns are illustrated in Figure 1.3.

Some or all of this effect could be attributed to flight, which is known to reduce mortality rates (Pomeroy 1990). We therefore repeated the analysis with the bats removed, but the effect of arboreality is retained ($F_{[2, 12]} = 8.96, P < 0.01$, for relative longevity; $F_{[2, 8]} = 4.84, P < 0.05$, for relative age at maturity). Also, we examined the relationship within the order Primates,

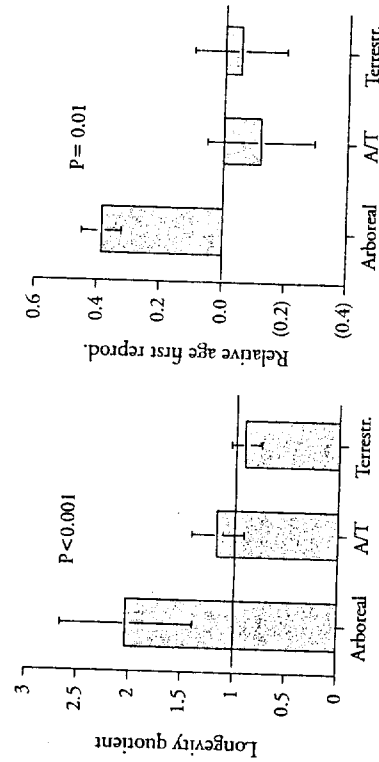


Figure 1.3. The effect of arboreality on life history at the level of orders of nonmarine eutherian mammals. Longevity quotient taken from Austad and Fischer (1992); relative age of first reproduction from Read & Harvey (1989).

where data on substrate use by wild animals is fairly extensive. Among primates, an independent contrast analysis shows the expected relationship between terrestriality and life history (using relative AFR), although it is only marginally significant (Figure 1.4). (The data for this analysis come from Deaner and colleagues [in press]; literature data on percent time spent terrestrially were compiled mainly by Charles Nunn.) Earlier, Ross (1988) had found that size-corrected primate life history speed is correlated with habitat. Species living in savannas, forest edge, and secondary forest were found to have faster life histories. Habitats were classified along these lines to test the predictions of the $r-K$ model for life history evolution, but this model has now been abandoned because experiments failed to find the density-dependent changes in life history predicted by the model (Stearns 1992). In retrospect, the correlation with terrestrial locomotion is apparent.

These findings indicate that both arboreality and the ability to fly reduce mortality and slow life history. Overall, then, animals that are off the ground

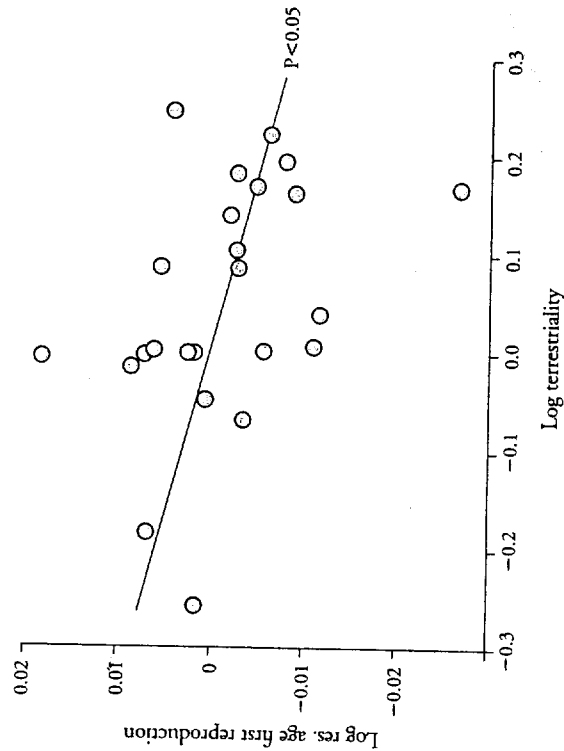


Figure 1.4. The effect of the percentage of time spent as terrestrial on life history (residual age of first reproduction) among primates, using independent contrasts. Life history data are from Deaner et al. (in press); substrate use from C. Nunn (personal communication).

have slower life history (compare Prothero & Jürgens 1987), most likely because they face lower mortality risks. Thus the relative encephalization of the earliest primates can be attributed to the fact that they were one of the few arboreal mammalian radiations (Shea 1987).

One implication of this argument is that there should be a relationship between arboreality and relative brain size. Contrary to this prediction, we did not find any effect of terrestriality on relative brain size in our primate sample. However, at the ordinal level, there is a significant effect after bats are removed ($F_{(2,9)} = 2.12$, n.s.; after bats are removed, $F_{(2,8)} = 10.29$, $P < 0.01$). Also, several more limited comparisons did find the expected increase in relative brain size among more arboreal species or even subspecies, compared with the terrestrial counterparts in the same lineage (compiled in Table 1.2).

There are various ways to interpret the absence of a universal effect of arboreality on relative brain size, in spite of the clear-cut effect on life history. A plausible interpretation is that brain size tends to evolve, ratchet-like, in one direction. Throughout the evolutionary history of mammals, there is a

Table 1.2. Relation between arboreality and relative brain size (EQ as defined by Jerison [1973] or Eisenberg [1981]) in mammalian lineages, using (A) comparisons between EQ of terrestrial and arboreal species (t -tests); and (B) Pearson correlations with degree of arboreality across species or subspecies (in *Promyscus*)

A				
	Terrestrial	Arboreal	Significance	Source
Neotropical edentates	0.84 ($n = 2$)	1.025 ($n = 2$)	n.s.	Eisenberg 1981
S. African myomorphs	0.33 ($n = 5$)	0.52 ($n = 3$)	$P = 0.01$	Bernard & Nurton 1993
Sciurids	0.96 ($n = 16$)	1.84 ($n = 17$)	$P < 0.0001$	Meier 1983

B				
	Correlation with arboreality	Number of species	Significance	Source
Didelphimorpha	+0.72	13	$P < 0.01$	Eisenberg & Wilson 1978
<i>Promyscus maniculatus</i>	+0.67	18	$P < 0.01$	Lemen 1980
<i>P. leucopus</i>	+0.70	8	$P < 0.05$	Lemen 1980

distinct trend of increasing relative brain size (Jenison 1973), suggesting that once large brains have evolved, they become such an integral and vital part of the organism's functioning that they cannot be reduced by moderate increases in the speed of life history. The testable implication of this suggestion is that transitions toward increased arboreality should be accompanied by increases in relative brain size whereas transitions toward more terrestriality are not necessarily accompanied by reductions in relative brain size. Future work should test this prediction.

Why Do Life History and Cognition Undergo Correlated Evolution?

At this point, we must examine what it is about life history that causes correlated evolution with the brain. All other things being equal, natural selection will favor faster life history because genotypes that reproduce faster will replace others in the population. Thus, there must be positive benefits for slowing down. The advantage most commonly considered is that slower development leads to larger body size, which in turn tends to produce both lower adult mortality rates (thus sustaining a slowing down) and, once reproduction has started, either higher rates of infant production or larger-sized infants. However, as we noted, the fast-slow continuum is retained even if adult body size is statistically removed, so there must also be size-independent benefits to slowing down life history.

We can envisage two possible size-independent benefits. First, if immature mortality is very high relative to adult mortality, selection will favor long life span (but not necessarily delayed maturity) and thus, because of the tradeoff between reproduction and survival (e.g., Stearns 1992), a reduced reproductive effort (Cole 1954). For instance, in sea turtles, infant mortality is orders of magnitude higher than adult mortality. Increased reproductive effort in a single reproductive event (resulting in death) would therefore be unlikely to produce another surviving adult, and hence long life spans and modest reproductive effort would be favored by selection. These conditions are especially likely for species in which entry into the adult niche is extremely difficult because of the absence of parental care, such as in sea turtles.

However, we don't expect these conditions to apply generally to primates or other mammals with extensive parental care. Hence, a second size-independent benefit of slow life history is needed: females that have delayed maturation may produce offspring that are of better quality (Stearns 2000). The nature of this benefit remains largely unexplored (Pagel & Harvey 1993), and tends to be referred to as "experience" (Harvey et al. 1989).

We review various hypotheses that insert some biology into the experience-based, size-independent benefits of slow life history (for complete discussion see Deaner et al. in press). The first two assume that animals evolving larger brains are also expected to evolve slower life histories. The maturational constraints hypothesis claims that immature nervous systems cannot function at the adult level. Thus, large-brained animals whose brain development would not be complete until after commencing reproduction benefit from delaying the onset of reproduction until this is achieved. This hypothesis, then, assumes that slow life history was an evolutionary compromise forced onto animals that were evolving larger brains. The cognitive buffer hypothesis posits that large brains are adaptive because they reduce mortality, especially among adults, thus allowing a slowdown of life history. This hypothesis, then, suggests that slow life history evolved because it was made possible by larger brain size.

The second class of hypotheses assumes that slow life histories relax the costs of brain enlargement, or even favor it. The brain malnutrition risks hypothesis argues that the growing brain's vulnerability to nutrient and energy shortages made it easier to select for larger brain size in organisms with slow life history, because if brains developed rapidly in an energy-poor environment, a considerable proportion of adults would be cognitively impaired and thus unfit. The delayed benefits hypothesis sees slow life history as a critical precondition for the evolution of larger brains. Specifically, it argues that investment in organs that provide their fitness benefits well after they have developed produces greater fitness payoffs in animals with slow life history.

These nonexclusive hypotheses are logically coherent and make assumptions that are reasonably well supported. Their predictions are not all equally supported in all taxa (Deaner et al. in press), perhaps because of the poor quality of life history data (especially longevity), particularly in nonprimates, or because the hypotheses do not apply equally to all taxa (e.g., only to those above a minimum brain size). The hypotheses all suggest that brains and life history evolve in lock-step, but also that the relationship is not quite symmetrical: large-brained organisms must have slow life history to produce demographically viable organisms, but not all animals with slow life histories need necessarily evolve larger brains (as we saw in bats). The delayed benefits hypothesis, after all, assumes there are distinct benefits to the cognitive adaptations that outweigh the obvious developmental costs.

Life history therefore acts as a filter (see Figure 1.5): the same selective pressure will lead to enhanced cognition, and hence enlarged brain size, in a species with slow life history, but not in an otherwise identical species with

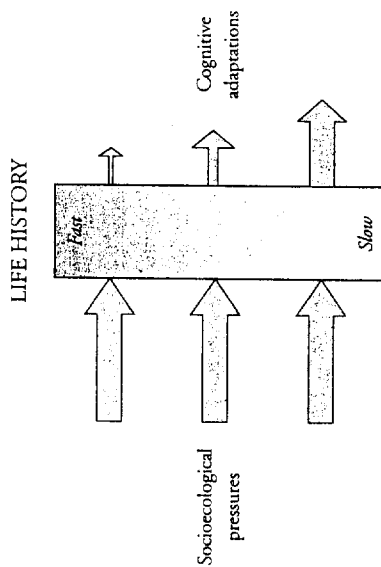


Figure 1.5. Life history as a filter: organisms with slow life history are more likely to respond to social or ecological demands by evolving cognitive adaptations. Various kinds of cognitive adaptations therefore accumulate in organisms with slow life history.

fast life history. The life history perspective thus provides a useful general over-arching framework for cognitive evolution. It does not obviate the need to develop hypotheses that postulate cognitive adaptations to specific external demands, but it does explain which kinds of organisms can attain these adaptations when exposed to the selective pressure, and which cannot. A broader comparative perspective also suggests that there may be numerous possible cognitive benefits, many of them taxon-specific, as explained below.

Reexamining the Selective Advantages of Cognition

Distinguishing among Multiple Hypotheses

It is well known that comparative tests of hypotheses for cognitive evolution face a variety of problems, but our examination of the impact of life history has just made these problems even more daunting. First, statistical models must now explicitly incorporate the interaction effect due to life history. Second, the hypotheses are not mutually exclusive, and statistical models must accordingly be multivariate rather than bivariate (testing hypotheses one by one). We must therefore find ways to improve the resolution of the tests. One way to achieve this is to identify better proxy variables for the socioecological demands and the cognitive variables, as this would reduce the consequences of unequal error variances in multiple regressions.

Another way to improve comparative tests might be to increase the taxonomic scope of the taxa in the test, since this provides more degrees of freedom. However, inclusion of a larger array of taxa also requires explicit recognition of a larger array of hypotheses. All hypotheses listed in Table 1.1 were developed with primates in mind. Some apply only to primates, or even a subset of primates (e.g., the arboreal clambering hypothesis), but others may apply more broadly. On the other hand, in other taxa other benefits may apply. Unfortunately, there have not been many suggested pacemakers for cognitive evolution in nonprimates. Mace and Eisenberg (1982) suggested that intensity of interspecific competition affected relative brain size among rodents, whereas Gittleman (1994) proposed, for carnivores, that unassisted maternal care posed unique cognitive challenges. The important message here is that tests of cognitive evolution require proper identification of all the potentially relevant benefits. So far, we have not reached this stage.

A very different way to sort out the pacemakers of cognitive evolution may therefore be worth considering. One promising avenue is the examination of striking phylogenetic contrasts, in which both cognition and life history show a major divergence between sister species or clades. In principle, the most striking cognitive contrasts should be accompanied by the most easily identified lifestyle differences that have served as the evolutionary facilitators for the cognitive divergence between the two sister taxa. These pacemakers could be divergences in ecology, mating system, social behavior, or any other aspects of their lifestyle that might affect cognition. Having identified the key differences, we can then build a likely scenario that can subsequently be tested for consistency, or add them to a multivariate statistical model.

To illustrate this approach, let us briefly examine one of the most striking phylogenetic contrasts among primates. In primates, the contrast between *Homo* and *Pan* is perhaps the most pronounced, and involves a long list of possible socioecological pacemakers (compare Gibson 1999). Compared to chimpanzees, humans generally rely more on technology for foraging and food processing, show more complex social organization involving more cooperation and exchange, show an amazing capacity for culture, and have an infinitely flexible communication system in language. All of these differences involve cognition. Thus, humans no doubt show more advanced technical intelligence (Byrne 1997), are much better at imitation of complex actions (Tomasello 1999), show more evidence for a theory of mind and multiple levels of intentionality (Dennett 1996), and, Kanzi notwithstanding (Savage-Rumbaugh & Lewin 1994), show much greater linguistic abilities. Thus, there are at least four different major components to the cognitive contrast,

the last two almost certainly unique among primates, though not necessarily among mammals more generally (compare cetacea: Tyack 1999).

Both the social strategizing and the food processing hypotheses are implicated in this list of contributing selective benefits, but so are other traits that involve cognition, namely imitative abilities and language. The latter two are not part of the list of general selective advantages for increased cognitive skills among mammals or primates. In other words, it seems as if a unique set of "customized" hypotheses is needed to fully explain this contrast.

If these preliminary analyses are indicative of the general trend, we expect that all better studied contrasts will involve some rare elements. Thus, while it is necessary to make improvements to the comparative tests of the existing hypotheses for cognitive evolution, there is also a need to generate more relevant ones, including perhaps cognitive benefits that may be lineage-specific.

Social Strategizing and Life History

Examination of the interaction between life history and cognition has led us to emphasize the diversity of possible contributing factors, including cognitive benefits that may be fairly idiosyncratic, and thus only relevant to particular lineages. Nonetheless, slow life history may exert a more direct selective influence on cognition that can be placed under the rubric of social strategizing. In general, long-lived animals, unless they are nomadic, will be more prone to form long-term associations with known individuals, leading to many opportunities for social interactions and long-term relationships. Such a setting forms the precondition for social complexity. Moreover, various reproductive parameters are causally linked to life history, but also to the potential for sexual coercion: harassment and infanticide. If this intersexual conflict produces social challenges with possibly cognitive solutions, it may thus affect cognitive evolution.

First, slow life history implies longer interbirth intervals, which in general lead to more male-biased operational sex ratios because fewer females will be ready to conceive at any moment in time. This, in turn, means more potential for intersexual conflict, such as polyandrous mating by females despite attempts at monopolization by dominant males. It may be that behavioral strategies to deal with these problems (by both males and females) have led to solutions that involve social strategizing, including deception.

Second, the benefit of infanticide to the male depends on making the female return to receptivity earlier than without it; and this benefit should

strongly depend on the relative duration of lactation and gestation. The relative length of lactation has recently been shown to affect the risk of infanticide by males in mammals (van Schaik 2000). Slow life history leads to slowed-down post-natal development and increased lactation relative to gestation (Figure 1.6). It is conceivable that behavioral strategies to deal with infanticide risk (by both males and females) have led to solutions that involve cognition. If that is so, the threat of infanticide has favored cognitive evolution.

The Evolution of Domain-General Cognition

Most students of cognitive evolution have stressed that cognitive adaptations are domain-specific (e.g., Shettleworth 1998), although cognition in primates may appear to be fairly domain-general (e.g., Johnson et al. in press). We believe that the life history perspective may shed some light on this possi-

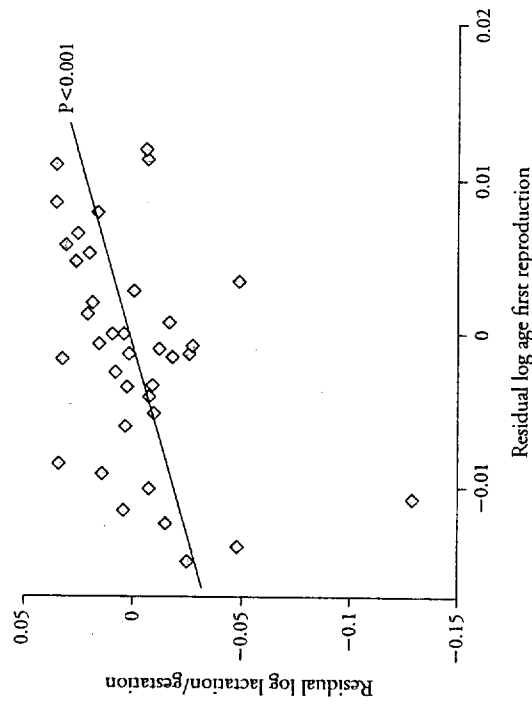


Figure 1.6. The effect of life history (as proxied by residual age of first reproduction) among primates on the length of lactation relative to gestation (also corrected for body weight by taking residuals), using independent contrasts. Life history data are from Deaner et al. (in press); reproductive data from van Schaik (2000).

ble difference. Domain-generality may be real in the sense that different cognitive adaptations share many neural mechanisms (compare Chapter 7), so that selection for one ability also produces improved abilities in another domain. However, domain-generality may also be an illusion. Assuming that approximately the same set of selective pressures operates in species with fast and slow life histories, species with slow life histories will be able to respond to more of them (compare Figure 1.5), leading to an accumulation of various kinds of domain-specific cognitive adaptations in these organisms. As a result, cognitive abilities in various different domains (e.g., ecological, social) will become concentrated in taxa with slow life histories. In taxa with fast life histories, in contrast, most abilities will be absent, and the few that are found will therefore be interpreted, correctly, as domain-specific cognitive adaptations.

True domain-generality can subsequently and gradually arise, or be strengthened, in organisms with slow life histories. Indeed, the presence of multiple specific cognitive adaptations may be a precondition for the evolution of domain-generality, because only in those organisms will there be selection on economizing on the neural substrates for cognition by sharing neural structures and pathways. Domain-general cognitive abilities, i.e., intelligence; may therefore be limited to species with sufficiently slow life histories. It will not be easy to test this speculation because it is hard to distinguish true domain-generality from accumulated domain-specific adaptations. Perhaps the difference can be demonstrated at the neuroanatomical level, or by exploring correlations in cognitive performance on a battery of tests across individuals of the same species.

Conclusion

Recently, the suggestion that cognition evolved in response to social demands has led to great interest in cognitive evolution, especially among primatologists. Although the idea that social strategizing provided the main selective pressure in primate cognitive evolution is now quite popular, we have argued that it is premature to consider the case closed. First, other non-exclusive benefits to cognition exist that may be important in some taxa. Second, all current hypotheses ignore the costs of cognitive adaptations, and therefore overlook the possibility that these adaptations may not evolve in certain taxa in spite of the obvious benefits. We showed that life history and relative brain size have undergone correlated evolution among primates and

among mammals in general, implying that only organisms with a slow life history could evolve significant cognitive adaptations.

The life history perspective has already yielded various new insights in cognitive evolution. First, because arboreal ancestry is a major correlate of life history among mammals, the unusual cognitive abilities of primates among mammals can be seen as the outcome of arboreal ancestry. Second, a life history approach suggests that a wide variety of factors may favor cognitive evolution, depending on the details of the taxon's natural history—a suggestion supported by a preliminary examination of the *Homo-Pan* contrast. Third, slow life history also may produce a variety of challenges directly or indirectly linked to social strategizing, e.g., via sexual coercion, strengthening the possibility that social strategizing was a major pacemaker. Fourth, the life history perspective also offers suggestions for the evolution of domain-general cognition.

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