INTRODUCTION

Great apes and humans are the largest-brained primates. Aside from a few extinct subfossil lemurs, they are also the largest in body mass. Body size is a key aspect of a species’ biology, a large organism having different energetic, ecological, and physical constraints than a small one. Brain size, in so far as it determines abilities to acquire, process, and act on information, is also a key aspect of a species’ biology and is linked to body size. Large animals have different informational problems to solve than do small ones, hence their respective sensory organs and nervous systems are sized and organized differently.

Mammalian body and brain size scale consistently with each other (Figure 18.1). This relation is generally described by allometric exponents that vary between 2/3 and 3/4 (e.g., Bauchot & Stephan 1966, 1969; Hofman 1982; Jerison 1973; Lande 1979; Martin 1981; Martin & Harvey 1985, Stephan 1972). From a paleontological perspective, the body–brain size relation offers an appealing way to evaluate the cognitive abilities of fossil taxa, a problem of particular importance for understanding hominid evolution.

A convincing theoretical basis for this general allometric statistical pattern, however, remains elusive (Deacon 1997; Harvey & Krebs 1990). Body mass is not a strict determinant of brain size, as species of similar size can have different brain sizes and cognitive abilities (Pagel & Harvey 1989). In addition, comparative analyses indicate considerable variation among taxa from general mammalian patterns (Pagel & Harvey 1989). Hominid brains, for example, are double or more their expected size as mammals. There are also phylogenetic differences in typical brain–body size relations within primates that reflect grade shifts in encephalization across taxa (Armstrong 1985a, b; Martin & Harvey 1985, Pagel & Harvey 1989).

One reason for the lack of a universal brain–body size correlation among mammalian species is that factors other than body mass or metabolism, such as locomotion, diet, predation risk, social structure, and life history, affect relations between body and brain size (see recent reviews in de Waal & Tyack 2003; other chapters in this volume). All of these factors and others may contribute to selective pressures for cognitive abilities. As such, allometric scaling models developed from analyses of relations between physical variables such as metabolic rate and body mass may not be appropriate models for relations between body and brain size.

Evolving a large brain depends upon a complex balance of costs and benefits, which vary from species to species. There are not likely to be simple explanations based upon simple physical principles. Observed correlations between brain size and body size, the variability in these relations, and the reasons underlying phylogenetic differences, require consideration of both direct and indirect influences. Direct influences include structural and metabolic constraints on encephalization and size-related needs: large-bodied animals are better able to support large crania and energetically expensive neural tissue than are small-bodied animals, and larger bodies may require more neurons to control. If this were all there was to the relation between body size and brain size, then we would expect simple and consistent statistical associations. However, additional indirect influences can independently affect both body size and intelligence, including the effects of selective pressures shaping other aspects of a species’ biology, such as locomotion, diet, predation risk, social interactions, and life history. If these indirect influences are important for determining brain–body size relations, then we expect more
complex and variable statistical patterns, as indicated by analyses of inter-taxon differences (Martin & Harvey 1985).

Because of the apparent complexities of brain–body relations and neurobiological differences among extant mammals, simple consideration of relative brain size provides only an incomplete picture of the cognitive abilities of fossil species. To understand scaling relations among body size, brain size, cognition, and other aspects of a species’ adaptation, we need first to understand the underlying selective pressures shaping cognitive function and related variables. Complex models involving ecological and social factors are required. Such models may provide new insights into the causal relations underlying statistical associations between body and brain size.

This chapter first examines the interrelations among multiple relevant variables and their relations with cognitive capacities and brain size that apply generally in primates, especially those linked with body size. This puts us in a stronger position to interpret the cognitive capabilities of extinct taxa, and therefore to understand the evolution of intelligence in the hominids.

PREVIOUS HYPOTHESES RELATING BODY MASS TO INTELLIGENCE

Logarithmic scaling between brain size and body size in mammals is often interpreted to suggest that increases in body size result in increases in brain mass in the absence of any selection for a particular brain function (Hofman...
Body size and intelligence in hominoid evolution

1983; Jerison 1973; Martin 1981, 1983) (Figure 18.1). The scatter about the line is interpreted as a change in brain mass that must be explained by some other factors. The questions to be answered are: (1) why do these observed scaling relations exist? and (2) why do some species depart from them?

Somatic factors: size, scaling and metabolism

A possible answer to the first question is that having a larger body with more sensory receptors sending input and more motor units to control requires greater processing power, hence larger brain size. This appears unlikely, however, because animals of similar size can vary dramatically in brain–body size relations. As an example among catarrhines, *Theropithecus oswaldi*, a large fossil papionin, was similar in body size to chimpanzees and female gorillas, with estimates ranging from about 20 to 128 kg (Delson et al. 2000; Martin 1993; and C. V. Ward unpublished data). Direct estimates of the cranial capacity of three specimens with body sizes ranging from 32 to 70 kg are 154, 155 and 200 cc (Martin 1993). Chimpanzees and gorillas of about the same body mass range, on the other hand, have brain sizes of roughly 275–580 cc (Tobias 1971). This variability, and the grade shifts in this relation evident among taxa (Begun & Kordos, Chapter 14, this volume), undermine the interpretation that brain size and body size are related by simple physical or physiological laws.

A related possibility is that somatic brain regions, which govern somatic and autonomic sensorimotor function, should scale with body size because larger bodies with their greater number of cells might need more neurons to receive input and send output (Abottiz 1996; Fox & Wilczynski 1986). In contrast, extrasomatic regions of the brain concerned with higher cognitive processing, such as the neocortex, are expected not to follow any fixed scaling pattern. Somatic regions of the brain correlate weakly with body size ($r = 0.5$), suggesting that a larger body does not require a larger somatic brain (Rilling & Insel 1998). Non-somatic regions show even weaker correlations.

A frequently cited explanation for observed brain–body size correlations is metabolic rate of either the individual or its mother (Jerison 1973; Martin 1983). Smaller animals have higher metabolic rates, limiting the size of metabolically expensive brain tissue. There are significant problems with this hypothesis, however. Taxa do not always scale as predicted. Metabolic rate is not always correlated with adult brain size (Harvey & Krebs 1990) or neonatal brain size (Pagel & Harvey 1988). Furthermore, taxa with similar metabolic structures and body masses can have markedly different trajectories of postnatal brain growth (Periera & Leigh 2002). Maternal or individual metabolic rates do not seem to constrain brain size tightly.

A small-bodied organism faces stricter structural, metabolic, and other constraints on attaining large brain size than a large-bodied one. A large body is necessary for attaining large brain size (Dunbar 1993). Smaller animals are usually subject to higher extrinsic mortality rates than are larger ones, decreasing the selective advantages of growing a larger brain at the expense of rapid generational turnover times. They also tend to have relatively faster metabolisms than do larger animals (Kleiber 1932), so maintaining a large brain would pose a relatively greater burden on them. Large body size results in both a slower metabolism and less predation risk, decreasing costs associated with growing and maintaining a large brain. Therefore, one mechanism for being able to afford a large brain in the presence of cognitive selection pressures would be to increase body size (Dunbar 1993). This would alter the cost–benefit ratio of increasing brain size by decreasing metabolic costs, and accordingly facilitate brain expansion. In addition, selection for slower life history or increased body size would decrease constraints imposed by life history and metabolism on brain size (van Schaik & Deaner 2003; Kelley, Chapter 15, van Schaik, Preuschoft & Watts, Chapter 11, this volume), easing constraints on brain expansion in species facing selection for increased intelligence.

Because the brain is so metabolically expensive, consuming up to 10% of calories for most mammals and up to 20% for modern humans (Armstrong 1990), it should be as small as possible for a given body mass and set of species-specific cognitive demands (Geary & Huffman 2002). The only way for an expanded brain to be retained by selection is if the benefits to the individual of improved cognitive processing outweigh the metabolic and structural costs. The expensive nature of brain tissue may partially explain why brain regions expand differentially in taxa responding to different information-processing demands (e.g., Adolphs 2003; Armstrong 1985b; Barton & Harvey 2000; de Winter & Oxnard 2001; Purves 1994; Semendeferi & Damasio 2003; Jerison 1973; Martin 1981, 1983) (Figure 18.1). The scatter about the line is interpreted as a change in brain mass that must be explained by some other factors. The questions to be answered are: (1) why do these observed scaling relations exist? and (2) why do some species depart from them?
Another factor arguing against evolution of a large, unspecified cortex of the sort proposed by Finlay and Darlington (1995), Finlay et al. (2001) or Barton (1999) is that the energetic costs of maintaining a large brain would not necessarily be balanced by significant functional improvements (Aboitiz 1996; cf. La Cerra & Bingham 1998). To expand the brain, neurons must increase in number rather than size to maintain conduction speed, as dendrite breadth must increase with the square power of length to maintain conduction velocity (Kaas 2000). With more neurons, each neuron will communicate with absolutely more but proportionately fewer neurons than before. Clusters of specialized neurons should appear with cortical expansion to permit fine-tuned processing of information or there can be relatively little improvement in cognitive sophistication (Geary & Huffman 2002; Kaas 2000; Nimchinsky et al. 1999; and see MacLeod, Chapter 7, this volume). For these reasons, areal specializations alongside greater interconnectedness both characterize the human and probably the great ape cortex (MacLeod, Chapter 7, this volume). Great apes and humans have larger neocortices, the area primarily responsible for flexible problem solving, than less socially complex species (Adolphs 2003; Barton 1996; Clark, Mitra & Wang 2001; de Winter & Oxnard 2001; Dunbar 1993; Dunbar & Bever 1998; Preuss 2001; Sawaguchi 1997), and also have augmented neocerebellar structures compared with other anthropoids that may be related to their especially complex behavioral challenges (MacLeod, Chapter 7, this volume).

Variation among mammal species in relative brain size and cognitive potential suggests that selection for overall or regional brain size increase affects metabolic rate or metabolic tradeoffs within an organism. A species under selective pressure to increase its cognitive complexity may experience selection to modify diet, altering calorie or nutrient intake to support brain expansion. Metabolic rate can also vary among mammalian species of similar body size, so it can also be modified by selection. For example, platyrhines have higher rates of oxygen metabolism than do strepsirhines of similar sizes (Armstrong 1990). This appears to have happened in the evolution of Homo, which reduced its gut size, diverting more metabolic energy to the brain (Aiello & Wheeler 1995). That the extra energy from a reduced gut was devoted to the brain and not to increasing reproductive output or some other reproductively valuable function can only be explained if brain size, and by inference intelligence, was under strong selective pressure.

### Locomotion

Povinelli and Cant (1995) argued that great apes, as large-bodied arboreal primates, face unique challenges in negotiating arboreal substrates due to increased substrate unpredictability and compliance, and face severe costs of failing to support their body weight high in the trees. These conditions would pose selective pressures for especially flexible and complex mental calculations during locomotion that would have survival and therefore reproductive consequences, and could have resulted in selection for negotiating safer movement in an arboreal setting. This led, they propose, to the evolution of self-concept and its supporting mental representation capabilities in the great ape lineage. However, as noted by Begun, Chapter 2, Gebo, Chapter 17, Hunt, Chapter 10, and Russon, Chapter 1, this volume, large bodied arboreal hominoids can be small brained (Oreopithecus), self-concepts may occur in mainly terrestrial hominids (Gorilla), and travel on highly compliant branches with deliberate, slow, non-stereotypical clambering occurs in small primates as well (some prosimians).

### Diet

Diet and body size are associated in primates (Clutton-Brock & Harvey 1977; Milton & LeMay 1976). Because larger animals tend to have relatively slower metabolic rates than smaller ones (Kleiber 1932), however, body size can affect the types and amounts of food in which a species will specialize. Very small primates are insectivorous, large ones are folivorous, and frugivores are typically intermediate in size (Kay 1984). When size and phylogenetic factors are controlled for, there is no set relation between diet and metabolism in primates, with folivores and frugivores often having similar metabolic rates (Elgar & Harvey 1987). There is also no correlation between encephalization and dietary quality or challenge, as measured by percentage of fruit in the diet (Ross, Chapter 8, this volume) or seasonality (Parker &
Gibson 1977, 1979), or between extractive foraging and neocortex size in primates (Barton & Dunbar 1997; Dunbar 1992). Identifying dietary features related to intelligence, however, may require more specific dietary measures (Ross & Jones 1999). Neither of these diet measures considers the particular form of frugivory in which great apes specialize, which is extended to include foods higher in protein and fat and non-fruit fallback foods on a seasonal basis to survive recurrent periods of fruit scarcity (Yamagiwa, Chapter 12, this volume). Even so, dietary pressures alone are unlikely to explain the evolution of enhanced intelligence in the great apes.

Social complexity

As a consequence of selection to cope with ecological pressures, most primates live in social groups (Wrangham 1980). Resource distribution affects the cost–benefit equation of living in groups, so dietary specializations can affect grouping size and patterns (Alexander 1974). Body size also affects social systems by altering susceptibility to predators, conspecific competition, resource availability and distribution, and habitat use.

The social brain hypothesis proposes that cognitive enhancements in anthropoid primates are associated with social complexity and is supported broadly across primates by comparative analyses (Barton & Dunbar 1997; Dunbar 1992; review in van Schaik et al., Chapter 11, this volume). These analyses typically find that group size and proxy measures for brain size (e.g., cranial capacity, neocortex ratios) are associated in a wide range of primates (e.g., Kudo & Dunbar 2001; Pawlowski, Lowen & Dunbar 1998; van Schaik & Deaner 2003). The social brain hypothesis as initially presented, however, fails to explain why primates with great-ape-like social systems, such as capuchins and macaques (Preuschoft & van Schaik 2000; Thierry, Wunderlich & Gueth 1989; Perry 2003), are not as intelligent as great apes or why great apes, with group sizes typical of other anthropoids, consistently show more complex cognition than all other anthropoids (in this volume, see Russon, Chapter 1). Closer examination, however, reveals that despite apparent social similarities, living great apes face more dynamic social problems than other nonhuman primates (van Schaik et al., Chapter 11, this volume), and so ancestral hominids may have been under stronger selective pressure to become better equipped for flexible social problem-solving abilities (Dunbar 1996; Whiten 1997; van Schaik et al., Chapter 11, this volume). Why great apes are more complex socially has not been made clear by the social brain model.

Social complexity may be related to patterns of sexual dimorphism in body size. Males are selected to grow to large size in taxa for which size is an advantage in male–male competitions that affect mating success, and this makes for rigid social structures. In monogamous primates where mating competition is minimal (e.g., gibbons), or where male–male coalitions are a significant component of their competition (e.g., Pan, hominins, capuchins), body size dimorphism is reduced. Gibbons are not relatively more intelligent than other primates so reduced size dimorphism alone is not directly correlated with greater intelligence. In species in which decreased body size dimorphism is related to coalitional behavior, however, the situation may be different. The social complexities of building and maintaining effective kin and non-kin coalitions, as documented among humans, male chimpanzees, and capuchin monkeys (Pawlowski et al. 1998; Wrangham 1999), may have selected for increased cognitive capacities (van Schaik et al., Chapter 11, this volume).

This particular combination of body mass and social factors may in part explain encephalization in Pan and Homo, but it does not explain the roughly equal levels of encephalization in Gorilla, Pongo, and probably Dryopithecus, Sivapithecus, and Australopithecus, all of which were strongly sexually dimorphic (Begun 2002; Kelley 2002; McHenry 1982). The combination of unusually complex coalitional behavior and reduction of body size dimorphism may have happened independently in Pan and Homo, since Australopithecus, which is more closely related to Homo, lacks at least some of these features (Ward et al. 1999). While complex coalitional behavior represents an aspect of social complexity that may select for intelligence, it is not the sole factor influencing selection for enhanced intelligence in hominids because encephalization preceded reduction in sexual dimorphism in hominids.

Life history

Body size is related to brain size via life history in several ways, in addition to easing metabolic constraints on brain growth as outlined above. Large body size tends to decrease extrinsic mortality by reducing susceptibility
to predators (Williams 1957; and see recent reviews in van Schaik & Deaner 2003; van Schaik et al. Preuschoft & Watts, Chapter 11, this volume). Large bodies take longer to grow, and a longer growth period may favor relatively larger brains by prolonging brain growth and programming (Barton 1993; Kelley, Chapter 15, this volume; Ross, Chapter 8, this volume; van Schaik & Deaner, 2003). Slow life histories have been hypothesized to allow longer time for brain growth or the learning involved to become a successful adult in humans (Dobzhansky 1962; Hallowell 1963; Mann 1975) and nonhumans (Joffe 1997; van Schaik & Deaner 2003; and see Ross, Chapter 8, this volume). However, time to reproductive maturity is not tightly related to rate or timing of brain development. Primates with the longest juvenile periods (humans), complete most of their brain size growth in infancy, well before the most complex learning tasks are tackled (Pereira & Leigh 2003; Ross, Chapter 8, this volume). Thus, prolonged juvenility may allow for brain growth, brain maintenance, experiential learning, or all three, depending on the species. While life history is an important correlate of intelligence and body size, slowing life history alone will not automatically result in increases in brain size and encephalization, but will only provide a conditions necessary for doing so when there is a fitness advantage to increased intelligence (see Kelley, Chapter 15, this volume).

A SYNTHESIS TO EXPLAIN BRAIN–BODY SIZE RELATIONS IN THE HOMINOMIDS

We suggest that body size and brain size co-evolved in significant but complex ways during hominin evolutionary history. Observed correlations between body and brain size are real. Allometry, however, does not signify a single universal constraint or scaling law. Instead, observed relations reflect a multi-factorial and often mutually reinforcing set of selective pressures. The specific allometric relation for each taxon depends on its phylogenetic history and its particular ecological and social circumstances. Considering only one or a subset of these circumstances will contribute to unsatisfying explanations for the relation between body and brain sizes.

Observed brain–body size scaling relations in hominids, as in other primates and non-primate mammals, result from parallel selection on both brain size and body size. Because selection for body size is related to selection for many other aspects of a species’ biology, such as metabolism, diet, habitat, life history, and social behavior, selection can produce similar combinations of traits. Situations favoring increased intelligence are often similar to those favoring increased body size. This would produce correlations independent of direct causal relations. Because closely related taxa share other adaptations that can affect and be affected by size, and these sets of adaptations often co-evolve, common patterns across taxa could result in the general relations generated by allometric analyses. One would not expect all taxa to share exactly the same relations, given different selective pressures and adaptive constraints faced by each. Species therefore should vary about a statistically derived line (as in Figure 18.1). Only by elucidating patterns of selection shaping many parts of a species’ biology and behavior can we hope to determine these relations and predict why and how variables are interrelated, and hence why observed scaling relations occur.

Selection pressures for enhancing cognition derive from situations that require increased flexibility and complexity in behavior and problem-solving (Geary & Huffman 2002). They concern biotic more than abiotic situations because the former are generally more variable, complex, and unpredictable. Broadly speaking, the most challenging may be predator–prey interactions and dynamic situations within social groups (Geary & Huffman 2002; West-Eberhard 2003). The more complex these become, the more complex and flexible cognition must be. Extant hominids face the most complex foraging challenges and the most sophisticated social interactions and relationships known in nonhuman primates (see many contributions in this volume).

Body size affects the cost–benefit ratio of evolving enhanced cognitive capacities by affecting susceptibility to predators and conspecific competitors, as well as diet, habitat use, the social system broadly, and life history, it also alters physical influences on brain size. Body size is associated with ecological dominance (Alexander 1989, 1990), a situation in which Darwin’s traditional hostile forces of nature (predation risk, food shortages, disease, and climate) decrease in their effects on differential reproduction relative to competition with conspecifics. Ecological dominance is accomplished in different ways by different species, but large body size is a common avenue. It represents a gradient, with some taxa being more ecologically dominant than others. An increase in body size reduces susceptibility to predation.
and lowers metabolic rate, potentially increasing ecological dominance, as well as relaxing energetic constraints on encephalization. Increases in intelligence can also increase ecological dominance, as they render individuals better able to locate and obtain food resources, evade predators, and otherwise modify their environments. The relative reduction in differential reproduction due to decreased extra-specific costs also effectively increases the fitness value of sophisticated social problem-solving abilities, in species for which sociality is most relevant to reproductive success.

This spiral of ecological dominance and increased social competition may have contributed to the evolution of the human grade of cognitive abilities (Alexander 1990; Flinn, Ward & Geary in press). Examples of non-human species with relatively high ecological dominance include elephants, dolphins, orcas, sperm whales, lions, and the great apes. Intraspecific interactions have significant fitness effects on individuals in most primate species (Alexander 1990; Flinn et al. in press), providing an initial condition in which an increase in ecological dominance will increase social competition and lead to more intense intra-specific arms races in social intelligence.

When social competition has significant fitness effects, relatively intelligent individuals who are able to negotiate their social and environmental settings better then their less cognitively sophisticated conspecifics stand to achieve higher net fertility. If a species’ social and physical environments are such that greater intelligence does not have significant fitness benefits, then large brains are not expected. Examples of long-lived, relatively large, relatively asocial, but not particularly encephalized species include Galapagos tortoises and rhinoceroses. One apparent exception to this rule, orangutans, who are often characterized as asocial yet highly intelligent, are actually more social than often supposed and show social complexity comparable to other great apes (see van Schaik et al., Chapter 11, this volume); they also share other key cognitive challenges with other great apes, such as especially complex foraging problems (see Yamagiwa, Chapter 12, this volume).

In terms of the model proposed here, *Oreopithecus* may be an exception that proves the rule. *Oreopithecus* probably was highly folivorous (Singleton, Chapter 16, this volume) and insular, and probably experienced little ecological competition or predator pressure due to its island habitat (Harrison & Rook 1997). Although it fits the large size–low predation pattern, its folivorous diet would have made it difficult to obtain adequate caloric and other nutrient resources to maintain a large brain. This and its comparatively unchallenging ecology would have made a large brain an attribute that it neither needed nor could afford, resulting in selection for a smaller brain, and correspondingly reduced cognitive abilities. Outside of primates, river dolphins and male angler fish are other examples suggesting that evolution can act to diminish brain size in the absence of positive selective pressures.

Most anthropoid primates tend to be frugivorous and experience social competition, although some taxa have undergone stronger selective pressure to negotiate more complex social systems than others. Great apes, because of their size and largely frugivorous diets, live in societies that tend to especially flexible fission–fusion with relatively high subordinate leverage and complex non-kin social relations that can affect social and therefore reproductive success (review in van Schaik et al., Chapter 11, this volume). This social complexity could favor enhanced cognitive abilities, and presumably brain size, until these increases are in turn constrained by other factors, and individuals are then selected to allocate energy to other efforts, such as parental effort. This arms race is species specific, because different ecological conditions and phylogenetic histories affect different species, and it explains phylogenetic differences in scaling patterns. Capuchin monkeys may share many aspects of their social system with chimpanzees, but a capuchin is only selected to out-compete other capuchin monkeys. It does not have to be as intelligent as a chimpanzee, reflecting its different phylogenetic heritage. The immediate ancestor of chimpanzees was already more encephalized than capuchins, and presumably more socially complex. Differences in such evolutionary starting points of intra-specific arms races, coupled with other constraints on different taxa, affects their ultimate trajectories.

The multiple covariates of selection may explain the lack of a tight correlation with social complexity and brain size. Because competition is relative to species, one should not predict equivalence in encephalization (i.e., EQ or neocortical index) or intelligence between taxa as mediated solely by social systems (e.g., Pawlowski et al. 1998; Preuschoft & van Schaik 2000; van Schaik et al., Chapter 11, this volume). Instead, among close phylogenetic relatives, we should see more socially complex species having relatively larger brains (or neocortices and
associated structures). Living catarrhines are generally more encephalized than platyrrhines and tend to have more complex social systems, though the most encephalized platyrrhines share some complex social features with cercopithecids. Among catarrhines, papionins are generally more encephalized than other cercopithecines, and hominids are more encephalized than hylabatids, after accounting for body mass (Gibson, Rumbaugh & Beran 2001; Begun & Kordos, Chapter 14, this volume). Generally, their higher encephalization levels are associated with greater social complexity, with levels of social complexity broadly tracking these encephalization differences (e.g., Dunbar 1996).

The neocortex is the primary site of learning and higher level cognitive processing, although other components such as the amygdala have supportive functions (Adolphs 2003; Siegal & Varley 2002). The cerebellum is also important, appearing to coordinate with the cortex to produce complex cognition (Rilling & Insel 1998; and see MacLeod, Chapter 7, this volume). The neocortex and the cerebellum are the two largest regions of the primate brain (MacLeod, Chapter 7, this volume); the cerebellum is disproportionately enlarged in apes over other nonhuman anthropoids and both enlarge at greater rates relative to the brain as a whole than more conservative components (see MacLeod, Chapter 7, this volume). Expansion of the brain to achieve enhanced cortical and cerebellar function would result in greater increases in overall brain size than would expansion driven by the functions of other regions. Doubling the neocortex results in a larger brain than doubling the hippocampus, for example. This is an important reason for the generally high association between behavioral complexities and brain size, with both social and ecological problems being important sources for these complexities.

In summary, particular combinations of diet, life history, social system, intelligence, and body size are likely to co-evolve, resulting in broad allometry between body and brain size. Some combinations appear unlikely. Large brains are costly for small-bodied primates, which are usually under selection for a high reproductive rate and fast life history due to high extrinsic mortality rates. Small primates are more likely to rely on insects for food, and coupled with high predation risks, this results in increased costs of grouping, and thus solitary life or small groups. Similarly, large primates are not expected to be relatively small branined. For primates, large size reduces predation risk, enabling flexibility in foraging party size. In great apes, even the comparatively solitary orangutan, it enables unusually flexible fission–fusion societies with high subordinate leverage and complex kin and non-kin interactions, all of which require exceptional cognitive sophistication (van Schaik et al., Chapter 11, this volume). Foraging patterns in great apes also tend to be especially complex. During hominoid evolution, constraints lifted by increasing body mass, combined with concomitant increases in ecological dominance in inherently social species, contributed to selecting for increased social and cognitive complexity.

**IMPLICATIONS FOR THE EVOLUTION OF HOMINID INTELLIGENCE**

Our ability to infer the cognitive capacities of fossil primates depends on the assessment of brain size, body size, dimorphism, diet, life history, and social system. The evolution of body mass in fossil apes is somewhat difficult to assess given uncertainties in determining phylogenetic relations of some taxa, and the diverse range of sizes of Miocene apes. Extant great apes range from about 33 to 170 kg in body mass (Smith & Jungers 1997). Basal catarrhines were considerably smaller, with propliopithecids (including *Aegyptopithecus zeuxis*) ranging from 5 to 7 kg (Fleagle 1999). Thus, it is likely that hominoids evolved from fairly small-bodied ancestors.

*Proconsul*, a stem hominoid with no direct evolutionary relation with extant apes (Begun, Ward & Rose 1997), ranged in size from about 9 to 60 kg (Table 18.1). Other apparently stem hominoids (*Afropithecus*, *Morotopihecus*) are also within this range, though toward the upper end. While a few possible stem hominoids (e.g., *Micropithecus*) are as small or smaller than gibbons, most stem hominoids are larger than siamangs, and it is likely that hylabatids are phylogenetic dwarfs (Begun, Chapter 2, this volume). This range does not follow any temporal or spatial patterning, however, and no trends are readily apparent. Among extant hominoids and their fossil relatives, only hylabatids are less than 20 kg in body mass. *Dryopithecus*, suggested to share a particularly close phylogenetic relation with hominids, is known from four species that all tend to be slightly smaller than chimpanzees in size (Begun 2002). Their 25–45 kg range is the likely ancestral condition for African hominoids, as australopithecine females also fall within this range. This is interesting, as *Pan* female body mass means range from 33.2 to 45.8 kg (Smith & Jungers 1997), suggesting that loss of significant body mass dimorphism in *Pan* may have involved females increasing size
in addition to or even instead of males decreasing in size.

Most hominoid taxa, living and fossil, are primarily frugivorous, although different species had relatively higher dependence on leaves (Kay & Ungar 1997) and some show use of hard foods (Singleton, Chapter 16, this volume). All extant hominids have anatomical and behavioral adaptations for processing especially challenging foods, often used as fallback resources in times of primary food scarcity (Bryne, Chapter 3, Russon & Begun, Chapter 19, Yamagiwa, Chapter 12, this volume). Most fossil hominids also have anatomical indications of an enhanced ability to exploit fallback foods, either in the form of large or specialized anterior teeth or large, thickly enameled molars and robust jaws (Russon & Begun, Chapter 19, Singleton, Chapter 16, this volume).

Early Miocene stem hominoids were not suspensory like extant hominoids, though a possible case has been made for *Morotopithecus* (Gebo, Chapter 17, this volume). Among middle and late Miocene hominids *Dryopithecus* had a clearly extant hominoid-like below-bran branch adaptation conceivably associated with the shift to a great-ape-sized brain and intelligence (i.e., Povinelli & Cant 1995). *Sivapithecus*, however, did not have the same type of below-bran positional behavior characteristic of extant great apes (reviews in Rose 1997; Ward 1997) and *Oreopithecus* was highly suspensory but small brained. This diversity suggests that locomotor pattern alone is not correlated in a straightforward manner with the evolution of intelligence.

The prolonged life histories and periods of immaturity characteristic of modern apes first appeared in the Miocene. The only basal hominoid for which evidence is available is *Proconsul heseloni*, which appears to have had a developmental trajectory, defined using timing of the eruption of the first molar, more like that of a hylabatid than a hominid (Beynon et al. 1998; Kelley 1997). Life history evolution seems to parallel the evolution of encephalization in hominoids. *Proconsul heseloni*, the only basal hominoid for which data are available, had a relative cranial capacity roughly like that of a similarly sized cercopithecids (Begun & Kordos, Chapter 14, this volume; Walker et al. 1983). *Afropithecus*, larger than *P. heseloni* and close in size to *P. nyanzae*, appears to have a delayed age of first molar eruption (Kelley & Smith 2003; Kelley, Chapter 15, this volume). Its brain size is unknown, but if similar to the similarly sized *P. nyanzae*, which is possible given the anatomy of the cranium, it may provide evidence than an extended life is a necessary but not a sufficient factor to account for brain size increases (see also...
Kelley, Chapter 15, Russon & Begun, Chapter 19, this volume). *Dryopithecus* has a further delayed age of first molar eruption, a life history change correlated to increased brain size, and is known to have had a great-ape-sized brain (Begun & Kordos, Chapter 14, Kelley, Chapter 15, this volume). *Sivapithecus* also had a delayed age at first molar eruption, though no direct evidence of brain size exists in this otherwise well-known taxon (Kelley, Chapter 15, this volume).

All living and fossil hominoids for which there are data available are highly sexually dimorphic in body mass except for hyllobatids, *Pan*, and *Homo*, implying intense mate competition and some level of group complexity (Plavcan 2001; Yamagiwa, Chapter 12, this volume). This suggests that polygynous mating systems with fairly high levels of male–male competition for access to females represent the ancestral hominoid condition. Reduced size body mass dimorphism is associated with monogamy in hyllobatids. *Pan* and *Homo* have independently reduced body mass dimorphism levels yet increased (perhaps both) or at least maintained (in *Pan*) significant levels of encephalization, suggesting that their male–male coalitional behavior is associated with the dimorphism changes.

In addition to coalitionary behavior, chimpanzees, orangutans, and *Homo* share the traits of tool use and manufacture. If chimpanzees and orangutans are more intelligent than other apes, this would involve some as yet undetected brain attribute other than mass to account for cognitive differences, because brain mass alone does not distinguish among great apes, and no significant cognitive differences have been documented. This has profound implications for interpreting fossil hominin behavior and for the suitability of chimpanzees as a source of behavioral models of human evolution.

If *Pongo* and *Gorilla* are as intelligent as *Pan*, it may be that the presence of coalitions maintain and even reinforce encephalization in *Pan* and *Homo* but that other factors achieve the same end in other fossil and living hominids. For *Pongo* and *Gorilla* it could be foraging challenges, other social problems or, at least in the case of *Pongo*, very slow reproductive turnover. All great apes appear to share fission–fusion tendencies rendered more complex by the effects of large body size (increased social leverage, less rigid dominance, enhanced social tolerance), so complex social problems may simply manifest themselves in other ways. It is also the case that *Pan* shares dietary complexities with the other great apes associated with seasonal fruit scarcities, so shared ecological pressures may be among the forces behind their encephalization. Once achieved, encephalization is likely to be maintained if social interactions remain important, although there is no reason a priori to believe that only one mechanism is involved.

In summary, the evolution of hominoid intelligence can best be studied by examining a combination of many types of data. The last common ancestor of hominoids was likely the size of a large cercopithecid, perhaps a baboon, with a similar life history and frugivorous diet. The hominid last common ancestor increased its brain size and body size, extended periods of its life history, and altered its diet. It also may have begun further restructuring its brain to improve cognitive function internally, leading to the more complex cortical structure, both internally and externally, of extant great apes (Adolphs 2003; McLeod, Chapter 7, this volume; Nimchinsky et al. 1999; Semendeferi & Damasio 2000). The increased ecological dominance resulting from large body mass resulted in social interactions having increased relative roles in determining individual reproductive success, resulting in selection for increased intelligence. This process tapered off somewhat through the late Miocene and early hominin evolution, when other constraints on cognitive abilities appear to have been reached (see Potts, Chapter 13, and Begun & Kordos, Chapter 14, this volume). The process of encephalization later took off again in *Homo*.

**CONCLUSIONS**

Complexities in brain–body size relations make predictions of brain size from body size and assessment of cognitive capacities from brain–body size ratio more complicated than once supposed. To track the evolution of intelligence in the fossil record, one cannot simply calculate EQ and have the whole story. However, recognition of the interrelations between body size, metabolism, ecological dominance, sociality, life history, diet, and other factors help explain previously enigmatic aspects of brain size and scaling relations within primates. With more complex models incorporating these other adaptive links, we can better explain variations in brain size, body size, and cognitive abilities among extant animals. If we can identify some of these other aspects of species’ biology in the fossil record, we can then more accurately track changes in intelligence over evolutionary time.

Many of these factors have been identified as correlates of intelligence. Here, we suggest that the concepts
of ecological dominance and intra-specific arms races in
cognitive capacities (Alexander 1989) are important, yet
hitherto unrecognized, phenomena. Ecological domi-
nance alters selective pressures in regard to predation
and to sociality. Given possible associations between
body size, longevity, and diet on the one hand, and ecol-
logical dominance on the other, increased selective pres-
sure for mental adaptations to a complex social and ecol-
ogical environment may result in increased brain size.

The recognition of the importance of social compe-
tition for sophisticated cognitive capacities may explain
some broad intertaxic scaling patterns, such as why
platyrrhines and catarrhines with similar social systems
are not similarly encephalized. Social competition is
relative within a species, with individuals competing
against conspecifics and not against an external factor.
If levels of intelligence are reached as a consequence
of social arms races, they are necessarily dependent on
lineage history and phylogenetic starting points. Most
primates, particularly haplorhines, are inherently social,
and when ecological dominance is increased by reduc-
predation, increasing dietary quality, or changing
other factors such as locomotion, social competition
increases in relative importance for individual reproduc-
tive success. This produces within-species arms races in
social skills that will continue until capped by other con-
straints, whether ecological, metabolic, or structural.

The evolution of body size in great apes influenced
the evolution of great ape intelligence. Size decreased
metabolic constraints on encephalization as it increased
ecological dominance by reducing predation risk. It
also led to longer life histories, which in turn favored
increased cognitive capacities. All of these factors are
interrelated, and feed back on one another. It is in this
context that we are in an improved position to study how
and why intelligence evolved in great apes.

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