



Chapter 18

Body Size and Intelligence in Hominoid

Evolution

chapter

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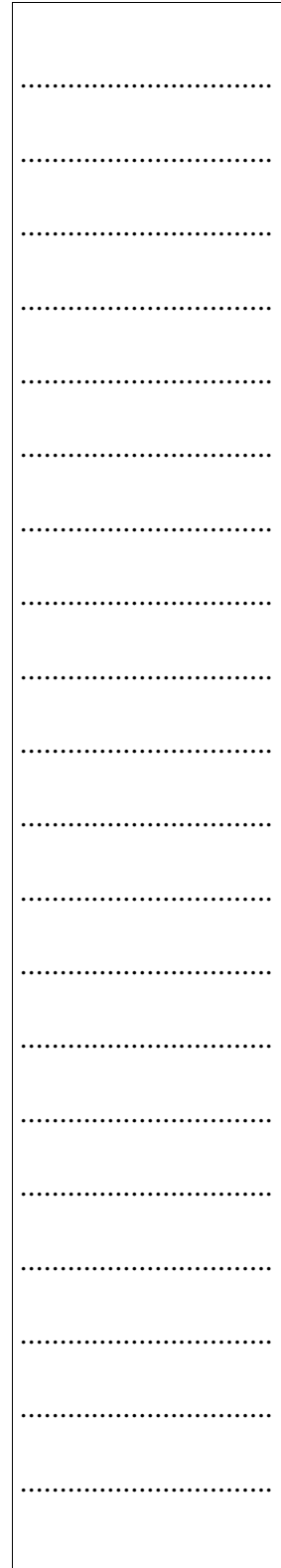
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1 A convincing theoretical basis for this general allometric statistical
2 pattern, however, remains elusive (Deacon 1997; Harvey & Krebs 1990).
3 Body mass is not a strict determinant of brain size, as species of similar
4 size can have different brain sizes and cognitive abilities (Pagel & Harvey
5 1989). In addition, comparative analyses indicate considerable variation
6 among taxa from general mammalian patterns (Pagel & Harvey 1989).
7 Hominid brains, for example, are double or more their expected size as
8 mammals. There are also phylogenetic differences in typical brain-body
9 size relations within primates that reflect grade shifts in encephalization
10 across taxa (Armstrong 1985a, b; Martin & Harvey 1983, Pagel & Harvey
11 1989).

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

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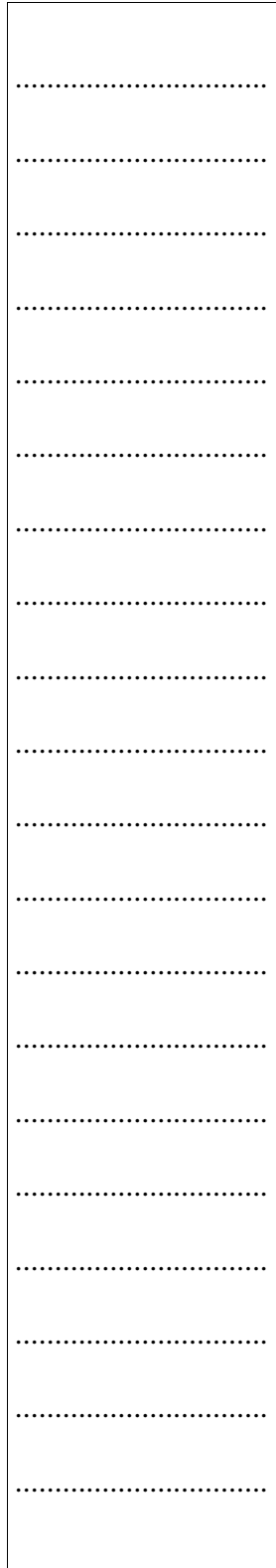
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1 neurobiological differences among extant mammals, simple consideration
2 of relative brain size provides only an incomplete picture of the cognitive
3 abilities of fossil species. To understand scaling relations among body size,
4 brain size, cognition and other aspects of a species' adaptation, we need to
5 first understand the underlying selective pressures shaping cognitive
6 function and related variables. Complex models involving ecological and
7 social factors are required. Such models may provide new insights into the
8 causal relations underlying statistical associations between body and brain
9 size. This chapter first examines the interrelations among multiple relevant
10 variables and their relations with cognitive capacities and brain size that
11 apply generally in primates, especially those linked with body size. This
12 puts us in a stronger position to interpret the cognitive capabilities of
13 extinct taxa, and therefore to understand the evolution of intelligence in the
14 hominids.



A-Head

15 **Previous hypotheses relating body mass to intelligence**

16 Logarithmic scaling between brain size and body size in mammals is often
17 interpreted to suggest that increases in body size result in increases in brain
18 mass in the absence of any selection for a particular brain function

1 have markedly different trajectories of postnatal brain growth (Periera &
2 Leigh 2002). Maternal or individual metabolic rates do not seem to
3 constrain brain size tightly.

4 A small-bodied organism faces stricter structural, metabolic, and other
5 constraints on attaining large brain size than a large-bodied one. A large
6 body is necessary for attaining large brain size (Dunbar 1993). Smaller
7 animals are usually subject to higher extrinsic mortality rates than are
8 larger ones, decreasing the selective advantages of growing a larger brain at
9 the expense of rapid generational turnover times. They also tend to have
10 relatively faster metabolisms than do larger animals (Kleiber 1932), so
11 maintaining a large brain would pose a relatively greater burden on them.
12 Large body size results in both a slower metabolism and less predation
13 risk, decreasing costs associated with growing and maintaining a large
14 brain. Therefore, one mechanism for being able to afford a large brain in
15 the presence of cognitive selection pressures would be to increase body
16 size (Dunbar 1993). This would alter the cost/benefit ratio of increasing
17 brain size by decreasing metabolic costs, and accordingly facilitate brain
18 expansion. In addition, selection for slower life history or increased body
19 size would decrease constraints imposed by life history and metabolism on

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1 brain size (van Schaik & Deaner 2003; Kelley, van Schaik *et al.* this
2 volume), easing constraints on brain expansion in species facing selection
3 for increased intelligence.

4 Because the brain is so metabolically expensive, consuming up to
5 10% of calories for most mammals and up to 20% for modern humans
6 (Armstrong 1990), it should be as small as possible for a given body mass
7 and set of species-specific cognitive demands (Geary & Huffman 2002).
8 The only way for an expanded brain to be retained by selection is if the
9 benefits to the individual of improved cognitive processing outweigh the
10 metabolic and structural costs. The expensive nature of brain tissue may
11 partially explain why brain regions expand differentially in taxa responding
12 to different information processing demands (e.g., Adolphs 2003;
13 Armstrong 1985b; Barton & Harvey 2000; MacLeod, this volume; Purves
14 1994; Semendeferi & Damasio 2000; Whiting & Barton 2003; de Winter &
15 Oxnard 2001; *contra* Finlay & Darlington 1995, Finlay *et al.* 2001; Rakic
16 1988; 1995b): it is too costly to sustain expansions that are not strictly
17 necessary.

18 Another factor arguing against evolution of large, unspecified cortex
19 of the sort proposed by Finlay and Darlington (1995), Finlay *et al.* (2001)

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1 or Barton (1999) is the energetic costs of maintaining a large brain would
2 not necessarily be balanced by significant functional improvements
3 (Aboitiz 1996; cf. La Cerra & Bingham 2002). To expand the brain,
4 neurons must increase in number rather than size to maintain conduction
5 speed, as dendrite breadth must increase with the square power of length to
6 maintain conduction velocity (Kaas 2000). With more neurons, each
7 neuron will communicate with absolutely more but proportionately fewer
8 neurons than before. Clusters of specialized neurons should appear with
9 cortical expansion to permit fine-tuned processing of information, or there
10 can be relatively little improvement in cognitive sophistication (Geary &
11 Huffman 2002; Kaas 2000; Nimchinsky *et al.* 2002; and see MacLeod this
12 volume). For these reasons, areal specializations alongside greater
13 interconnectedness both characterize the human and probably the great ape
14 cortex (MacLeod this volume). Great apes and humans have larger
15 neocortices, the area primarily responsible for flexible problem solving,
16 than less socially complex species (Adolphs 2003; Barton 1996; Clark *et*
17 *al.* 2001; Dunbar 1993; Dunbar & Bever 1998; Preuss 2001; Sawaguchi
18 1997; de Winter & Oxnard 2001), and also have augmented neocerebellar
19 structures compared to other anthropoids that may be related to their
20 especially complex behavioral challenges (MacLeod this volume).

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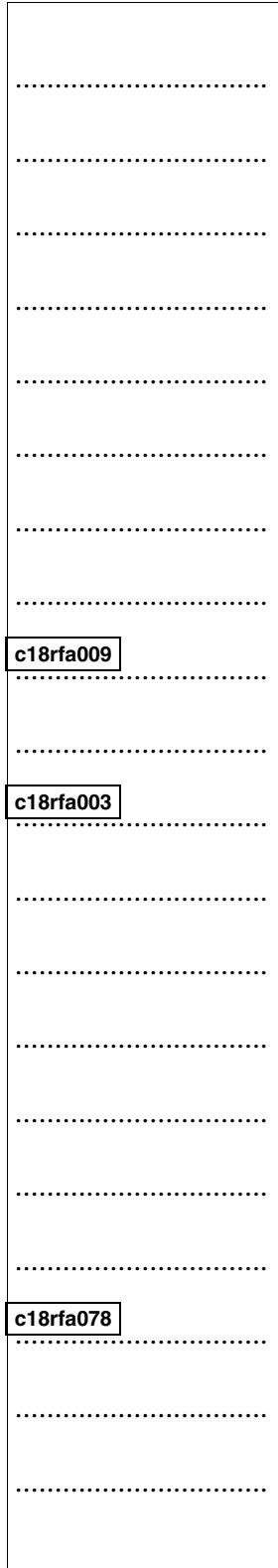
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1 Variation among mammal species in relative brain size and cognitive
2 potential suggests that selection for overall or regional brain size increase
3 affects metabolic rate or metabolic tradeoffs within an organism. A species
4 under selective pressure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



B-Head

16 Locomotion

17 Povinelli and Cant (1995) argued that great apes, as large-bodied arboreal
18 primates, face unique challenges in negotiating arboreal substrates due to
19 increased substrate unpredictability and compliance, and face severe costs

1 folivorous, and frugivores typically intermediate in size (Kay 1984). When
2 size and phylogenetic factors are controlled for, there is no set relation
3 between diet and metabolism in primates, with folivores and frugivores
4 often having similar metabolic rates (Elgar & Harvey 1987). There is also
5 no correlation between encephalization and dietary quality or challenge, as
6 measured by percent fruit in diet (Ross this volume) or seasonality (Parker
7 & Gibson 1977, 1979), or between extractive foraging and neocortex size
8 in primates (Dunbar 1992; Barton & Dunbar 1997). Identifying dietary
9 features related to intelligence, however, may require more specific dietary
10 measures (Ross & Jones 1999). Neither of these diet measures considers
11 the particular form of frugivory in which great apes specialize, which is
12 extended to include foods higher in protein and fat and non-fruit fallback
13 foods on a seasonal basis to survive recurrent periods of fruit scarcity
14 (Yamagiwa this volume). Even so, dietary pressures alone are unlikely to
15 explain the evolution of enhanced intelligence in the great apes.

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B-Head

16 Social complexity

17 As a consequence of selection to cope with ecological pressures, most
18 primates live in social groups (Wrangham 1980). Resource distribution
19 affects the cost-benefit equation of living in groups, so dietary

1 specializations can affect grouping size and patterns (Alexander 1974).
2 Body size also affects social systems by altering susceptibility to predators,
3 conspecific competition, resource availability and distribution, and habitat
4 use.

5 The social brain hypothesis proposes that cognitive enhancements in
6 anthropoid primates are associated with social complexity and is supported
7 broadly across primates by comparative analyses (Barton & Dunbar 1997;
8 Dunbar 1992; review in van Schaik *et al.* this volume). These analyses
9 typically find that group size and proxy measures for brain size (e.g.,
10 cranial capacity, neocortex ratios) are associated in a wide range of
11 primates (e.g., Kudo & Dunbar 2001; Pawlowski *et al.* 1998; van Schaik &
12 Deaner 2003). The social brain hypothesis as initially presented, however,
13 fails to explain why primates with great ape-like social systems, such as
14 capuchins and macaques (Preuschoft & van Schaik 2000; Thierry *et al.*
15 1989; Perry 2003), are not as intelligent as great apes or why great apes,
16 with group sizes typical of other anthropoids, consistently show more
17 complex cognition than all other anthropoids (in this volume, see Russon
18 a). Closer examination, however, reveals that despite apparent social
19 similarities, living great apes face more dynamic social problems than
20 other nonhuman primates (van Schaik *et al.* this volume), and so ancestral

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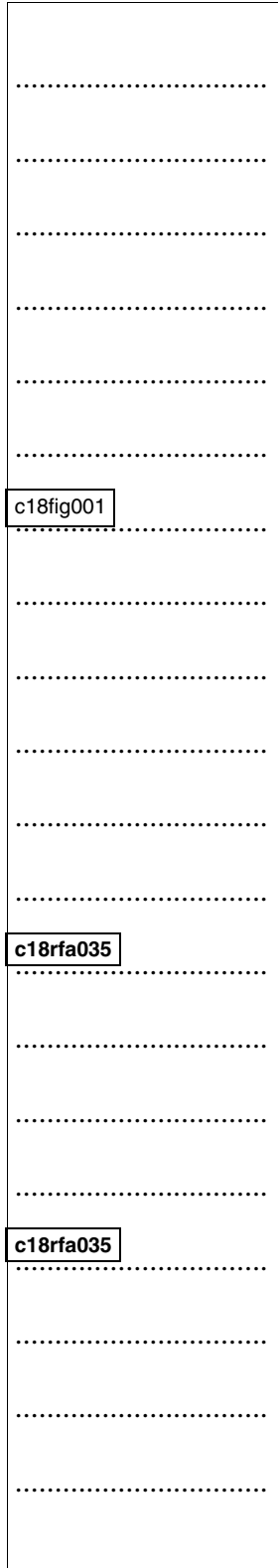
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1 taxa share other adaptations that can affect and be affected by size, and
2 these sets of adaptations often co-evolve, common patterns across taxa
3 could result in the general relations generated by allometric analyses. One
4 would not expect all taxa to share exactly the same relations, given
5 different selective pressures and adaptive constraints faced by each.
6 Species therefore should vary about a statistically derived line (as in Figure
7 18.1). Only by elucidating patterns of selection shaping many parts of a
8 species' biology and behavior can we hope to determine these relations and
9 predict why and how variables are interrelated, and hence why observed
10 scaling relations occur.

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



1 primates (see many contributions in this volume)

2 Body size affects the cost-benefit ratio of evolving enhanced cognitive

3 capacities by affecting susceptibility to predators and conspecific

4 competitors, as well as diet, habitat use, the social system broadly, and life

5 history' it also alters physical influences on brain size. Body size is

6 associated with ecological dominance (Alexander 1989, 1990), a situation

7 in which Darwin's traditional hostile forces of nature (predation risk, food

8 shortages, disease, and climate) decrease in their effects on differential

9 reproduction relative to competition with conspecifics. Ecological

10 dominance is accomplished in different ways by different species, but large

11 body size is a common avenue. It represents a gradient, with some taxa

12 being more ecologically dominant than others. An increase in body size

13 reduces susceptibility to predation and lowers metabolic rate, potentially

14 increasing ecological dominance, as well as relaxing energetic constraints

15 on encephalization. Increases in intelligence can also increase ecological

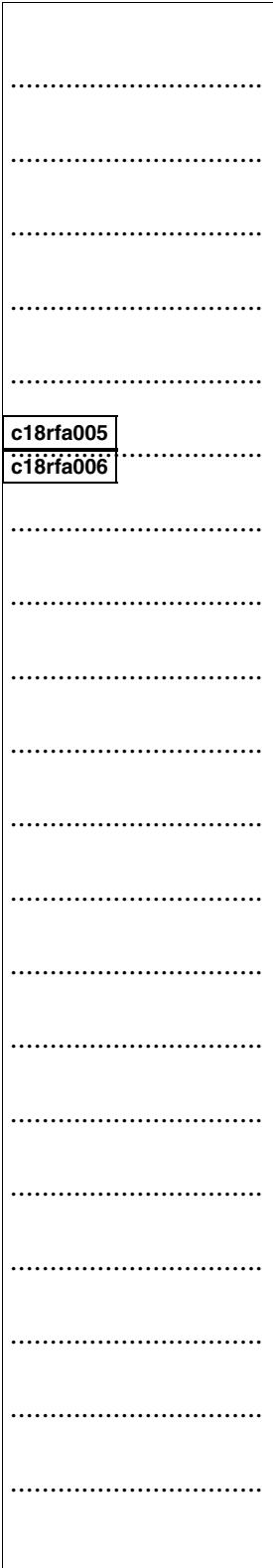
16 dominance, as they render individuals better able to locate and obtain food

17 resources, evade predators, and otherwise modify their environments. The

18 relative reduction in differential reproduction due to decreased

19 extra-specific costs also effectively increases the fitness value of

20 sophisticated social problem solving abilities, in species for which sociality



1 is most relevant to reproductive success.

2 This spiral of ecological dominance and increased social competition
3 may have contributed to the evolution of the human grade of cognitive
4 abilities (Alexander 1990; Flinn *et al.* in prep). Examples of nonhuman
5 species with relatively high ecological dominance include elephants,
6 dolphins, orcas, sperm whales, lions, and the great apes. Intraspecific
7 interactions have significant fitness effects on individuals in most primate
8 species (Alexander 1990; Flinn *et al.* in prep), providing an initial
9 condition in which an increase in ecological dominance will increase social
10 competition and lead to more intense intraspecific arms races in social
11 intelligence.

12 When social competition has significant fitness effects, relatively
13 intelligent individuals who are able to negotiate their social and
14 environmental settings better than their less cognitively sophisticated
15 conspecifics stand to achieve higher net fertility. If a species' social and
16 physical environments are such that greater intelligence does not have
17 significant fitness benefits, then large brains are not expected. Examples of
18 long-lived, relatively large, relatively asocial, but not particularly
19 encephalized species include Galapagos tortoises and rhinoceroses. One
20 apparent exception to this rule, orangutans, who are often characterized as

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1 asocial yet highly intelligent, are actually more social than often supposed
2 and show social complexity comparable to other great apes (see van Schaik
3 *et al.* this volume); they also share other key cognitive challenges with
4 other great apes, such as especially complex foraging problems (see
5 Yamagiwa this volume).

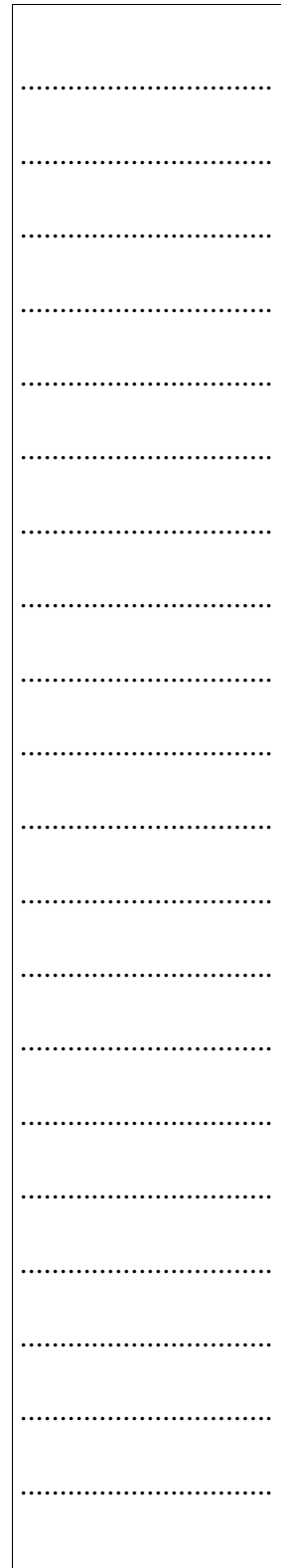
6 In terms of the model proposed here, *Oreopithecus* may be an
7 exception that proves the rule. *Oreopithecus* probably was highly
8 folivorous (Singleton this volume) and insular, and probably experienced
9 little ecological competition or predator pressure due to its island habitat
10 (Harrison &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

19 Most anthropoid primates tend to be frugivorous and experience
20 social competition, although some taxa have undergone stronger selective

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

20 The multiple covariates of selection may explain the lack of a tight



1 correlation with social complexity and brain size. Because competition is
2 relative to species, one should not predict equivalence in encephalization
3 (i.e., EQ or neocortical index) or intelligence between taxa as mediated
4 solely by social systems (e.g., Pawlowski *et al.* 1998; Preuschoft & van
5 Schaik 2000; van Schaik *et al.* this volume). Instead, among close
6 phylogenetic relatives, we should see more socially complex species
7 having relatively larger brains (or neocortices and associated structures).
8 Living catarrhines are generally more encephalized than platyrrhines and
9 tend to have more complex social systems, though the most encephalized
10 platyrrhines share some complex social features with cercopithecids.
11 Among catarrhines, papionins are generally more encephalized than other
12 cercopithecines, and hominids are more encephalized than hylobatids, after
13 accounting for body mass (Gibson *et al.* 2001; Begun & Kordos this
14 volume). Generally, their higher encephalization levels are associated with
15 greater social complexity, with levels of social complexity broadly tracking
16 these encephalization differences (e.g., Dunbar 1996).

17 The neocortex is the primary site of learning and higher level
18 cognitive processing, although other components such as the amygdala
19 have supportive functions (Adolphs 2003; Siegal & Varley 2002). The
20 cerebellum is also important, appearing to coordinate with the cortex to

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1 (including *Aegyptopithecus zeuxis*) ranging from 5–7 kg (Fleagle 1999).
2 Thus, it is likely that hominoids evolved from fairly small-bodied ancestors.
3 *Proconsul*, a stem hominoid with no direct evolutionary relation with
4 extant apes (Begun *et al.* 1997), ranged in size from about 9 to 60
5 kilograms (Table 18.1). Other apparently stem hominoids (*Afropithecus*,
6 *Morotopithecus*) are also within this range, though toward the upper end.
7 While a few possible stem hominoids (e.g., *Micropithecus*) are as small or
8 smaller than gibbons, most stem hominoids are larger than siamangs, and it
9 is likely that hylobatids are phylogenetic dwarfs (Begun this volume). This
10 range does not follow any temporal or spatial patterning, however, and no
11 trends are readily apparent. Among extant hominoids and their fossil
12 relatives, only hylobatids are less than 20 kg in body mass. *Dryopithecus*,
13 suggested to share a particularly close phylogenetic relation with hominids,
14 is known from four species that all tend to be slightly smaller than
15 chimpanzees in size (Begun 2002). Their 25–45 kg range is the likely
16 ancestral condition for African hominoids, as australopithecine females
17 also fall within this range. This is interesting, as *Pan* female body mass
18 means range from 33.2–45.8 kg (Smith & Jungers 1997), suggesting that
19 loss of significant body mass dimorphism in *Pan* may have involved
20 females increasing size in addition to or even instead of males decreasing

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1 of extant great apes (reviews in Rose 1997; Ward 1997) and *Oreopithecus*
2 was highly suspensory but small brained. This diversity suggests that
3 locomotor pattern alone is not correlated in a straightforward manner with
4 the evolution of intelligence.

5 The prolonged life histories and period of immaturity characteristic of
6 modern apes first appeared in the Miocene. The only basal hominoid for
7 which evidence is available is *Proconsul heseloni*, which appears to have
8 had a developmental trajectory, defined using timing of the eruption of the
9 first molar, more like that of a hylobatid than a hominid (Beynon *et al.*
10 1998; Kelley 1997). Life history evolution seems to parallel the evolution
11 of encephalization in hominoids. *Proconsul heseloni*, the only basal
12 hominoid for which data are available, had a relative cranial capacity
13 roughly like that of a similarly sized cercopithecids (Begun & Kordos this
14 volume; Walker *et al.* 1993). We have no information, however, on brain
15 size or life history of larger sized basal hominoids with which to explore
16 variation in these parameters. *Dryopithecus* has a further delayed age of
17 first molar eruption, a life history change correlated to increased brain size,
18 and is known to have had great ape-sized brain (Begun & Kordos, Kelley
19 this volume). *Sivapithecus* also had a delayed age at first molar eruption
20 though no direct evidence of brain size exists in this otherwise well known

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1 taxon (Kelley 1997, this volume).

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

14 In addition to coalitionary behavior, chimpanzees, orangutans and
15 *Homo* share the traits of tool use and manufacture. If chimpanzees and
16 orangutans are more intelligent than other apes, this would involve some as
17 yet undetected brain attribute other than mass to account for cognitive
18 differences, because brain mass alone does not distinguish among great
19 apes, and no significant cognitive differences have been documented. This
20 has profound implication for interpreting fossil hominin behavior and for

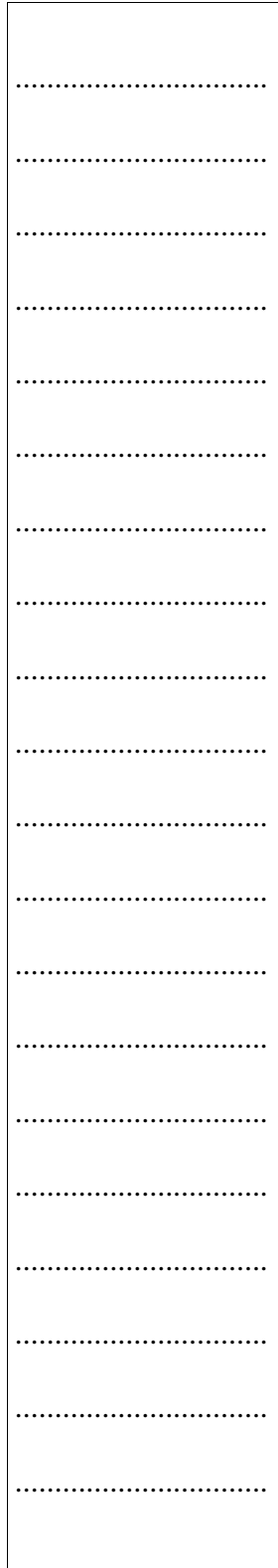
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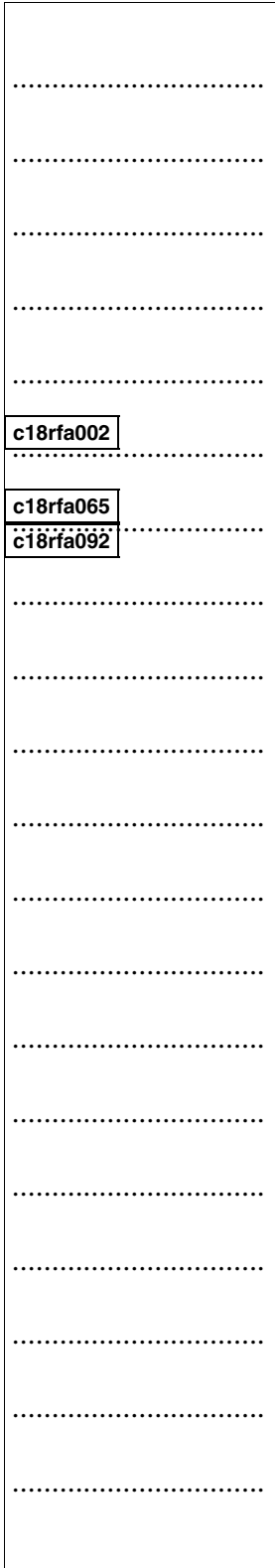
1 the suitability of chimpanzees as a source of behavioral models of human
2 evolution.

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

18 In summary, the evolution of hominoid intelligence can be best
19 studied by examining a combination of many types of data. The last
20 common ancestor of hominoids was likely the size of a large cercopithecoid,



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



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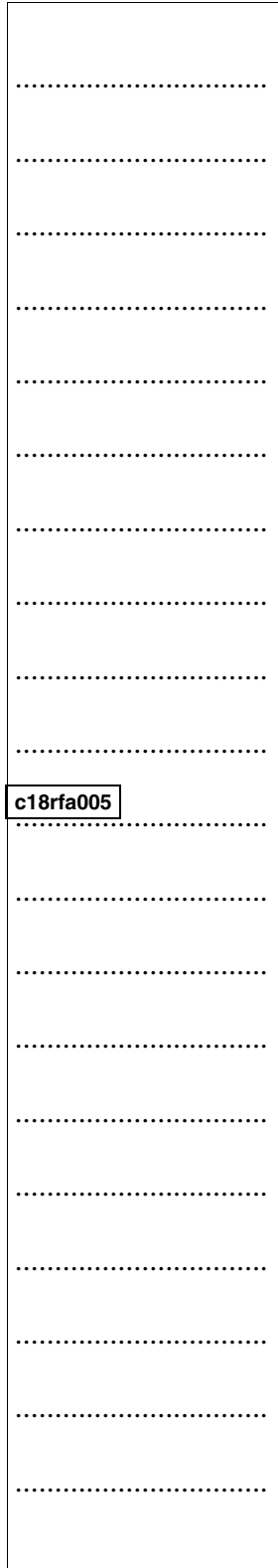
15 **Conclusions**

16 Complexities in brain-body size relations make predictions of brain size
17 from body size and assessment of cognitive capacities from brain/body size
18 ratio more complicated than once supposed. To track the evolution of
19 intelligence in the fossil record, one cannot simply calculate EQ and have

1 the whole story. However, recognition of the interrelations between body
2 size, metabolism, ecological dominance, sociality, life history, diet, and
3 other factors help explain previously enigmatic aspects of brain size and
4 scaling relations within primates. With more complex models incorporating
5 these other adaptive links, we can better explain variations in brain size,
6 body size and cognitive abilities among extant animals. If we can identify
7 some of these other aspects of species' biology in the fossil record, we can
8 then more accurately track changes in intelligence over evolutionary time.

9 Many of these factors have been identified as correlates of
10 intelligence. Here, we suggest that the concepts of ecological dominance
11 and intraspecific arms races in cognitive capacities (Alexander 1989) are
12 important, yet hitherto unrecognized, phenomena. Ecological dominance
13 alters selective pressures in regard to predation and to sociality. Given
14 possible associations between body size, longevity, and diet on the one
15 hand, and ecological dominance on the other, increased selective pressure
16 for mental adaptations to a complex social and ecological environment
17 may result in increased brain size.

18 The recognition of the importance of social competition for
19 sophisticated cognitive capacities may explain some broad intertaxic
20 scaling patterns, such as why platyrrhines and catarrhines with similar



1 social systems are not similarly encephalized. Social competition is
2 relative within a species, with individuals competing against conspecifics
3 and not against an external factor. If levels of intelligence are reached as a
4 consequence of social arms races, they are necessarily dependent on
5 lineage history and phylogenetic starting points. Most primates,
6 particularly haplorhines, are inherently social, and when ecological
7 dominance is increased by reducing predation, increasing dietary quality,
8 or changing other factors such as locomotion, social competition increases
9 in relative importance for individual reproductive success. This produces
10 within species arms races in social skills that will continue until capped by
11 other constraints, whether ecological, metabolic, or structural.

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

A-Head

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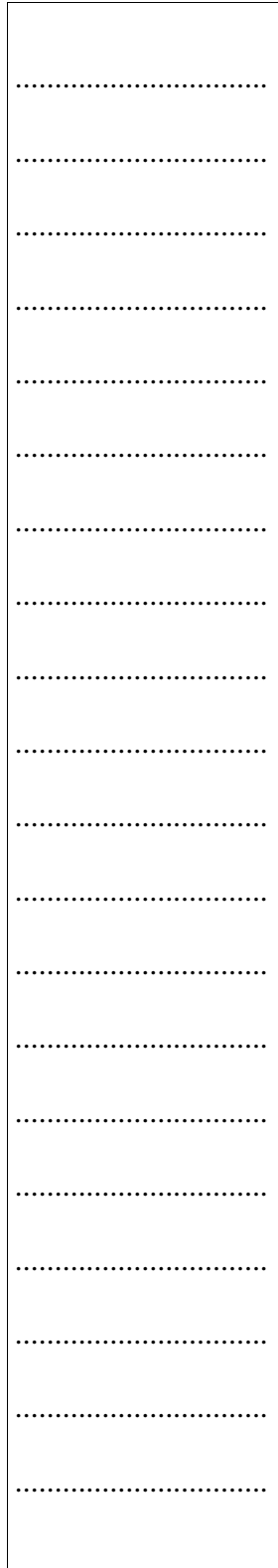
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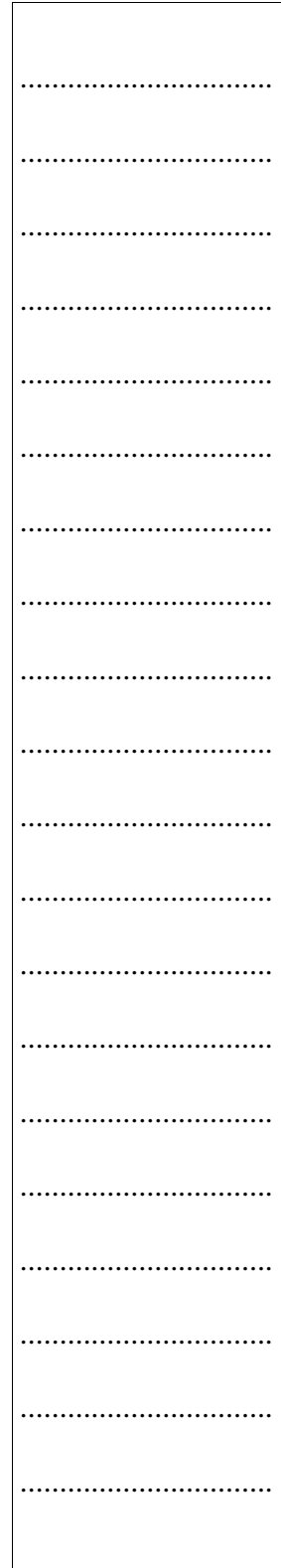
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c18tab001

Table 18.1. *Ballpark body mass estimates (kg) for fossil hominoids discussed in this chapter*

	Males	Females	Evidence
<i>Proconsul heseloni</i>	?	10	Dental, cranial & postcranial
<i>Proconsul nyanzae</i>	35	15	Dental, palatal & postcranial
<i>Micropithecus clarki</i>	?	3.5	Dental and palatal
<i>Afropithecus</i>	35	?	Dental, facial & postcranial
<i>Morotopithecus</i>	54	?	Dental, facial & postcranial
<i>Dryopithecus laietanus</i>	35	20	Dental, cranial and postcranial
<i>Dryopithecus brancoi</i>	40	25	Dental, cranial and postcranial
<i>Sivapithecus punjabicus</i>	40	20	Dental, cranial and postcranial
<i>Sivapithecus parvada</i>	60	?	Dental, postcranial
<i>Oreopithecus</i>	30	15	Dental, cranial and postcranial
<i>Australopithecus*</i>	70	31	Postcranial

* *Australopithecus afarensis*. Based on estimates from Fleagle (1999), Gebo *et al.* (1997), Harrison (1989), Jungers (1987), Leakey & Walker (1997), McHenry (1988), Ruff *et al.* (1989), Walker *et al.* (1993) and personal observations (which authors).

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