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The Evolution of Diet, Brain and Life History among Primates and Humans

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Introduction

This paper presents a theory of the brain and lifespan evolution and applies it to both the primate order, in general, and to the hominin line, in particular. To address the simultaneous effects of natural selection on the brain and on the lifespan, it extends standard life history theory (LHT) in biology, which organizes research into the evolutionary forces shaping age-schedules of fertility and mortality (Cole, 1954; Gadgil and Bossert, 1970; Partridge and Harvey, 1985). This extension, *the embodied capital theory* (Kaplan, 1997; Kaplan et al., 2000b; Kaplan and Robson, 2001b), integrates existing models with an economic analysis of capital investments and the value of life.

The chapter begins with a brief introduction to embodied capital theory, and then applies it to understanding major trends in primate evolution and the specific characteristics of humans. The evolution of brain size, intelligence and life histories in the primate order are addressed first. The evolution of the human life course is then considered, with a specific focus on the relationship between cognitive development, economic productivity, and longevity. It will be argued that the evolution of the human brain entailed a series of co-evolutionary responses in human development and aging. It concludes with a discussion of several unresolved issues raised at this workshop.

The embodied capital theory of life history evolution

According to the theory of evolution by natural selection, the evolution of life is the result of a process in which variant forms compete to harvest energy from the environment and convert that energy into replicates of those forms. Those forms

that can capture more energy than others and can convert the energy they acquire more efficiently into replicates than others become more prevalent through time. This simple issue of harvesting energy and converting energy into offspring generates many complex problems that are time-dependent.

Two fundamental tradeoffs determine the action of natural selection on reproductive schedules and mortality rates. The first tradeoff is between current and future reproduction. By growing, an organism can increase its energy capture rates in the future and thus increase its future fertility. For this reason, organisms typically have a juvenile phase in which fertility is zero until they reach a size at which some allocation to reproduction increases lifetime fitness more than growth. Similarly, among organisms that engage in repeated bouts of reproduction (humans included), some energy during the reproductive phase is diverted away from reproduction and allocated to maintenance so that it can live to reproduce again. Natural selection is expected to optimize the allocation of energy to current reproduction and to future reproduction (via investments in growth and maintenance) at each point in the life course so that genetic descendents are maximized (Gadgil and Bossert, 1970). Variation across taxa and across conditions in optimal energy allocations is shaped by ecological factors, such as food supply, disease and predation rates.

A second fundamental life history tradeoff is between offspring number (quantity) and offspring fitness (quality). This tradeoff occurs because parents have limited resources to invest in offspring, and each additional offspring produced necessarily reduces the average investment per offspring. Most biological models operationalize this tradeoff as number vs. survival of offspring (Lack, 1954; Smith and Fretwell, 1974; Lloyd, 1987). However, parental investment may not only affect survival to adulthood, but also the adult productivity and fertility of offspring. This is especially true of humans. Thus, natural selection is expected to shape investment per offspring and offspring number so as to maximize offspring number times their average lifetime fitness.

The embodied capital theory generalizes existing life history theory by treating the processes of growth, development and maintenance as investments in stocks of somatic, or embodied, capital. In a physical sense, embodied capital is organized somatic tissue – muscles, digestive organs, brains, etc. In a functional sense, embodied capital includes strength, speed, immune function, skill, knowledge and other abilities. Since such stocks tend to depreciate with time, allocations to maintenance can also be seen as investments in embodied capital. Thus, the present-future reproductive trade-off can be understood in terms of optimal investments in own embodied capital vs. reproduction, and the quantity-quality trade-off can be understood in terms of investments in the embodied capital of offspring vs. their number.

The brain as embodied capital

The brain is a special form of embodied capital. Neural tissue is involved in monitoring the organism's internal and external environment, and organizing physiological and behavioural adjustments to those stimuli (Jerison, 1976). Portions (particularly the cerebral cortex) are also involved in transforming past and present experience into future performance. Cortical expansion among higher primates, along with enhanced learning abilities, reflects increased investment in transforming present experience into future performance (Armstrong and Falk, 1982; Fleagle, 1999).

The action of natural selection on neural tissue involved in learning and memory should depend on costs and benefits realized over the organism's lifetime. Three kinds of costs are likely to be of particular importance. First, there are the initial energetic costs of growing the brain. Among mammals, those costs are largely borne by the mother during pregnancy and lactation. Second, there are the energetic costs of maintaining neural tissue. Among infant humans, about 65% of all resting energetic expenditure supports maintenance and growth of the brain (Holliday, 1978). Third, certain brain capacities may actually decrease performance early in life. Specifically, the ability to learn and increased behavioural flexibility may entail reductions in "pre-programmed" behavioural routines. The incompetence with which human infants and children perform many motor tasks is an example.

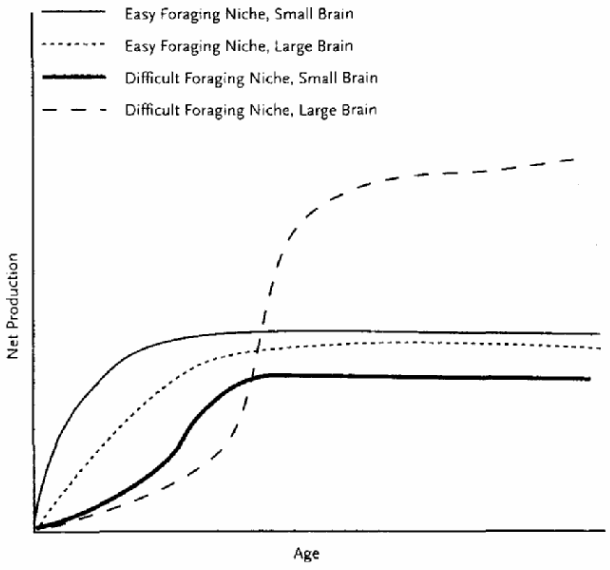

Fig. 1. Age-specific effects of brains on net production: easy and difficult foraging niches.

Some allocations to investments in brain tissue may provide immediate benefits (e.g., perceptual abilities, motor coordination). Other benefits of brain tissue are only realized as the organism ages. The acquisition of knowledge and skills has benefits that, at least in part, depend on their impact on future productivity. Figure 1 illustrates two alternative cases, using as an example the difficulty and learning-intensiveness of the organism's foraging niche. In the easy feeding niche where there is little to learn and information to process, net productivity (excess energy above and beyond maintenance costs of brain and body) reaches its asymptote early in life.

There is a relatively small impact of the brain on productivity late in life (because there has been little to learn), but there are higher costs of the brain early in life. Unless the lifespan is exceptionally long, natural selection will favour the smaller brain.

In the difficult food niche, the large-brain creature is slightly worse off than the small-brain one early in life (because the brain is costly, and learning is taking place), but much better off later in life. The effect of natural selection will depend upon the probabilities of reaching an older age. If those probabilities are sufficiently low, the small brain will be favoured, and if they are sufficiently high, the large brain will be favoured. Thus, selection on learning-based neural capital depends not only on its immediate costs and benefits, but also upon mortality schedules which affect the expected gains in the future.

Selection on mortality schedules

In standard LHT models, mortality is generally divided into two types: (1) extrinsic mortality (i.e. mortality that is imposed by the environment and is outside the organism's control, such as predation or winter) and (2) intrinsic mortality (hazards of mortality over which the organism can exert some control over the short run or which is subject to selection over longer periods). In most models of growth and development, mortality is treated as extrinsic (Kozlowski and Wiegert, 1986; Charnov, 1993) and therefore as a causal agent, not subject to selection. Models of aging and senescence (Promislow, 1991; Shanley and Kirkwood, 2000) typically focus on aging-related increases in intrinsic mortality. From this point of view, extrinsic mortality is thought to affect selection on rates of aging, with higher mortality rates favouring faster aging.

This distinction between types of mortality is problematic. Organisms can exert control over virtually all causes of mortality in the short or long run. Susceptibility to predation can be affected by vigilance, choice of foraging zones, travel patterns and anatomical adaptations, such as shells, cryptic coloration and muscles facilitating flight. Each of those behavioural and anatomical adaptations has energetic costs (lost time foraging, investments in building and maintaining tissue) that re-

duce energy available for growth and reproduction. Similar observations can be made regarding disease and temperature. The extrinsic mortality concept has been convenient, because it has provided a causal agent for examining other life history traits, such as age of first reproduction and rates of aging. However, this has prevented the examination of how mortality rates themselves evolve by natural selection.

Since all mortality is, to some extent, intrinsic or "endogenous", a more useful approach is to examine the functional relationship between mortality and the effort allocated to reducing it (see Figure 2). Exogenous variation can be thought of in terms of varying "assault" types and varying "assault" rates of mortality hazards. For example, warm, humid climates favour the evolution of disease organisms, and therefore the assault rate and diversity of diseases on organisms living in those climates are increased. Such exogenous variation would affect the functional relationship between actual mortality hazards such as disease and endogenous effort allocated to reduce it by mounting immunological defences. The outcome mortality rate is neither extrinsic nor intrinsic.

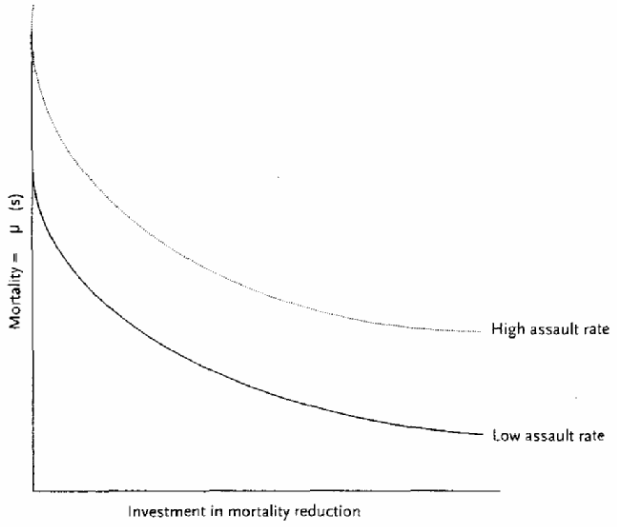

Fig. 2. Mortality rate as a function of investments.

Kaplan and Robson (2001a, 2001b) have developed formal models to analyze the simultaneous effects of natural selection on investments in both capital and reducing mortality. As a first step, it is useful to think of capital generally (interpreted as the bundle of functional abilities embodied in the soma). Organisms generally receive some energy from their parents (e.g., in the form of energy stored in eggs) to produce an initial stock of capital. Net energy acquired from the

environment grows at each age as a function of the capital stock, with diminishing returns to capital (as illustrated in Figure 3).

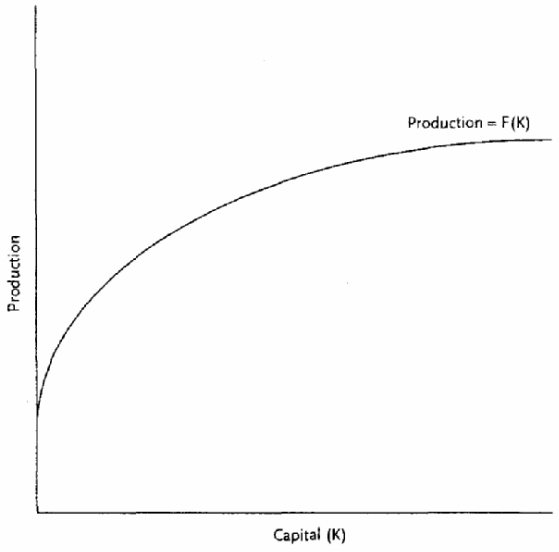

Fig. 3. Production as a function of the capital stock.

This energy can be used in three ways, which are endogenous and subject to selection. It can be reinvested in increasing the capital stock (e.g. growth of the body or brain). Some energy may also be allocated to reducing mortality (for example, in the form of increased immune function as illustrated above in Figure 2). The probability of reaching any age will be a function of mortality rates at each earlier age. Finally, energy can also be used for reproduction, which is the net excess energy available after allocations to capital investments and mortality reduction. An optimal life history programme would optimize allocations to capital investments, mortality reduction, and reproduction at each age so as to maximize total energy allocations to reproduction over the life course. This, of course, depends both on reproductive allocations and on survival.

The results of the analysis, which are presented and proven formally in Kaplan and Robson (2001a), are illustrated in Figures 4a, 4b, and 4c. During the capital investment period, the value of life (which is equal to total expected future net production) increases with age, since productivity grows with increased capital. The optimal value of investment in mortality reduction also increases, since the effect of a decrease in mortality increases as capital increases. This is illustrated in Figure 4a. At some age, a steady state is reached when capital is at its optimum level, and both capital and mortality rates remain constant.

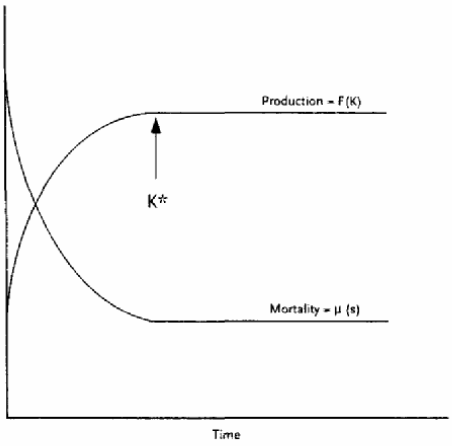

Fig. 4a. The optimal life history.

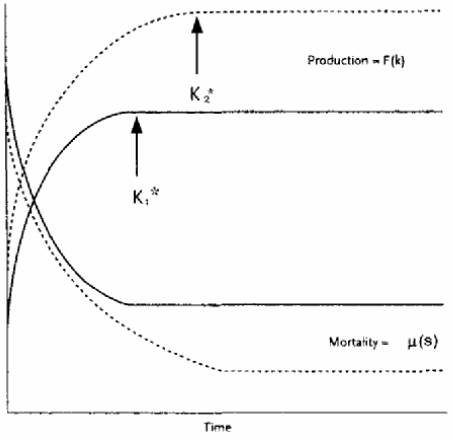

Fig. 4b. The optimal life history with a productivity shift.

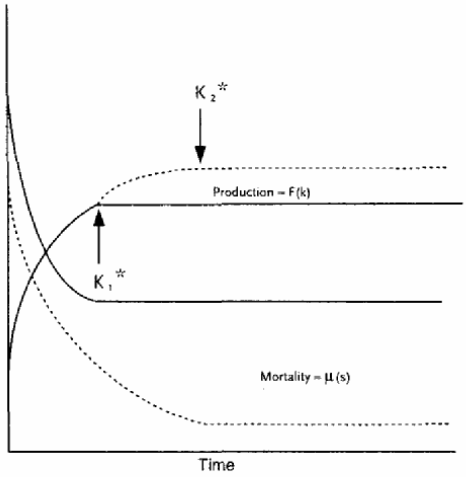

Fig. 4c. The optimal life history with a mortality shift.

Figures 4b and 4c show two important comparative results. In Figure 4b, the impact of a change in productivity is shown. Some environmental change that increases productivity (holding the marginal value of capital constant) has two reinforcing effects: it increases the optimal level of both capital investment (and hence the length of the investment period) and efforts to reduce mortality. Figure 4c shows the impact of a reduction in mortality rates, again with two effects. It increases the optimal capital stock (because it increases the expected length of life and hence the time over which it will yield returns) and produces a reinforcing increase in effort at reducing mortality, since the impact of a decrease in mortality is greater as mortality rates decrease.

Finally, the model shows that a shift in productivity from younger to older ages (for example, an increased reliance on learning that lowers juvenile energy production but increases adult production) increases the value of living to older ages and therefore optimal effort at reducing mortality. This has the effect of increasing the expected lifespan. Our theory is that brain size and longevity co-evolve for the following reasons. Ecological conditions favouring large brains also select for greater endogenous investments in staying alive. As the stock of knowledge and functional abilities embodied in the brain grow with age, so too does the value of the capital investment. This favours greater investments in health and mortality avoidance. In addition, holding the value of the brain constant, ecological conditions that lower mortality select for increased investment in brain capital for similar reasons; an increased probability of reaching older ages increases the value of investments whose rewards are realized at older ages. The next section applies this logic to the brain and lifespan evolution in the Primate order.

Brain and lifespan evolution among primates

The theoretical and empirical model

Relative to other mammalian orders, the Primate order can be characterized as slow-growing, slow-reproducing, long-lived and large-brained. The radiation of the order over time has involved a series of four directional grade shifts towards slowed life histories and increased encephalization (i.e. brain size relative to body size). Even the more "primitive" prosimian primates are relatively long-lived and delayed in reaching reproductive maturity compared to mammals of similar body size, which suggests the same of early primate ancestors. Austad and Fischer (1991, 1992) relate this evolutionary trend in the primates to the safety provided by the arboreal habitat and compare primates to birds and bats, which are also slow-developing and long-lived for their body sizes. Thus, the first major grade shift that separated the Primate order from other mammalian orders was a change to a lowered mortality rate and the subsequent evolution of slower senescence rates,

leading to longer lifespans and slightly larger brains.

The second major grade shift occurred with the evolution of the anthropoids (the lineage containing monkeys, apes and humans), beginning about 35 mya. Its major defining characteristic is the reorganization of the sensory system to one dominated by binocular, colour vision as opposed to olfaction and hearing in association with hand-eye coordination. These sensory changes co-occurred with an increased emphasis on plant foods (especially hard seeds and fruits), as opposed to insects (Fleagle, 1999; Benefit, 2000). The grade shift is also seen in brain size and life history. Regressions of log brain size on log body size (Barton, 1999) as well as log maximum lifespan on body size (Allman et al., 1993) show significant differences in intercept between strepsirhine (including most prosimians) and haplorhine (including all anthropoids and a few prosimian) primates. Relative to prosimians, anthropoids also have lower metabolic rates and longer gestation times (Martin, 1996).

The evolution of monkey and ape dietary adaptations in the Miocene and Pliocene appears to be based on an early adaptation for both groups to feed on hard seeds and green fruit (Benefit, 2000). In the Late Miocene/Early Pliocene cercopithecoids, which had been semi-terrestrial, cursorial, hard seed and green fruit eaters much like modern vervet monkeys, evolved new digestive adaptations allowing the colobines to digest mature leaves. Cercopithecoids also began to compete more directly with apes in both terrestrial and arboreal habitats. Miocene apes were highly diverse and found in many habitats but were essentially agile arboreal quadrupeds. By the Late Miocene apes had fully developed their characteristic shoulder girdle morphology, allowing suspension below branches that gave special access to ripe fruits for larger bodied animals. This dietary shift to dependence on ripe fruits, based on the morphological adaptation of arm suspension, moved apes into a new grade with an emphasis on feeding higher in the food pyramid on very nutritious food packets high in energy but spatially and temporally dispersed in an arboreal habitat. This new grade reduced direct competition with monkeys, ceded open terrestrial habitat to them, and greatly reduced the number and diversity of ape species. At the same time it put a premium on acquired knowledge about the location of ripe fruits and for skills for more complex extractive foraging of embedded and protected, high-energy and fatty foods such as nuts, insects, and hard-shelled fruits.

This third major grade shift marked the evolution of the hominoid lineage (leading to apes and humans). This grade shift entailed further encephalization, as revealed by a yet greater intercept of log brain size regressed on log body size and superior performance on most tasks reflecting higher intelligence (Byrne, 1995, 1997; Parker and McKinney, 1999). The divergence of the hominin line, and particularly the evolution of the genus *Homo*, defined the fourth major grade shift.

The brain size and lifespan of modern humans are very extreme values among mammals, and even among primates. Although the record is incomplete, it appears that brain enlargement and life history shifts co-occurred. Early *Homo ergaster* shows both significant brain expansion and a lengthened developmental period (Smith, 1993), but much less so than modern humans. Neandertals display both brain sizes and dental development that are in the same range as modern humans. Modern humans have a brain size about three times that of female gorillas of similar weight, and about double the maximum lifespan.

The proposal here is that both shifts in mortality risks and in the benefits of information storage and processing due to changes in feeding niche underlie these directional changes in the primate lineage through time. However, in addition to these large-scale shifts, there exists a great deal of adaptive variation among primates. Species of all four grades continue to co-exist, often sympatrically (especially monkeys, apes and humans). Moreover, not all evolutionary change has been in the direction of larger brains and longer lives. For example, smaller-brained monkeys appear to have replaced apes in some niches at the end of the Miocene (Fleagle, 1999; Benefit, 2000). If changes in mortality risks and the learning intensiveness of the feeding niche explain the grade shifts, the same factors might also explain variation within grades.

Figure 5 illustrates the theory and the empirical model that it generates, given the available data. On the left, the two rounded boxes represent exogenous ecological

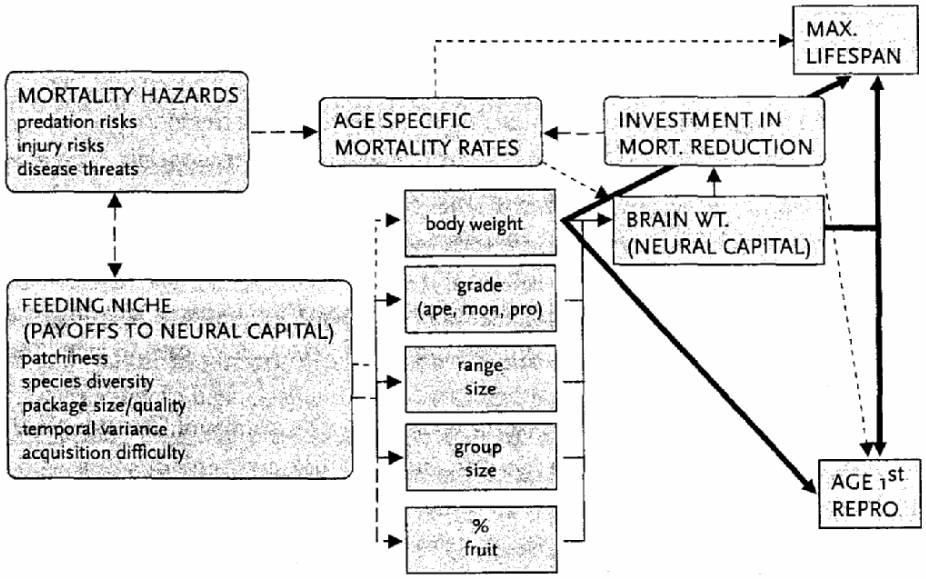

Fig. 5. A theoretical and empirical path model of primate brain evolution.

variables.[1] Some features of the feeding niche that are likely to affect the payoffs for information acquisition and processing (and hence, brain size) are listed in the lower box. Resource patchiness tends to be associated with larger home ranges and potentially greater demands on spatial memory. The number of different species consumed potentially adds to demands for spatial memory, learned motor patterns, processing of resource characteristics, and temporal associations (Jerison, 1973). Large, nutrient-dense packages (such as big, ripe fruits) tend to be patchily distributed in space and often with very short windows of availability (Clutton-Brock and Harvey, 1980; Milton, 1981, 1993). Year-to-year abundance and location of high-quality packages also appear to vary. Hence, diets with a greater relative importance of large, high-quality packages are probably associated with increased brain size through several routes: by increasing the number of species exploited, by increasing the size of the home range, and by increasing the importance of predicting the timing and location of availability. In addition, some high-quality foods, such as hard-shelled fruits, nuts, insects, and honey, must be extracted from protective casings, and their exploitation often requires learned strategies and tools. Features of the environmental/behavioural niche of the organism that are likely to affect mortality rates and the payoffs of investments in mortality reduction are listed in the upper left box. Life in or near trees probably increases injury risk, but decreases predation risk for overall lower mortality risks. Lowered risk of mortality due to predation is expected to increase investment in combating disease and, hence, decrease disease risks as well (though these have received little attention in primate studies to date). Lower mortality rates increase the probability of reaching older ages and therefore affect the payoffs for larger brains, holding the feeding niche constant.

The co-evolution of brain size and mortality patterns is shown in the path diagram (dashed arrows depict effects of unmeasured conceptual or latent variables). Both features of the feeding niche and mortality risks affect the optimal brain size. Brain size is expected to have both direct and indirect effects on lifespan and age of first reproduction. Larger brains may confer direct survival advantages through increased physiological efficiency and through learned predator avoidance (Jerison, 1973; Armstrong, 1982; Allman et al., 1993; Hakeem et al., 1996; Rose and Mueller, 1998). In addition, since larger brains are associated with greater relative productivity at older ages, brain size is expected to be associated with investment in mortality reduction. Similarly, the energetic costs of the brain reduce energy available for growth, and learning-based feeding niches may lower productivity during the juvenile period. This would produce slower growth rates and a later age of first reproduction, holding body size constant. The greater allocations to mortality reduction (e.g. increased immune function, reduced foraging time) would also slow the growth rates.

The rectangular boxes depict measured variables for which comparative data are available, and the solid arrows depict associations that can be tested empirically. The thinner lines represent the first stage in the model, predicting brain weight. Measures of feeding niche are captured by grade (ape, monkey, vs. prosimian), range size, and percentage of fruit in the diet. We also include body and group size in this first stage. In addition to directly affecting brain size, body size is likely to be associated with dietary niche. For example, larger bodies probably favour the exploitation of larger home ranges because of their greater locomotor efficiency. Larger body masses are also associated with larger home ranges since larger animals need to work harder to get enough food (Leonard and Robertson, 2000). Furthermore, larger home ranges may also be associated with larger groups, because holding resource abundance constant, a patchy environment will tend to produce both larger home ranges and a larger number of individuals feeding at each resource patch (Wrangham, 1979). Because the social intelligence hypothesis has figured so prominently in the literature (Byrne, 1995; Barton and Dunbar, 1997; Dunbar, 1998), the path between group size and brain size is also included. In addition, if social intelligence takes time to acquire and its benefits are weighted towards older ages (as may well be the case), embodied capital theory does predict that selection on social intelligence will co-evolve with longevity and mortality rates. For example, social intelligence might allow alpha males to retain their high status to older ages, and it might confer greater benefits on females when they

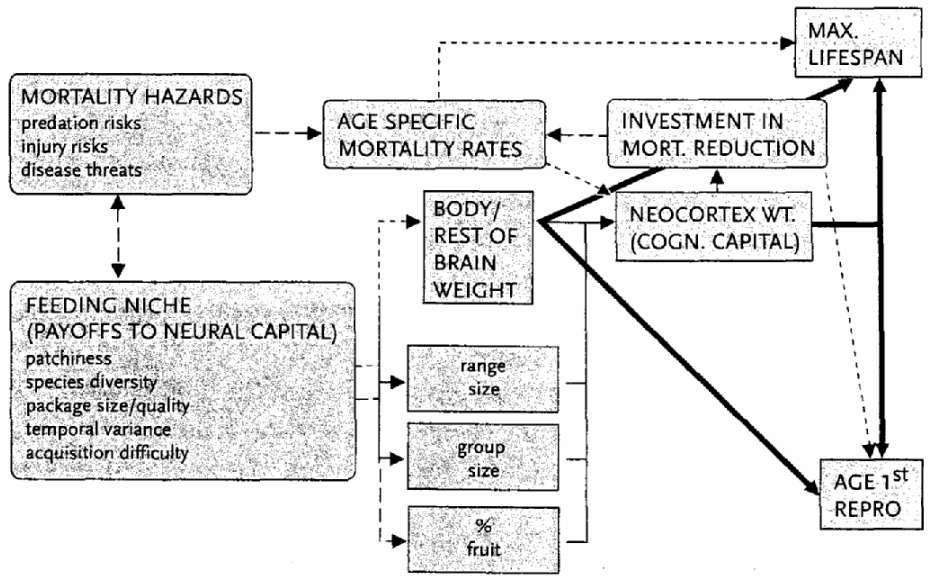

Fig. 6. A theoretical and empirical path model of neocortex evolution.

have many descendants (in the case of ranked matrilines). Such effects would also be consistent with the model. The second stage, shown with bold arrows, examines the effects of brain size and body size on age of first reproduction and maximum-recorded lifespan, respectively.

A second model will also be tested (see Figure 6). The logic of the embodied capital model suggests that the brain functions that are most involved in transforming present experience into future performance should have the greatest impact on the payoffs to living longer and allocating effort to mortality reduction. In addition, it has been argued that the association of brain size with lifespan in primates, after controlling for body size, is spurious and due to greater measurement error in body size than in brain size (Economos, 1980; Dunbar, 1998). However, Allman and colleagues (1993) have shown that brain size is a better predictor of lifespan than the size of other organs. To address these issues, the size of the neocortex will be disaggregated from the rest of the brain. The neocortex should better reflect the learning-intensiveness of the feeding niche and social system than the rest of the brain. In the second model, neocortex weight replaces brain weight, and the weight of the rest of the brain replaces body weight, as an instrument (since measurement error for neocortex and rest of brain weight, respectively, should be similar). Other people have measured the proportional ratio of neocortex to the rest of the brain (Dunbar, 1998). Rather than using a ratio that combines neocortex with the rest of the brain in one variable but is incapable of disentangling the independent effects of two different parts of the brain, we prefer placing both measures, the neocortex and the rest of the brain, in the regression analysis. Others have utilized the same approach looking at neocortex size but with a very small sample (Barton, 2000).

The primate sample

Data are available on the total adult brain weights (in grams) for 124 species, compiled from secondary sources (Harvey et al., 1987; Barton, 1999). From this sample, there are 95 species for which data are available on mean adult body weight (in grams), group size, age at first breeding for females (in months), maximum lifespan (in years), maximum home range (in hectares), and percent frugivory. Much of the data came from secondary sources (Harvey et al., 1987; Dunbar, 1992; Ross, 1992; Barton, 1996, 1999). These data differ, however, from previous analyses in a heavier reliance on primary field data for female age at first breeding, maximum home range, and percent frugivory (see details Kaplan et al., 2001). They may thus more accurately represent the selection pressures faced by wild individuals, which are assumed to be living under conditions much more representative of the context in which these features co-evolved.

Data analysis

A two-stage least squares regression analysis was performed to test the models. For the model in Figure 5, the first stage was conducted hierarchically. First, the natural logarithm of brain weight was regressed on the natural logarithms of body weight, range size, and group size, and on percentage of fruit in the diet. Then to capture other aspects of niche differentiation, grade (ape and monkey, compared to a prosimian baseline) was added as a fixed effect to determine if it significantly improved the model.

Results

The results are presented in Table 1. In the simple model without grade, body weight, range size and percentage of fruit in the diet are each positively related to brain weight, accounting for 94% of the variance. Group size was not significant. Grade significantly improved the model fit ($p<.0001$) with the model now accounting for 97% of the variance. In this model, percentage of fruit is no longer

Table 1. Two-stage model of brain size and life history.

A. Stage I, Brain Weight

	R^2=.94, N= 95				R^2=.97, N= 97			
Parameter	**B**	**Std. Error**	**t**	**Sig.**	**B**	**Std. Error**	**t**	**Sig.**
Intercept	-1.74	0.16	-11.22	0.0000	-1.74	0.16	-11.22	0.0000
Body wt.	0.68	0.03	23.01	0.0000	0.59	0.02	24.83	0.0000
Range size	0.05	0.03	1.95	0.0550	0.05	0.02	2.54	0.0130
Group size	0.07	0.04	1.64	0.1040	0.07	0.04	2.02	0.0468
Perc. fruit	0.00	0.00	2.65	0.0100	0.00	0.00	1.46	0.1484
Ape	.	.	.	0.87	0.10	8.73	0.0000	
Monkey	.	.	.	0.45	0.07	6.42	0.0000	
Prosimian	.	.	.	0.00	.	.	.	

B. Stage II

	Maximum lifespan, R^2=.52, N=80				Age of first reproduction, R^2=.74, N=79			
Parameter	**B**	**Std. Error**	**t**	**Sig.**	**B**	**Std. Error**	**t**	**Sig.**
Intercept	3.14	0.34	9.32	0.0000	2.78	0.37	7.58	0.0000
Body wt.	-0.24	0.10	-2.36	0.0208	-0.21	0.11	-1.99	0.0503
Brain wt.	0.53	0.13	4.12	0.0001	0.71	0.14	5.19	0.0000

significant, but group size is. The predicted values of log brain size from this full model are then used in the second stage of the analysis[2].

Part B of Table 1 shows the results of the second stage in which the natural logarithms of female age at first reproduction and maximum reported lifespan, respectively, were regressed on the logs of predicted brain weight and body weight. In both cases, brain weight explains most of the variance, and the effect of body weight is negative. When brain weight is not in the model, the association between body weight and both lifespan and age of first reproduction is, of course, strongly positive. It may be that after controlling for brain weight, larger bodied species eat lower quality diets (Milton, 1981, 1987, 1988, 1993; Milton and Demment, 1988; Aiello and Wheeler, 1995), which is associated with a relatively shorter lifespan and earlier age at first reproduction.

The results of decomposing brain weight into the neocortex and the rest of the brain (Figure 6) are shown in Tables 2 and 3. Using the same set of regressors as in the full model of brain size, the natural logarithms of the weights of the rest of the brain and of the neocortex (shown on the left and right sides of Table 2, respectively) are each treated as dependent variables. Body weight and grade are the only variables that significantly affect the weight of non-neocortical brain tissue, and the effect of grade is rather small. With respect to neocortex weight, however, both range size and grade have large effects. Thus, consistent with the above logic, feeding niche has a larger effect on neocortex weight than on the rest of the brain, which appears to be more a function of body weight.

In Table 3, the weight of the rest of the brain is used as an instrument for body weight in Stage 1 of the model. This model shows that neocortical weight increases more than proportionally with the rest of the brain (b = 1.1), and that both

Table 2. Neocortex and rest of brain weight.

	Rest of brain weight (brain wt-neocortex wt), R^2=.94, N=32				**Neocortex weight, R^2=.98, N=32**			
Parameter	**B**	**Std. Error**	**t**	**Sig.**	**B**	**Std. Error**	**t**	**Sig.**
Intercept	-2.03	0.30	-6.66	0.0000	-2.46	0.25	-9.68	0.0000
Body wt.	0.55	0.05	10.42	0.0000	0.57	0.04	13.02	0.0000
Range size	0.08	0.04	1.79	0.0860	0.12	0.04	3.41	0.0020
Group size	-0.05	0.07	-0.68	0.5010	0.02	0.06	0.28	0.7800
Perc. fruit	0.00	0.00	0.42	0.6810	0.00	0.00	0.77	0.4470
Ape	0.51	0.23	2.25	0.0330	0.89	0.19	4.64	0.0000
Monkey	0.27	0.16	1.73	0.0950	0.71	0.13	5.51	0.0000
Prosimian	0.00	.	.	.	0.00	.	.	.

Table 3. Two-stage model of neocortex size and life history.

Stage I				
Neocortex size, R^2=.996, N=32				
Parameter	**B**	**Std. Error**	**t**	**Sig.**
Intercept	-0.26	0.05	-5.03	0.0000
Rest of brain wt.	1.10	0.03	31.83	0.0000
Range size	0.01	0.02	0.76	0.4556
Group size	0.06	0.03	2.35	0.0270
Perc. fruit	0.00	0.00	0.88	0.3871
Ape	0.52	0.09	5.99	0.0000
Monkey	0.47	0.06	8.29	0.0000
Prosimian	0.00	.	.	.
Stage II				
Maximum lifespan, R^2=.70, N=32				
Parameter	**B**	**Std. Error**	**t**	**Sig.**
Intercept	2.66	0.11	25.21	0.0000
Rest of brain wt.	-0.20	0.24	-0.83	0.4122
Neocortex wt.	0.38	0.19	2.05	0.0506
Age of first reproduction, R^2=.79, N=32				
Intercept	2.49	0.14	17.42	0.0000
Rest of brain wt.	-0.30	0.31	-0.99	0.3304
Neocortex wt.	0.64	0.24	2.69	0.0119

grade and group size have large significant effects. In the second stage, predicted neocortical weight is positively associated with both age at first reproduction and maximum lifespan, while the rest of the brain is not significantly associated with the life history variables. This is also consistent with the model. These results should be treated with some caution, however, because the two measures of brain weight are highly collinear. In these analyses, species were treated as independent data points. We also conducted a similar set of analyses using independent phylogenetic contrasts. Here, we present results on contrasts that assume equal branch lengths (analyses using contrasts weighted by transformed branch lengths yielded similar results and are available from the authors upon request). In Stage 1 regressions, brain weight was positively predicted by body weight (t(Bailey) = 15.11, p < .001) and range size (t[86] = 3.99, p < .001). Neither group size nor percent fruit

in the diet independently contributed to prediction, both $t < 1$, ns. In Stage 2 regressions, brain weight predicted both maximum lifespan ($t[88] = 3.33$, $p < .005$) and age at first reproduction (brain weight: $t[88] = 2.39$, $p < .02$). Body weight did not predict either of these variables in these analyses (maximum lifespan: $t[88] = -1.36$, ns; age at first reproduction: $t[88] = .24$, ns).

The evolution of Homo: *chimpanzees and modern humans compared*

The same principles may explain the very long lives and the very large brains characteristic of the genus *Homo* and particularly of modern *Homo sapiens*. *Homo* has existed for about 2 million years. Figure 7 shows human ancestors experienced a dramatic increase in brain size, but a much less marked increase in body size, especially during the second half of this period. Using Martin's (Martin, 1981) measure of "Encephalization Quotient (*EQ*)" (i.e., brain weight corrected allometrically for body weight, with $EQ = \frac{(brain\ wt)}{11.22 * (body\ wt)^{.76}}$ one is the average value for a mammal), the large increases in brain size relative to body size are shown with the bold line. *Australopithecus*, the presumed evolutionary ancestor of *Homo*, coexisted with early *Homo*. *A. boisei*, in particular, had an *EQ* of just over two, which compares to about 3.5 for early *Homo*. Lifespans of extinct species are not directly observable, of course, but indirect evidence suggests the lifespan of australopithecines was much less than that of modern humans and comparable to that of chimpanzees (Smith, 1991), with early species in the genus *Homo* having lifespans that are intermediate between chimpanzees and modern humans (Smith, 1993).

Hominins have subsisted on hunting and gathering, perhaps supplemented by scavenging, for all but the last 10,000 years of our evolutionary history. Our proposal (Kaplan, 1997; Kaplan et al., 2000b; Kaplan and Robson, 2001b) is that the hunting and gathering way of life is responsible for the evolution of these extreme values with respect to brain size and longevity. Large brains and long lives are coevolved responses to an equally extreme commitment to learning-intensive foraging strategies and a dietary shift towards high quality, nutrient-dense, and difficult-to-acquire food resources. The following logic underlies this proposal. First, high levels of knowledge, skill, coordination, and strength are required to exploit the suite of high-quality, difficult-to-acquire resources humans consume. The attainment of those abilities requires time and a significant commitment to development. This extended learning phase during which productivity is low is compensated for by higher productivity during the adult period, with an intergenerational flow of food from old to young. Since productivity increases with age, the time investment in skill acquisition and knowledge leads to selection for lowered

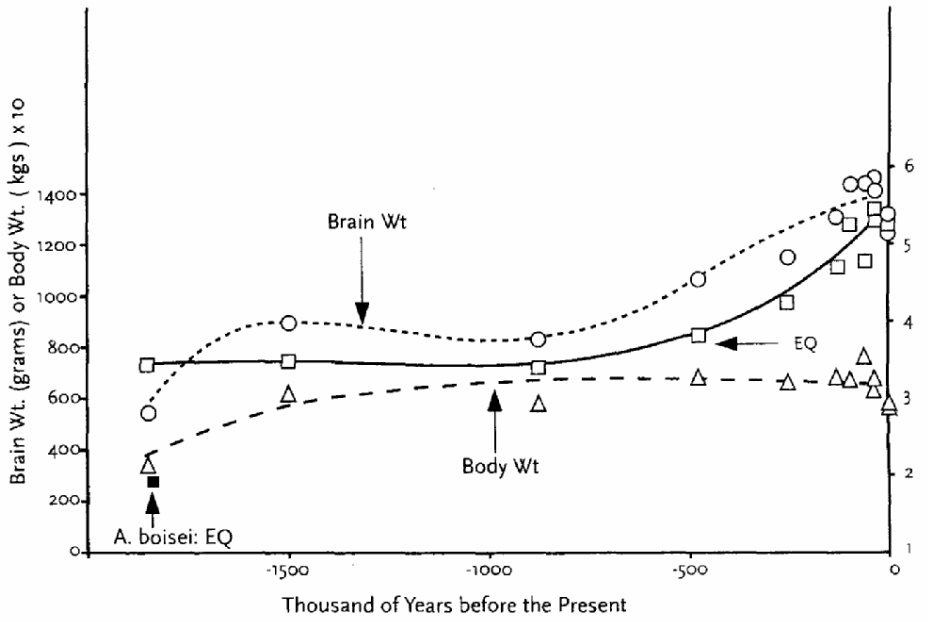

Fig. 7. Hominin brain size and body weight.

mortality rates and greater longevity, because the returns on the investments in development occur at older ages.

Second, the feeding niche specializing in large, valuable food packages, and particularly hunting, promotes cooperation between men and women and high levels of male parental investment, because it favours sex-specific specialization in embodied capital investments and generates a complementarity between male and female inputs. The economic and reproductive cooperation between men and women facilitates provisioning of juveniles, which both bankrolls their embodied capital investments and acts to lower mortality during the juvenile and early adult periods. Cooperation between males and females also allows women to allocate more time to childcare and raises nutritional status, increasing both survival and reproductive rates. Finally, large packages also appear to promote inter-familial food sharing. Food sharing assists recovery in times of illness and reduces risk of food shortfalls due to both the vagaries of foraging luck and the variance in family size due to stochastic mortality and fertility. These buffers against mortality also favour a longer juvenile period and higher investment in other mechanisms to increase lifespan.

Thus, the proposal is that the long human lifespan co-evolved with the lengthening of the juvenile period, increased brain capacities for information processing and storage, and intergenerational resource flows – all as a result of an important dietary shift. Humans are specialists in that they only consume the highest quality

plant and animal resources in their local ecology and rely on creative, skill-intensive techniques to exploit them. Yet, the capacity to develop new techniques for extractive foraging and hunting allows them to exploit a wide variety of different foods and to colonize all of the earth's terrestrial and coastal ecosystems.

The best available evidence for evaluating this theory is to compare wild living chimpanzees, human's closest living relatives, with contemporary hunter-gatherers who still depend on foraging for subsistence and who have little or no access to Western medicine. Both chimpanzees and contemporary foragers have been affected by current global trends, such as war, deforestation, population movements, and other effects of modern economies. They cannot be treated as replicas of the evolutionary past. Nevertheless, the differences in the diets, survival rates, and age-profiles of productivity between chimpanzees and contemporary hunter-gatherers are striking and consistent with the theory.

Diet, survival and age profiles of productivity among chimpanzees and contemporary hunter-gatherers

Diet

There are ten foraging societies and five chimpanzee communities for which caloric production or time spent feeding were monitored systematically (Kaplan et al., 2000b). Modern foragers all differ considerably in diet from chimpanzees. Measured in calories, the major component of forager diets is vertebrate meat. This ranges from about 30% to around 80% of the diet in the sampled societies with most diets consisting of more than 50% vertebrate meat (equally weighted mean = 60%), whereas chimpanzees obtain about 2% of their food energy from hunted foods.

The next most important food category in the forager sample is extracted resources, such as roots, nuts, seeds, most invertebrate products, and difficult to extract plant parts such as palm fiber or growing shoots. They may be defined as non-mobile resources that are embedded in a protective context such as under the ground, in hard shells or bearing toxins that must be removed before they can be consumed. In the ten foraging societies sampled, extracted foods accounted for about 32% of the diet, as opposed to 3% among chimpanzees.

In contrast to hunted and extracted resources, which are difficult to acquire, collected resources form the bulk of the chimpanzee diet. Collected resources, such as fruits, leaves, flowers, and other easily accessible plant parts are simply gathered and consumed. They account for 95% of the chimpanzee diet, on average, and only 8% of the forager diet.

The data suggest that humans specialize in rare but nutrient-dense resource packages or patches (meat, roots, nuts), whereas chimpanzees specialize in ripe fruit and low nutrient density plant parts. These differences in nutrient density of

foods ingested are also reflected in human and chimpanzee gut morphology and food passage time, with chimpanzees specialized for rapid processing of large quantities and low nutrient, bulky, fibrous meals (Milton, 1999).

The age profile of acquisition for collected, extracted, and hunted resources

In most environments, fruits are the easiest resources that people acquire. Daily production data among Ache foragers show that both males and females reach their peak daily fruit production by their mid to late teens. Some fruits that are simply picked from the ground are collected by two- to three-year-olds at 30% of the adult maximum rate. Ache children acquire five times as many calories per day during the fruit season as during other seasons of the year (Kaplan, 1997). Similarly, among the Hadza, teenage girls acquired 1650 calories per day during the wet season when fruits were available and only 610 calories per day during the dry season when fruits were not. If we weight the wet and dry season data equally, Hadza teenage girls acquire 53% of their calories from fruits, compared to 37% and 19% for reproductive-aged and post-reproductive women, respectively (Hawkes et al., 1989).

In contrast to fruits, the acquisition rate of extracted resources often increases through early adulthood as foragers acquire the necessary skills. Data on Hiwi women show that root acquisition rates do not asymptote until about age 35-45 (Kaplan et al., 2000b) and the rate of 10-year-old girls is only 15% of the adult maximum. Hadza women appear to obtain maximum root digging rates by early adulthood (Hawkes et al., 1989). Hiwi honey extraction rates by males peak at about age 25. Again the extraction rate of 10-year-olds is less than 10% of the adult maximum. Experiments done with Ache women and girls clearly show that young adult girls are not capable of extracting palm products at the rate obtained by older Ache women (Kaplan et al., 2000b). Ache women do not reach peak return rates until their early 20s. !Kung (Ju/'hoansi) children crack mongongo nuts at a much slower rate than adults (Blurton Jones et al., 1994), and Bock (1995) has shown that nut cracking rates among the neighbouring Hambukushu do not peak until about age 35. Finally, chimpanzee juveniles also focus on more easily acquired resources than adult chimpanzees. Difficult to extract activities such as termite and ant fishing or nut cracking are practiced less by chimpanzee juveniles than adults (Silk, 1978; Hiraiwa-Hasegawa, 1990; Boesch and Boesch, 1999).

Human hunting differs qualitatively from hunting by other animals and is the most skill-intensive foraging activity. Unlike most animals that either sit and wait to ambush prey or use stealth and pursuit techniques, human hunters use a wealth of information to make context-specific decisions, both during the search phase of hunting and then after prey are encountered. Specifically, information on ecology, seasonality, current weather, expected animal behaviour, and fresh

animal signs are all integrated to form multivariate mental models of encounter probabilities that guide the search and are continually updated as conditions change (Liebenberg, 1990). Various alternative courses of action are constantly compared and referenced to spatial and temporal mental maps of resource availability (ibid.). This information is collected, memorized and processed over much larger spatial areas than chimpanzees ever cover. For example, interviews with Ache men show that fully adult men (aged 35+) had hunted in an area of nearly 12,000 km^2 of tropical forest in their lifetimes. Almost all foragers surveyed use more than 200 km^2 in a single year, and many cover more than 1,000 km^2 in a year (Kelly, 1995, Table 4.1). Male chimpanzees, on the other hand, cover only about 10 km^2 in a lifetime (Wrangham, 1975; Wrangham and Smuts, 1980).

In addition, humans employ a wide variety of techniques to capture and kill prey, using astounding creativity (Kaplan et al., 2000b). Those kill techniques are tailored to many different prey under a wide variety of conditions. For example, from 1980 to 1996 our sample of weighed prey among the Ache includes a minimum of 78 different mammal species, at least 21 species of reptiles and amphibians, probably over 150 species of birds (more than we have been able to identify) and over 14 species of fish. Finally, human hunters tend to select prey that is in prime condition from the perspective of human nutritional needs rather than prey made vulnerable by youth, old age or disease as do so many carnivorous animals (Stiner, 1991; Alvard, 1995).

The skill-intensive nature of human hunting and the long learning process involved are demonstrated dramatically by data on hunting return rates by age. Hunting return rates among the Hiwi do not peak until age 30-35 with the acquisition rate of 10-year-old and 20-year-old boys reaching only 16% and 50% of the adult maximum, respectively. The hourly return rate for Ache men peaks in the mid-30s. The return rate of 10-year-old boys is about 1% of the adult maximum, and the return rate of 20-year-old juvenile males is still only 25% of the adult maximum. Marlowe (unpublished data) obtains similar results for the Hadza. Also, boys switch from easier tasks, such as fruit collection, shallow tuber extraction and baobab processing, to honey extraction and hunting in their mid to late teens among the Hadza, Ache and Hiwi (Blurton Jones et al., 1989, 1997; Kaplan et al., 2000b). Even among chimpanzees, hunting is strictly an adult or sub-adult activity (Teleki, 1973; Stanford, 1998; Boesch and Boesch, 1999).

Survival and net food production

Figure 8 (Kaplan et al., 2000b) shows probabilities of survival and net production (i.e. food acquired minus food consumed) by age. The chimpanzee net production curve shows three distinct phases. The first phase, to about age 5, is the period of complete to partial dependence upon mother's milk and of negative net produc-

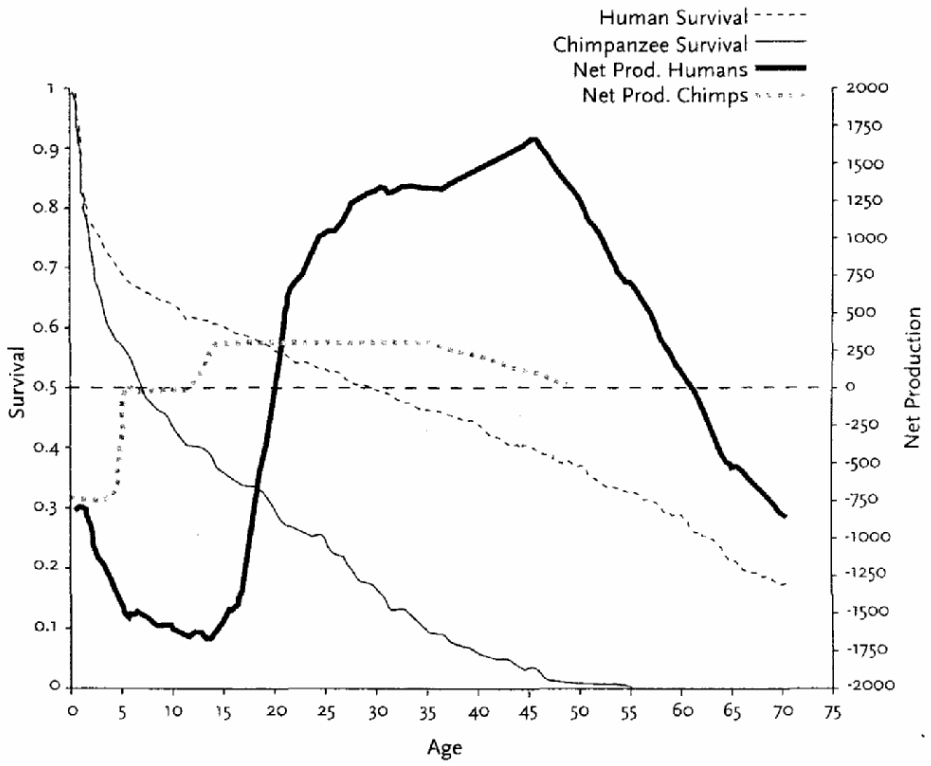

Fig. 8. Survival and net food production: human foragers and chimpanzees. On the left vertical axis is the probability of survival and on the right, is net production in calories per day. The data on chimpanzee survival are derived from averaging age-specific mortality rates from all five study sites where systematic data on births and deaths are recorded (Hill et al., 2001); data on chimpanzee food consumption and production are from Gombe (Goodall, 1986). Human survival rates are averaged from Ache (Hill and Hurtado, 1996), Hiwi (Kaplan et al., 2000a), and Hadza (Blurton Jones et al., 2002). Net production data are from the same groups (details on all sources and estimation procedures for the both human and chimpanzee production and consumption data are in Kaplan et al., 2000b.

tion. The second phase is independent juvenile growth, lasting until adulthood, during which net production is zero. The third phase is reproductive, during which females, but not males, produce a surplus of calories that they allocate to nursing.

Humans, in contrast, produce less than they consume for about 20 years. Net production becomes increasingly negative until about age 14 and then begins to climb. Net production in adult humans is much higher than in chimpanzees and peaks at a much older age, reflecting the payoff of long dependency. More precisely, human peak net production is about 1,750 calories per day, reached at about age 45. Among chimpanzee females, peak net production is only about 250 calo-

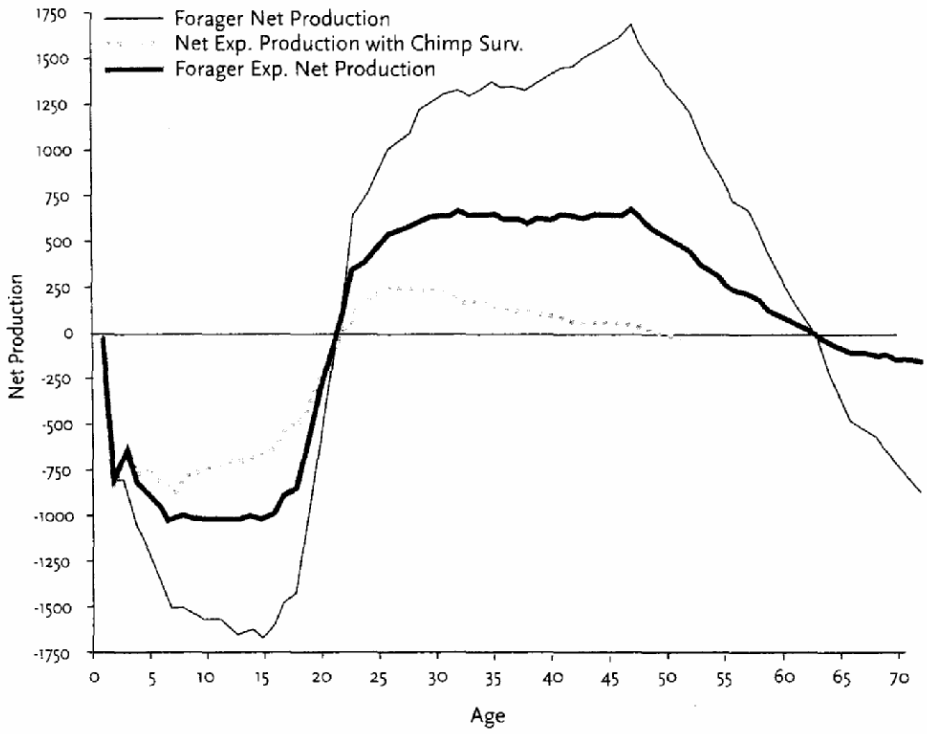

Fig. 9. Expected net production.

ries per day, and since fertility decreases with age, net productivity probably decreases throughout adulthood.

The survival curves, using the scale on the right-hand y-axis of Figure 8, reveal why the human age-profile of productivity requires a long adult lifespan. Only about 30% of chimpanzees ever born reach 20, the age when humans produce as much as they consume. Less than 5% of chimpanzees reach 45 when human net production peaks, but more than 15% of hunter-gatherers survive to age 70. By age 15, chimpanzees have consumed 43% and produced 40% of their expected lifetime calories, respectively; in contrast, humans have consumed 22% and produced only 4% of their expected lifetime calories!

The relationship between survival rates and age-profiles of production is made even clearer in Figure 9. The thin solid line plots net production by age for foragers (as in Figure 8). The bold line shows expected net production for foragers, which is net production at each age multiplied by the probability of being alive at each age. The area of the "deficit" period, prior to age 20, is about the same size as the surplus after age 20. The dashed line shows the hypothetical "contrary to fact" expected net production profile of a human forager with a chimpanzee survival

function. The area of the deficit is now much larger than the area of the surplus, since very few individuals survive to the highly productive ages. This shows that the human production profile would not be viable with chimpanzee survival rates, because expected lifetime net production would be negative.

Development and cognitive function among monkeys, apes and humans

Although it has long been recognized that human intelligence is our most distinctive specialization as a species, it is now becoming increasingly clear that our larger brains and greater intellectual capacities depend upon the elongation or stretching out of development at every stage. The production of cortical neurons in mammals is limited to early foetal development and compared to monkeys and apes, human embryos spend an additional 25 days in this phase (Deacon, 1997; Parker and McKinney, 1999). The greater original proliferation of neurons in early foetal development has cascading effects in greatly extending other phases of brain development, ultimately resulting in a larger, more complex, and effective brain. For example, in monkeys, such as macaques, myelination of the brain begins prenatally and is largely complete within a few months after birth, but in humans continues to at least 12 years of age (Gibson, 1986). Dendritic development is similarly extended to age 20 or greater in humans.

The timing of cognitive development is extended in chimpanzees relative to monkeys, and in humans relative to apes (Parker and McKinney, 1999). In terms of Piagetian stages, frequently used by comparative cognitive psychologists, macaque monkeys traverse only two subperiods of cognitive development regarding physical phenomena by about six months of age and peak in their logical abilities by about three years of age; however, they fail to be able to represent objects symbolically, to classify objects hierarchically, or to recognize themselves in a mirror. Chimpanzees traverse three to four subperiods of cognitive development by about 8 years of age3. They can recognize themselves in a mirror and are much better at classification than macaques, but are not capable of constructing reversible hierarchical classes and abstract, logical reasoning. Human children traverse eight subperiods of cognitive development over 18-20 years.

It is interesting to note that even though humans take about 2.5 times as long to complete cognitive development as do chimpanzees, humans actually learn faster than chimpanzees. In most cognitive spheres, especially language, a two-year-old child has the abilities of a four-year-old chimpanzee, even with intensive training. Humans appear to have much more to learn and their brains require more environmental input to complete development. Formal abstract logical reasoning does not emerge until age 16 to 18. This is the age when productivity begins to in-

crease dramatically among modern hunter-gatherers (see below). The ability to construct abstract scenarios and deduce logical relationships appears to allow for the growth in knowledge that results in peak productivity in the mid-30s.

Elongated development in humans is also associated with slowed aging of the brain. Macaques exhibit physiological signs of cognitive impairment, as evidenced by the appearance of Alzheimer-like neuropathology (senile plaques, neurocytoskeletal abnormalities) and cerebral atrophy by age 22-25, and chimpanzees by age 30, in contrast to humans for whom such changes are rare until age 60 (<1%) and only common (>30%) by age 80 (Finch, 2002).

Discussion and conclusions

The analyses in this paper have applied embodied capital theory to understanding primate radiations in brain size and longevity, and the evolution of the human life course. Embodied capital theory organizes the relationships of ecology, brain size and longevity among primates, which existing debates about primate brain size evolution have failed to do. Most studies of brain evolution have ignored longevity, and focused either on the benefits or on the costs of brains, but not both. The liveliest current debate concerns whether the benefit of a large brain is to solve ecological or social problems (Clutton-Brock and Harvey, 1980; Byrne and Whiten, 1988; Allman et al., 1993; Milton, 1993; Barton and Dunbar, 1997; Dunbar, 1998). On the cost side, another debate concerns, for example, whether larger brains require smaller guts or lower metabolic rates (Foley and Lee, 1991; Aiello and Wheeler, 1995; Martin, 1996; Barton, 1999).

Studies examining the relationship between the brain and longevity fail to model simultaneous selection. One focus has been on whether the relationship between brain size and longevity is real or a statistical artifact (Economos, 1980; Foley and Lee, 1991; Allman et al., 1993; Martin, 1996; Barton, 1999). Another has been on the metabolic costs of growing large brains (Foley and Lee, 1991; Martin, 1996) and its indirect relationship to lifespan through body size. Others have focused either on the direct impacts of the brain on lifespan or on the benefits of a longer lifespan. For example, Sacher offers two proposals: (1) brains directly increase lifespan by ensuring more precise homeostasis of bodily functions and (2) brains delay maturation and lower the reproductive rate, therefore requiring an extension of the lifespan (Sacher, 1975). Other hypotheses are: (A) larger brains are beneficial to longer-lived animals because they are likelier to experience food shortages when knowledge of the habitat would facilitate survival (Allman et al., 1993); (B) larger brains decrease ecological vulnerability to environmental risks and select for increased longevity (Rose and Mueller, 1998); and (C) larger brains help maintain tissue differentiation and slow the process of entropy leading to senes-

cence (Hofman, 1983). The embodied capital theory shows how features of ecology, including both mortality risks and information processing demands, interact in determining optimal allocations to the brain and survival.

Issues raised at this workshop and directions for future research

Several unresolved questions were discussed at the workshop. To conclude, we would like to address four of those questions, all of which are interrelated, with suggestions for future research:

1. the timing of changes in diet, brain function and longevity since the split between ape and hominid lineages;
2. the specific evolutionary processes by which diet, brain size and longevity changed over time, and the extent to which those changes occurred simultaneously;
3. sex-based specialization in economic roles, male parental investment and the relative importance of selection on females and males, respectively, in producing these macro-evolutionary trends; and
4. the relative importance of, and the relationship between, social and dietary factors in brain evolution.

Timing and measurement

With respect to the timing and tempo of evolutionary change in diet, brain and the life course, two major issues must be addressed. The first is descriptive: how can the important changes be measured, given the nature of the fossil, archaeological and molecular genetic record? The second is explanatory: what factors were responsible for the timing of the sequence of changes, and how did they vary across space? From a descriptive perspective, the documentation of changes in brain size appears the most straightforward, since the record of fossil crania is expanding and provides reasonably accurate measures of brain volume. The problem, of course, is that we are interested in brain function as well as size. It has long been recognized that changes in the internal organization of the brain may have been associated with large changes in brain function, but such changes may be largely invisible by examining fossil crania (Holloway, 1978, 1979). Our results raise another important, but perhaps more easily solved, problem. Although the sample of post-cranial fossil remains is rather sparse and unfortunately not well associated to the sample of crania, there is clear evidence of large changes in body size and muscularity over time and space in the hominid lineage (Kappelman, 1996; Ruff et al., 1997).

It is also well known, as discussed above, that it is important to take allometries between brain and body size into account when assessing changes in cognition and

other neurally based capabilities. Allometry can be viewed in two ways. The first is as a simple bivariate statistical relationship, estimated from the slope of the regression of log brain weight on log body weight. The second is conceptual or causal, and here the issue is how much an increase in body size causally contributes to (or requires) an increase in brain size. The estimated slope for all nonhuman primates is close to 0.75, but within each major grade (prosimians, monkeys and apes), the slope is closer to 0.67. One might therefore view these associations as supporting one of the explanations for them, even if it is unclear which one. But the explanations for these increases are conceptual and causal, and therefore should apply to regression slopes with other variables included in the model. Our analysis shows that the estimated slope decreases to about 0.5, after controlling for life history and ecological variables. We suspect that with better measures of our predictor variables (which are probably measured with greater error than body size), the estimated slope for body size would be even lower; that is, we assume that the effects of these measurement errors would counteract the underestimation of the slope due to error in body size (Nunn and Barton, 2000). Hence, the proportional increase in brain size necessary to support an increase in body size may be much lower than either the surface area or metabolic rate theories would suggest. It is interesting to note that within-species differences in body weight due to sexual dimorphism (e.g. among gorillas and orangutans) result in very small increases in brain size, with coefficients closer to 0.20-0.25. Using standardized encephalization quotients, male gorillas are less encephalized than the average mammal, and female gorillas are exceptionally encephalized. The life history model presented here provides a reason why statistical associations between brain and body size may provide upwardly biased estimates of the proportional increase in brain size necessary to support an increase in body size. If both optimal brain size and body mass are sensitive to length of lifespan, they may coevolve positively at a greater rate than would be expected by the neural requirements of a larger body size. If standard allometric coefficients are upwardly biased, this would mean that early members of the genus *Homo* may have been more encephalized with greater cognitive capacities than current models suggest. The same could be said for Neandertals as well. It is especially important to determine whether changes in muscularity produce smaller or larger changes in brain size than do changes in mass due to increased skeletal length. Clearly, more empirical and theoretical work on brain-body size allometry is needed.

Measuring changes in diet across time and space is also problematic, but novel techniques, such as isotopic analysis of fossil bone (Sponheimer and Lee-Thorp, 1999; Richards, this volume) or bone collagen (Sponheimer and Lee-Thorpe, 1999) and analysis of dental microwear patterns (Grine, 1986) promise to provide increased precision in our ability to estimate ancient diets. We simply wish to pro-

vide some suggestions about the evaluation of evidence. The evidentiary basis of early arguments about hunting and food sharing during early hominin evolution (Isaac, 1976) has received increasing scrutiny in the last decade and a half (Binford, 1981; Schoeninger et al., 2001; Lupo and O'Connell, 2002; O'Connell et al., 2002). The role of hunting in the diets of early *Homo* has been re-evaluated, and many scholars favour a much greater role for scavenging (Bunn and Kroll, 1986; Bunn and Ezzo, 1993; Speth and Tshernov, 1998; O'Connell et al., 2000) and for female-based plant gathering (O'Connell et al., 1999; Wrangham et al., 1999). While we think that such re-evaluation is of great importance, it is also important to utilize the same high standards for evidence when evaluating the scavenging and gathering hypotheses. The lack of solid, incontrovertible evidence about hunting should not be taken to imply that scavenging or collecting must have been important, since the evidence about the quantitative importance of scavenging is equally weak, and there is virtually no evidence regarding plant product consumption. At this point, we should be agnostic about the composition of early hominin diets. In addition, much emphasis has been placed on evidence regarding the hunting of large game. Given the prey size chosen by chimpanzees, we suggest that more attention should be placed on examining assemblages in terms of small game, which may have been easier for early hominins to hunt (Stiner et al., 2000). With respect to longevity, we must be careful about using dental evidence, which may provide clearer evidence about rates of development than length of lifespan. Among primates, there are strong associations both between age of first reproduction and adult mortality rates (Charnov, 1993) and between rates of dental development and maximum lifespan in captive populations (Smith, 1991). Some new evidence suggests that early *Homo*, as represented by WT 15000, may have developed more rapidly than previously thought (Smith, 1991, 1992, 1993; Smith and Tompkins, 1995). It should be pointed out, however, that when chimpanzees are compared to modern foraging populations, the length of pre-adult development increased proportionally less than did lifespans or life expectancies at adulthood. For example, average age of first reproduction among chimpanzees has been estimated to occur at age 13 and among modern foragers at about age 18-19. This is approximately a 50% increase. However, life expectancy at adulthood for chimpanzees is about 14 additional years, whereas among humans it is just over 30 years, more than a 100% increase. Estimates of maximum lifespan also suggest such a doubling. Even though the two are highly correlated, it would be very useful to investigate factors that have independent effects on rates of development and longevity among nonhuman primates and to develop new methods for assessing longevity in the fossil record.

Neandertals may turn out to be an interesting case in point to evaluate the timing of changes in diet, brain function and longevity. Recent research suggests that Ne-

andertals may have undergone rapid maturation on the basis of their dental growth in comparison to modern humans (Rozzi and Castro, 2004). They also appear to have been quite efficient hunters and rank as highly active, top-level carnivores (Richards et al., 2000; Sorensen and Leonard, 2001). Much more needs to be learned as to how this pattern might relate to changes in mortality risks and learning-intensiveness of their feeding niche (Anwar et al., this volume).

Timing and evolutionary mechanisms

The model we propose is silent about the timing of changes in different hominin lineages across time and space. Nevertheless, it is clear that there were progressive changes in brain size and presumably in other features of the human adaptive complex over time, at least in some lineages. Moreover, the data show that some features of the contemporary human adaptive niche absolutely require the presence of other features. The long period of juvenile low productivity (1) and costly brain growth (2) could not be supported without a long adult lifespan (3) in which both men (4) and women (5) contribute to the energetic support of juveniles. These five co-adapted traits can be thought of as an adaptive peak, *sensu* Sewall Wright (1932). One question is whether hominin evolution can be characterized by the traversing of several adaptive peaks, separated by adaptive valleys.

One view would be that long-term juvenile dependence, brain size, longevity, and increased parental investment evolved in small steps, to some extent independently within some range. In this case, the additive phenotypic effects of genes contribute to the selective environment of other genes. For example, the phenotypic effects of genes affecting brain development and function increase foraging returns for high-quality, nutrient-dense foods during adulthood. The ensuing diet and age profile of production then constitute the selective environment for genes affecting dietary physiology (e.g. the size of the large intestine) and rates of aging (e.g. accumulation of plaque and free radicals). At the same time, the phenotypic effects of those latter genes affect the selective environment for genes affecting brain tissue and brain development. This could result in a "ratcheting" process, in which both sets of genes change over time, resulting in non-random associations of brains and longevity at the species level. Such a process may take some time to unfold, but does not imply adaptive valleys.

Another view is that these traits are more tightly linked and that changes in one would not be favoured without a concurrent change in one or more of the others. This would imply that adaptive valleys would have to be traversed by some process, such as genetic drift. In this case, some population demes would by chance have founders who were extreme on one of the traits, such as brain size. This could have entailed a net fitness cost with prolonged development or parental provisioning, albeit it could only have been relatively small. Through further ran-

dom events and population drift, some descendants would possess genotypes coding for higher levels on the other traits, leading to a new adaptive peak and population expansion. This piecemeal process would presumably have taken even longer, and would also imply greater divergence among hominin lineages at the same point in time.

From a mechanistic perspective, some trait associations could be due to pleiotropy (i.e., single genes influencing more than one trait) and/or linkage disequilibrium (sets of genes jointly assorting during meiosis). Research into brain aging and longevity suggests that some genes may have such pleiotropic effects. The apolipoprotein (apoE) allele system is a good example since this seems to affect neurite growth and the aging of both the brain and the cardiovascular system. (The discussion here is based on Finch and Sapolsky, 1999, which gives the original sources). Brain aging, as in the symptoms of Alzheimer's disease, is common in long-lived mammals. These signs of brain aging are delayed in humans relative to apes and in apes relative to monkeys. In humans, apoE has at least three variants (apoE 2, 3 and 4) whereas all nonhuman primates that have been studied have the same variant, most similar to human apoE 4. Interestingly, this variant is a risk factor for both Alzheimer's disease and coronary artery disease, suggesting that the apoE 2 and 3 variants may have evolved to slow down both brain and cardiovascular aging. These other variants also promote neurite growth in cultured neurons, suggesting they also stimulate greater brain development and complexity.

Pleiotropic effects of this nature could evolve by a similar ratcheting process. The sensitivity of one tissue type (e.g. neurons) to a gene product could affect selection on the sensitivity of other tissue types (e.g. vascular tissue) to that same gene product, and vice versa. To the extent that associations between brains and longevity are due to pleiotropic effects, this would generate correlations at the individual level as well as at the species level. Given the growing body of data suggesting that such individual-level associations exist among humans, pleiotropy deserves careful consideration.

A third possibility is that environmental conditions changed over time in a way that systematically changed the benefits and/or the costs of cognitive abilities. Either the changes in environmental conditions would have to have been directional, or those changes could have interacted with one of the two processes mentioned above. Some mix of environmental change and incremental change in co-adapted trait bundles is perhaps the most likely scenario. In any case, each of those possibilities deserves further theoretical and empirical attention.

Timing and the role of men

There are several other proposals that attempt to explain the evolution of human life histories, especially longevity. One model, recently proposed by Hawkes and

colleagues (Hawkes et al., 1998), often referred to as the "Grandmother Hypothesis", proposes that humans have a long lifespan because of the assistance that older post-reproductive women contribute to descendant kin through the provisioning of difficult-to-acquire plant foods. Women, therefore, are selected to invest in maintaining their bodies longer than chimpanzee females. This model offers no explanation of why men live so long. In contrast to this female-centred view, Marlowe (2000) proposes that reproduction by males late in life selects for the lengthening of the human life course, with effects on females being incidental. The embodied capital theory proposes an explanation for why both men and women live long lives. Both men and women exploit high-quality, difficult-to-acquire foods (females extracting plant foods and males hunting animal foods), sacrificing early unskilled productivity for later skilled productivity at much higher rates, with a life history characterized by an extended juvenile period where growth is slow and much is learned, and a high investment in mortality reduction to reap the rewards of those investments in growth and learning.

Discrimination among these alternative proposals requires more data and a clear set of alternative predictions. Of course, it is also possible that each may be relevant for different times in the course of hominin evolutionary history. It is plausible that some of the early shifts in brain size or life history occurred primarily through shifting roles of women as they aged. One possibility is that a shift to more extractive foraging increased the benefits of three-generational resource flows among female kin. On the other hand, since some of the populations living in cold climates during the Middle and Late Pleistocene must have depended almost exclusively on meat (Hoffecker, 1999), men must have played a much larger role in the energetic support of reproduction and parental investment in those populations (Mussi, this volume). The large differences among ape mating and parental investment systems and between contemporary foraging populations and all ape species suggest that they are highly malleable and depend on the details of the food acquisition strategy and local ecology. The fact that all human peoples live in multi-male, multi-female groups with restricted sexual access mediated through some form of marriage highlights the importance of understanding the evolutionary origins of this pattern, especially since it appears to be a necessary condition to support the human life history adaptation (Rodseth and Wrangham, 2004). Uncovering its distribution over space and evolutionary time represents one of the most difficult challenges. Palaeo-molecular genetics, as it develops, may turn out to provide the best source of information on this problem.

Socio-ecology and brain evolution

As mentioned above, the liveliest current debate concerns whether the benefit of a large brain is to solve ecological or social problems (Clutton-Brock and Harvey,

1980; Byrne and Whiten, 1988; Allman et al., 1993; Milton, 1993; Barton and Dunbar, 1997; Dunbar, 1998; Dunbar, this volume). In general, proponents of the social view tend to formulate the problem in terms of *Machiavellian intelligence*, the idea that intelligence evolves to manipulate others for selfish ends in an evolutionary arms race. We wish to offer a somewhat different perspective on this debate.

There is growing environmental evidence that human populations experienced tremendous variability in climate during the Pleistocene (Potts, 1996a; Richerson and Boyd, 2000; and Binford, this volume). In fact, it has been argued that much of the selective pressure on brain size (Potts) and on the emergence of culture (Richerson and Boyd) derives from coping with high-magnitude and rapid shifts in temperature and their ecological sequelae. It is also clear that contemporary foragers also experience large fluctuations in energy gain rates over much shorter stretches of time, due to the vagaries of hunting luck. Much of this latter variability can be unsynchronized across individuals, greatly increasing the benefits of food sharing to mitigate risk and inter-temporal variation in food consumption (Kaplan and Hill, 1985; Kaplan et al., 1990; Winterhalder, 1990; Winterhalder, 1996). Moreover, as mentioned above, people also experience variation in food capture due to illness and injury, and during those periods, they are frequently subsidized by fellow members of their group (Gurven et al., 2000; Sugiyama and Chacon, 2000). Finally, contemporary human foragers can often experience great gains from cooperative pursuit of game animals (Kaplan and Hill, 1985; Bailey and Aunger, 1989; Bailey, 1990; Gurven et al., 2000; Alvard, 2001; Hill, 2002), some of which can simply not be captured by lone hunters.

Those observations may help explain some exciting new findings in experimental economics and cognitive neuroscience. Humans appear to possess a strong bias towards entering into cooperative relationships and to punish individuals who "defect" in cooperative activities. This bias has been termed strong reciprocity, (see Gintis and colleagues for a collection of papers detailing this phenomenon [Gintis et al., 2004]), that is characterized by a strong tendency to cooperate in one-shot prisoner's dilemma, ultimatum and public goods games where the dominant strategy (in the sense of the individually maximizing one) is always to defect. Moreover, people are often willing and motivated to punish non-cooperators, at a cost to themselves, even when play is completely anonymous. This tendency to cooperate and to punish breaches of fairness has been documented in a diverse array of cultures, and the phenomenon is quite robust to variations in experimental design (Henrich et al., 2004). Cognitive neuroscientists, utilizing functional Magnetic Resonance Imaging (fMRI), have now begun to document areas of the brain involved in such behaviour and in resolving moral dilemmas (Sanfey et al., 2003).

Those results appear consistent with new comparative analyses of food-sharing systems among contemporary foragers. Band-wide food sharing that is completely egalitarian is actually rather rare among modern hunter-gatherers, and appears to be restricted to small groups and to circumstances in which individual return rates from foraging are sacrificed in order to increase group return rates (Gurven, 2004; Kaplan et al., 2004). In many groups, there is evidence of significant producer control over sharing and limited scope of partners. For example, among Hiwi foragers, hunters tend to exercise control over how much and with whom they share meat, restricting those who receive shares to some 15-20% of potential recipients in large groups (Gurven et al., 2000).

Our hypothesis is that one important use of human intelligence is to take advantage of gains from cooperation and, at the same time, be selective about when and with whom to cooperate based on individual assessments of the situation and the likelihood that others will reciprocate. According to this hypothesis, humans tend to cooperate in experimental games and to punish defectors for two reasons. The tendency to cooperate on the first move allows people to experience greater gains from cooperation and to demonstrate their quality as potential cooperators in future interactions. People have a moral approach to these problems because a more Machiavellian approach, which would take advantage of all opportunities for defection in one-shot games, is outcompeted by a moral psychology when there is uncertainty about the possibility of being detected as a defector, and the costs of being labelled as a cheater have great long-term consequences. Potentially, runaway selection on the ability to detect subtle signs of a Machiavellian strategy in the context of a food acquisition strategy that depends on cooperation and sharing may have been of great importance in the evolution of social intelligence and moral reasoning.

According to this view, both social and foraging intelligence are ecologically determined, and are a function of our dietary adaptation. The pursuit of large mobile packages of food engenders both risky outcomes and great gains from cooperation. However, cooperative strategies entail risks of defections; decisions about when and with whom to cooperate, and behaviours that facilitate being selected as a cooperative partner may have played a great role in individual and family food consumption patterns. Verbal language, via gossip and coordination communication, may have played a large role in this adaptive complex (Alvard and Nolin, 2002).

With respect to timing, several alternative scenarios may be distinguished. One possibility is that the ability to engage in abstract logical reasoning evolved in response to the cognitive demands of tool-based extractive foraging and knowledge-based hunting. Those internal symbolic abilities established a cognitive infrastructural pre-adaptation for symbolically based communication. Alternatively,

the gains from cooperation may have set the stage for the evolution of symbolically based communication systems that, in turn, served as a cognitive pre-adaptation for the evolution of abstract logical reasoning and its application to the food quest. A third possibility is another gradual, ratcheting co-evolutionary process, as described for the co-adaptation of life history, parental investment, and brain size. Distinguishing among such possible sequences is another difficult challenge facing human evolutionary scientists.[4]

To conclude, the human adaptation is broad and flexible in one sense, and very narrow and specialized in another sense. It is broad in the sense that as hunter-gatherers, humans have existed successfully in virtually all of the world's major habitats. This has entailed eating a very wide variety of foods, both plant and animal, and a great deal of flexibility in the contributions of different age and sex classes of individuals. The human adaptation is narrow and specialized in that it is based on extremely high investments in brain tissue and learning. In every environment, human foragers consume the largest, highest quality, and most difficult-to-acquire foods, using techniques that often take years to learn. It is this legacy that modern humans bring to the complex economies existing today, where education-based embodied capital determines income, and the economy is a complex web of specialization and cooperation between spouses, families and larger social units. We are only beginning to explore the implications of this legacy for understanding modern behaviour.

Notes

1. Although feeding niche is subject to selection, the suite of foods eaten are treated as givens in order to model how selection moulds life history traits, brain size and other features of phenotype in response to niche conditions.
2. Since brain size is endogenous, the problem of simultaneity can be addressed by using predicted brain size in this second regression. Similar results are obtained, however, when measured values are used instead of predicted values.
3. The fourth subperiod, such as conservation of quantities of liquids under container transformations, seems to require tutelage and symbolic training.
4. Similar reasoning may be applied to primate social intelligence. Co-evolutionary selection on brains and longevity due to the complexity and the navigational demands of the primate diet may have produced pre-adaptations for the evolution of social intelligence. Given that primates live long lives with enduring social relationships and given that many species of primates eat foods whose distribution generates within-group competition, there would be selection for the application of existing enhancements in memory and information processing abilities to the management of social interaction. Many animals live in social groups, but primates are notable in terms of the complexity

of their social arrangements. Perhaps, social pressures alone are not sufficient to select for markedly increased brain size, but they might select for the extension of existing abilities to social problems. This may be why apes display remarkable social intelligence, even though group size is not particularly large (Byrne, 1995; Byrne, 1997). Orangutans, for example, live in far-flung communities so are mostly solitary on a day-to-day basis, but it takes about seven years for a young orangutan to become independent of its mother (presumably because of the learning-intensive nature of the diet). If this view is correct, it also suggests that the assumption of extreme domain-specificity in intelligence may be unwarranted.