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ABSTRACT : The selective advantage of intelligence is found in the human breeding strategy, both in allowing young of different genotypes to be raised to the same optimum niche and in the manipulation of family size. Requirements of the model are consistent with the human properties of language, prolonged juvenility, adult conservatism, long life, menopause with subsequent prolonged survival of postreproductive females, and hidden ovulation. The alternate hypothesis of intelligence being selected for its use by clever foragers is rejected because this should violate the principle of niche-fixity. The model proposes that the selectively most important aspect of intelligence is the property of overriding innate behavior, for which the term Conscious Prevention of Stimulated Behavior (CPSB) is proposed. The model permits selection for intelligence to have been a rapid, punctuational event.

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I am unimpressed by all of what may be called "opposing thumb" models for the selection of intelligence. By "opposing thumb" I mean all models that assume an alliance between using a large brain and such avowed properties of our kind as grasping hands, or whatever others of our physical oddities take our fancy. I do not deny that modern humans use their brains to get the most out of the peculiar bodies they do have but I find profoundly unconvincing the argument that the use of these bodies in foraging promoted the evolution of large brains, and hence presumably intelligence itself.

Nor are social facilitation arguments entirely satisfactory alternatives. These are the models giving advantage to powers of abstract reasoning in social encounters, as in being able to ponder the question, "If I punch him on the nose, what might the harvest be?" Social facilitation models suggest that correct solution of this conundrum in time to prevent an unwise action would allow run-away selection towards the intelligent state (Jolly 1966, 1985; Humphrey 1976). This argument seems less than compelling when we note that numerous social animals cope with aggression and other interactions without abstract reasoning.

But both "opposing thumb" and "social facilitation" models encounter the, to me, insuperable difficulty that their mechanisms are likely to interfere with niche fixity. It is a cardinal principle of evolutionary ecology that selection works to enforce conformity of behavior with the species norm. To be clever is perilous because cleverness invites being different when being different is not allowed. This does not foreclose the possibility of learned behavior in a world fashioned by natural selection, but it does suggest definite limits to the scope of learning. The best evidence that the free use of a large brain is likely to lead to loss of fitness is that the trait appears to have been permitted but once in three thousand million years.

One of the many problems of human origins, then, is to find a true selective advantage for the use of a large brain which should confer the benefits of its intellectual powers without the unacceptable costs of aberrant behavior. I suggest that the package of traits yielding the necessary selective advantage is to be found in the human breeding strategy and that the use of large brains by reproductive females for the training of young largely increased infant survival and hence maternal fitness. At the same time, the increased learning and memory made possible by a large brain let humans regulate clutch to optimum size while retaining the long juvenile period inseparable from the prolonged learning involved. The selective advantage should be large, because resulting in a direct increase in numbers of offspring raised to maturity.

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If it is assumed that a large brain is a simple evolutionary step involving neoteny and a limited number of loci (Jerison 1973), then rapid evolution of traits yielding selective advantage from large brains should have kept pace with rapidly increasing brain size. The alternative model of gradual increase of brain size should allow eventual attainment of a critical minimum size. After brains of the required size were present, selection for the intelligent use of the large brain should proceed in parallel with the evolution of traits giving selective advantage to intelligence. Whether the size of brains of hominid precursors of humans increased gradually or rapidly, therefore, is irrelevant to an understanding of the package of traits required to give selective advantage to the emergent property of intelligence as a function of a large brain.

The proposed model allows selective advantage to be given entirely by applying advanced learning and knowledge amassed in preceding generations to reproductive traits already latent in the population and easily modified. The model thus suggests that selection for the intelligent use of a large brain was rapid and could be considered a "punctuational" event (Eldredge and Gould 1972). This is consistent with the possibility that the attainment of intelligence, and the emergence of humans as a species, were comparatively recent and compatible with a human origin in the order of 150,000 yr ago (Cann *et al* 1987). And it suggests rapid population growth for the matrilineal line in which intelligence evolved.

#### Intelligence and human properties allowable for analysis

Anthropological colleagues have insisted that I define intelligence, if I pretend to discuss it. I admit I cannot do this. Instead I propose to identify intelligence by some of the properties it confers on humans. The simplest of these is the trait of learning virtually all important behavioral parameters of niche. Other animals learn; some of them learn much; but the learning required of a human infant before it can be an effective breeding adult is uniquely large. A one-liner definition of the human species could well be, "The animal that learns its niche". So human intelligence can be recognized, in part, by an almost absolute reliance on learning for the acquisition of skills for survival, foraging, and reproduction.

But the second property of human intelligence is more compelling. This is our ability consciously to set aside what appear to be genetically constrained and innate behaviors and instead to do something different. Obvious examples are the ways in which we can overcome fear of heights or spiders, despite the fact that both are probably innate and genetically constrained conditions (Wilson 1975), in order to climb at the one or pick up the other. I shall call the human property of overriding genetic instructions as to how to behave in order to behave differently the **Conscious Prevention of Stimulated Behavior**, yielding the unmemorable acronym CPSB.

Through CPSB humans can and do override basic genetic instructions, letting them respond to fear, anger, pity, cold, hunger, threat and other stimuli in ways quite different from the responses suggested by innate behavior. I take both this property of CPSB and extreme niche-learning to be essential properties that must be explained by any model for the selective advantage of intelligence.

Conscious Prevention of Stimulated Behavior (CPSB) is a formal way of stating the principle of free will. Operationally the concept is particularly useful in letting a biologist examine the natural selection of human attributes without justly incurring the political wrath of those afraid that selective models of human behavior will have evil social consequences. Important human social behavior is learned or disciplined, not the result of genetic instruction. This is particularly clear, for instance, when studying human aggression, despite claims by ethologists to understand war as an extension of the agonistic behavior of animals (Lorentz 1966). Military experience suggests that anger has little place in warfare, and the staff colleges of the world have long taught that battles are won by soldiers disciplined to subdue anger, and to subdue as well impetuosity, excitement, fear, and other agonistic behavior in favor of trained and deliberate purpose. Aggressive military behavior, like most of the important things that modern humans do, is conscious, learned, and intentional. It is



1981). These alternatives are variants on a general mechanism, but classical character displacement itself does appear to have been firmly demonstrated as a population separating mechanism in at least one instance (Schluter, Price, and Grant 1985; Grant 1986).

The Lotka-Volterra-Gause logistic hypothesis predicts that individuals shall function in ways closely similar to their conspecifics and their parents. Individuals of deviant behavior are likely to suffer excess interspecific competition in addition to intraspecific competition, thus leaving less surviving offspring. Likewise, individuals that deviate from parental behavior court excess predation or environmental privation and again leave less surviving offspring than those that behave as their parents did. The result is relentless selection to conformity (Van Valen 1973). It is against this requirement of conformity that the emergence of life-styles acquired by learning must be judged.

The life-style to which individuals of a species conform is the species niche, where niche may be defined as a specific set of capabilities for extracting resources, for surviving hazard, and for competing, coupled with a corresponding set of needs (Colinvaux 1982). This is niche defined in the tradition of Grinnel (1904) and Gause (1934), and as also implied in the writings of Shelford (1911). Ecological advances from Lack's (1944) work on speciation in birds, through character displacement (Brown and Wilson, 1956), the Santa Rosalia essay (Hutchinson, 1959) and the coining of the term "competitive exclusion" (Hardin, 1960) all use the term "niche" in this sense. Elton's (1927) use of "niche", which was responsible for the widespread acceptance of the term, was slightly different in that it spoke to community function of individuals so that his "niche" could be filled by ecological equivalents in different communities. Operational definitions of niche as an "hypervolume of resource axes" (Hutchinson 1957) or "sets of conditions" (MacFadyen 1957) refer to limits on species function as defined here but do so in terms of the environmental space required for the fulfillment of those functions; a mirror image of the species niche as it were (Colinvaux 1986).

"Niche" as used in this paper, then, describes the functional properties of a species population. Description of the species niche becomes the significant description of the species itself, with the morphometry of the type specimen being no more than the structural manifestation of the functional niche. The genetic mechanism that isolates a population does so by controlling function; and natural selection removes individuals that deviate markedly from the normal function of the species. In other words the species niche is fixed by natural selection.

This fixity of niche meets the test for an "evolutionary stable strategy" (ESS) where an ESS is a strategy such that, if almost everyone else is doing it, it would not pay a mutant to do something different (Maynard Smith and Price, 1973). The dangers of straying from the parental niche include excess competition, excess predation, interrupted food supplies, environmental hazard, and social ostracism or other failure to find a mate.

The essential fixity of niche is contrived for most species directly by genes that narrowly program the capabilities, aptitudes, and behavior of individuals. But animals also learn some skills for living, and all the primates learn many of their foraging habits. This introduces the pleasing paradox that the niche, which must be fixed in the speciation process, is nevertheless partly learned in these animals. Learning suggests flexibility rather than fixity of niches.

The paradox of a learned niche which must be fixed can be resolved for learning animals if learning is completed in a juvenile period and is constrained in adults of reproductive age. This appears to be the general pattern. Birds that learn songs do so as young or juveniles, often with a definite and constrained period in which the song must be fixed. The advantage of this song-learning is apparently that of suiting individuals to local circumstance in a way impossible to program directly in genes. The learning actually fixes the niche more narrowly than is possible by genetic instruction alone (Hinde 1970; Marler and Mundinger 1971). Local learning of fixed and highly specialized foraging habits also is known in birds (Norton-Griffiths 1969).

Learning in non-human primates appears to serve the same function of fitting

individuals to local resources that it does for birds. Characteristic is the learning of food distribution in time and space without which year-round foraging in complex ecosystems like tropical rain forest or seasonal savannas would not be possible. Hylobatid apes, for instance, learn to use at least 260 species of plant food (Gittins and Raemaekers 1980). The patterns of ranging and feeding of apes using so many seasonal or scattered resources can be understood if the animals learn, and remember, the distribution and edibility of plants in the group home range (Clutton-Brock and Harvey 1977). But this learning does not violate the principle of a fixed niche, rather it is a way in which niche can be fixed onto a local pattern of resources.

As with birds, the learning to forage of apes is a phenomenon of youth, apparently associated with the prolonged juvenile period during which young apes live with parents and older conspecifics. And also as with birds this juvenile learning can result in subpopulations with different traits, like the local "cultures" identified in gorillas by Schaller (1963), that are closely analogous to populations of Norton-Griffiths' (1969) oyster-catchers with different skills.

Despite the large component of learning in primates, recent field work demonstrates how clearly individuals continue to conform to the species niche and how rigorously the niches within guilds are kept separate. Terborg (1983) shows how the behavior of five sympatric primate niches are kept separate, although most foraging and much social behavior is learned. Other studies of sympatric primates with similar conclusions are those of Hladik and Hladik 1972; Mittermeier and van Roosmalen 1981; Clutton-Brock 1975; Gautier-Hion 1978; Struhsaker and Leland 1979; and MacKinnan and MacKinnan 1980. The patterns of niche separation described in these studies are different in the Old World and the New, but actual niches, learned though the behavioral components might be, are distinct so that the species live in sympatry with competition minimized as predicted by the Lotka-Volterra-Gause hypothesis. It follows that learning has been used as a route to a fixed niche that is alternative to direct genetic instruction. The apparent paradox of the requirement for a fixed niche and the implications of learning is thus resolved.

#### The selective perils of intelligence

For an animal to learn more than apes or birds learn is inherently risky because likely to result in the loss of niche fixity. And yet this is what humans do. Furthermore, we add abstract reasoning and conscious setting aside of customary behavior (CPSB) to our basic trait of learning virtually all foraging and social habits. The combined effects of these several traits must tend to cause individual humans to respond to the common environment in severally different ways. The essential conformity of behavior of members of a species population should break down and all individuals would be deviant with the consequent cost to fitness.

Thus, to the extent that dawning intelligence brought nonconformity, it must have released strong adverse selection. Obviously this selective disadvantage to the clever must have been offset by compensating advantages, or intelligence could never have evolved at all, but the essential point is that learning beyond that of niche fixity of the kind seen in apes should not be advantageous to the forager. It is not self-evident that intelligence is a "good thing"; rather dawning intelligence is to be seen as dangerous to the animal that possesses the trait.

In the next section I suggest that compensating fitness gains resulted from the use of intelligence in the training of young and in regulating clutch. But the perils of cleverness through increased likelihood of deviant behavior are clear. Natural selection, therefore, should have favored traits that limited the possibilities for deviant behavior in an intelligent animal.

This can be restated as :

**HYPOTHESIS 1** : Learning will be permitted by natural selection only when linked to constraints that result in niche fixity comparable to that provided by genetic stereotyping

Clearly the prediction of this hypothesis is met for all non-human learners in the ways described earlier, essentially by restricting the time when learning is possible to a youthful interval when learning is constrained to a parental role-model. In non-human primates extensive learning is made possible by a prolonged juvenile period when the young are socially dependent on elders, up to the seven years of juvenility in Pongo. Apparently selection for advanced learning in humans worked to stretch this primate trait to require the two decades of apprenticed juvenility needed by humans before they are able to enter the adult population as individuals fully equipped to breed. Humans can acquire reproductive function, of course, before this juvenile apprenticeship is over, depending on such factors as nutrition, but sexual precocity cannot be equated with readiness to be a successful human parent and the onset of functional reproductive systems should not be confused with readiness for parenthood. Humans learn how to live for about twenty years before becoming fully-functioning adults.

Once they are adult members of the breeding population, humans are predicted by the hypothesis to be fixed in their ways and to learn no more of the essentials of how to live. That humans learn easily as infants and juveniles, but less easily as adults, is a condition well-known to pedagogy (literally child guiding). The phenomenon is at its strongest for items of fundamental social belief or matters of prime importance to a forager like food preferences. Examples of molding social beliefs in the young abound, as when Christian religious orders have worked on the principle that if they can train a child until the age of seven, its religious orientation will never change. Likewise various political tyrannies have used child-indoctrination as a way of finding recruits and providing stability for their regimes, an example notorious in recent history being the Hitler Youth. Thus it is possible to fix the social attitudes of the very young for life.

Also as predicted by the hypothesis are data on human reluctance to relearn fundamental niche parameters like food preferences as adults. It is almost an axiom of military practice, for instance, that soldiers campaigning in foreign countries fight best if provided with food to which they are used, and that they will sometimes go hungry rather than eat unfamiliar food. This is an example of a general phenomenon, that humans get "set in their ways" once they are part of the adult population. A more general example may be that social and revolutionary change characteristically starts with the young. It is the young that question new ideas, and it is to the rising generation that people look for new initiatives. These observations are so familiar as to risk being trite, yet it is not self-evident that only the young are to engage in new ideas; unless, as predicted by hypothesis 1, the ability to learn is a genetically constrained condition, granted to the young and withdrawn from adults.

Hypothesis 1 predicts not only that learning should be confined to a juvenile period but also that learning should be so constrained that the parental niche, and only the parental niche, shall be learned. This is a prediction that a social system shall be in place that ensures that learning by copying shall be from parents, or at least from individuals who act as the parents do. That early humans lived in close-knit groups of relatives is at least hard to falsify with current knowledge and seems to be part of present anthropological consensus (Foley and Lee 1989).

Thus the perilous possibilities of individuality raised by the possession of intelligence can be seen to be constrained as predicted by hypothesis 1. The correct human niche is learned from adult role models during a prolonged apprenticeship, after which further learning is curtailed. Sexual precocity during the learning process probably makes possible the refinement of even reproductive behavior under the influence of role models. And these necessary constraints are clearly but extended versions of similar traits possessed by other animals that learn essential niche parameters.

#### Selective advantage of intelligence to the breeding female

A sexual system exacts large costs to a female, even beyond the damage she may

suffer from the male or the half-share of her offspring she effectively donates to him. A principal extra cost results from the recombinant genetic load, or the fact that all offspring share genes with two parents and are not exact copies of either or of each other. In a sexual system, therefore, the young of a brood start with unequal chances for survival, making it virtually certain that some are doomed to die without issue. Since sexual systems are nearly ubiquitous in nature, there must be powerful selective advantages from sex for breeding females despite the large costs (Williams 1975; Maynard-Smith 1977). But whatever the advantage of sex, the costs remain. Any trait that reduces these costs should be preserved by natural selection.

Intelligence, coupled with prolonged juvenility and communication with older kin, should let females train each of their offspring to optimum behavior and habits, despite their having different genotypes. Theoretically females who train their young intelligently should be able to avoid the costs of genetic recombination almost entirely, the residual price being no more than offspring homozygous for lethal recessive alleles, or with other deleterious genotypes making them too nonviable to be trained.

An intelligent female, who could train all of her offspring to perform as well as herself despite their deviant array of genotypes should achieve greater fitness than a competing female for whom optimum performance was attained only by the selective removal of part of her brood. This will be true whether the training is for foraging behavior and food preference or for proper social response or for coping with enemies and accident. The advantage would be progressive as each increment in traits for training improves marginally the chances for the success of offspring. Female will compete with female in training skills, and selection for the intelligent traits that make training possible will proceed rapidly.

Thus we get;

**HYPOTHESIS 2:** the primary selective advantage of intelligence is that it increases effective female fecundity by allowing young with different genotypes to be programmed for the same optimal behavior in the next generation.

Necessary conditions for the training of young include: --provision of role models, a method of instruction, adequate time, and a system of punishment and reward. The rudiments of these four conditions can be found in all animals with significant niche-learning. Long juvenile periods are common, and both primates and mammalian carnivores fix various niche parameters through systems of apprenticeship to parental role models, a process that almost inevitably includes some semblance of instruction and punishment (Bonner, 1980; Pulliam and Dunford 1980).

The more extensive training of young envisaged in the model requires maximal provision to meet these conditions, evidently achieved, in part, by the prolonged human juvenility. Yet more than just prolonged juvenility is needed, if the advantage of training all young to be as good as the best is to be achieved. It is virtually mandatory that the young of a single parentage should be raised synchronously so that the members of the brood can be molded together. Humans, therefore, should raise clutches of young, rather than single infants at intervals, where a clutch is defined as a group of offspring, cared for by parents or representing a heavy parental investment per offspring, and raised synchronously. And yet primates, including humans, are generally thought to be iteroparous with a clutch-size of one, a condition not on the face of it conducive to clutch rearing.

Human infants are born one at a time in sequence such that undergraduate textbooks often cite humans as an example of an iteroparous species. Yet humans raise but one family in a life-time. Sequential human births are more properly likened to clutch building in birds when eggs are laid one at a time until the clutch is complete. Most birds produce many such clutches in a lifetime, and are properly called iteroparous. Humans produce but one. Building the human clutch requires many years because the gestation period is nine months and the young are both very large and demanding of much parental care, but the fact that the clutch is slow to build does not alter the result of a single clutch, or family, in the reproductive life-time of the human female.

The human family thus can be seen as the predictable result of selection for females able to train young to optimum performance. The iteroparous habits of ancestors are modified so that the sequential births are used to build a clutch of juveniles who can learn the parameters of their future niche together. Females can train young as they are raised. The result is a single, prolonged reproductive event in each female lifetime, despite the fact that births are intermittent and sequential. Humans are better called quasi-semelparous, rather than truly iteroparous, though a new term really is needed to describe the uniqueness of the human reproductive strategy. I offer the term semelracemous (literally "one-time cluster").

After little more than two decades of clutch-building, effectively one juvenile period, a human female reaches menopause and ceases to be reproductively active. She has, however, a further two decades of life expectancy, unless killed, in which to complete the training of her clutch. The phenomenon of menopause, therefore, serves as a condition that allows a female time to complete the training of her semelracemous clutch freed from sexual activities or births that could not lead to extra fitness.

Granted that there were physiological or metabolic constraints on life span of the hominid stock from which protohumans evolved, the institution of two decades of clutch-rearing could not be accommodated by indefinite life. Protohumans could not be made to live for ever, or even for some multiple of the juvenile period. With life-span stretched to its expedient limit selection should work to make as safe as possible the last two decades of life, or to provide surrogate mothers for the clutch that took so many years to build, if such were possible. Withdrawal of the female from the breeding population one juvenile period from expected death is a simple stratagem for increasing her survival, suggesting one of the original selection pressures for menopause. This logic suggests that at the time of menopause more fitness could be gained by training young already born than by further fecundity. Thus essential parameters of human life-history phenomena that are consistent with synchronous clutch-raising in humans include long juvenile period, menopause, and prolonged postreproductive lives of females (Table 1).

The summed effect of these selection pressures is the semelracemous human reproductive system. A female builds a single clutch in her lifetime by serial accretion of young, and raises those young synchronously. Her clutch-building is ended when she is withdrawn from the breeding population at menopause, but she continues in her vital function of trainer of young right through to their becoming parents themselves. These properties are all consistent with hypothesis 2, allowing the tentative conclusion that a prime selective advantage of intelligence to the first humans was that effective fecundity was increased through the training of young with different genotypes to optimum behavior for life in the prevailing niche.

#### Regulation of the human clutch

Animals that raise large young simultaneously maximize fitness if clutch size is regulated to an optimum for the resources available; one young too few and potential fitness is lost; but one young too many and the resulting thin spread of resources will endanger the whole clutch. A large ecological literature, particularly for birds, shows that clutch-sizes for animals with large altricial young are indeed optimal for the pattern of expected resources. For species in which clutch-size varies, individual clutch-size is set by the availability of food (Lack 1968; Krebs and Davies, 1978).

As evolving human populations acquired the trait of semelracemosity with their young raised simultaneously, so they necessarily incurred selection for mechanisms that should allow optimum regulation of clutch, which in turn requires estimation of resources for young-rearing. For an animal with a prolonged juvenile period, estimating resources requires forecasting the yields of all the future years of dependency. Initial requirements for clutch regulation in humans, therefore, are stringent and can be stated formally in hypothesis format as follows:

**HYPOTHESIS 3** : human females are provided with the means for predicting resources available for child rearing for 10 - 20 future years.



**HYPOTHESIS 4** : human females are provided with a mechanism for converting estimates of future resources into estimates of optimum clutch.

Classic examples of clutch regulation by birds depend only on estimates of current food supplies. Parental care lasts no more than a few weeks, essentially for one terrestrial season, and "food now" is an adequate voucher for the food supply throughout the rearing period. "Food now" can be measured either by maternal fat or by a simple behavioral response to food availability like the pecking rate. But "food now" is not an adequate measure of the resources available during the twenty or so years for which a human mother must plan.

Hypothesis 3, therefore, predicts the existence in humans of a system for estimating resources quite different from the simple measures of available food used by other species. This resource measure must describe living conditions expected across two future decades. The task is partly simplified by the human habit of building families by serial additions over several years, thus letting parents modify family size in the light of experience, but the task of forecasting future resources remains formidable. When the last infant is added to a family, more than a decade remains in which it will be a burden to parents or siblings, and longer still before it can itself be a successful parent.

Estimating future environments can be likened to weather forecasting, which in part it is. A stochastic component in the control of weather prevents accurate prediction by a deterministic model, requiring that weather forecasting predict the future through extrapolation from time-series data of the past. This appears to be the only way in which future environments can be predicted. It follows from hypothesis 3 that human clutch regulation must begin with measures of past resource fluctuations that are then extrapolated to serve as measures of future resources.

There appear to be three, and only three, possible mechanisms by which humans could record environmental data for a sufficient time-series:

1. By long prereproductive life during which the necessary data are accumulated.
2. By transfer of data from older conspecifics.
3. By use of paleoecological data.

Use of paleoecological data (3) is predicated on the preexistence of intelligence, with the additional development of science, and can be discounted. A long prereproductive life (1) has merit; an analogous mechanism is the prolonged juvenile periods of many seabirds that are apparently necessary while the juvenile gains sufficient skill in foraging to be able to provide for chicks. But the cost to fitness through increased mortality of subadult life for the time-span required (in the order of 20 years or more) between maturity and first reproduction would be high. The human life-span shows that this option was not taken. Hypothesis 3 thus predicts that humans assess resources by transfer of data from older conspecifics.

A system of data transfer between generations is inherent in the basic human trait of niche-learning and is not unique to humans. But the data needed to optimize clutch are of a new order of complexity and of a kind not transmitted by any other animal. And the quality of data transmission has large consequences in enhanced or reduced fitness for the individual female.

Long life, with overlapping generations living together, are minimal conditions for the required transfer of data, but these are not sufficient without an adequate method of communication. It is suggested that an immediate selective advantage of a large brain was that it made reproductive counsel across generations possible through the development of language. Language then made possible the transmission of resource estimates (hypothesis 3) and appropriate family size (hypothesis 4) as a single instruction of the clutch size that had yielded high survivorship in previous generations.

The analysis so far suggests that language and prolonged old age evolved in protohuman populations because they gave immediate selective advantage through the breeding effort. Records of long time-series of changing environments were preserved by oral tradition and memory, transferred by language, and made possible by living in

family groups. The experience of preceding generations thus could be used to ensure that the clutch-size chosen should be optimal, an advantage that was in addition to the primary selective advantage of intelligence, that of increasing infant survivorship through training all siblings to have optimal niche properties.

#### Manipulation of family size

Estimates of expected resources and desirable clutch passed on between generations must be converted into actual clutches of the desired size. From the general prediction that humans should regulate clutch, therefore, follows:

**HYPOTHESIS 5 :** human females are provided with a mechanism for converting estimates of optimum clutch into actual families of this size.

But as was shown in the last section the mechanism to set clutch at the required size must depend on the use of information transferred consciously. Hypothesis 5, therefore, can be supplemented as follows:

**HYPOTHESIS 6 :** the human reproductive system allows conscious or learned manipulation of family size.

Human reproductive phenomena include concealed ovulation, ovulation independent of environmental cues, ovulation by non-pregnant females every four weeks or so, and persistent or intermittent sexual activity (Table 1). On the face of it, these combined phenomena appear destined to lead to that iteroparity throughout the reproductive life of the female usually thought of as part of the human condition. In some modern peoples in cultural transition or cultural collapse this is indeed what appears to happen. But this system eminently has the potential to be manipulated by learned or conscious behavior either through contraception or through culling. The human sexual system is adaptive, therefore, because it ensures a sufficient number of live births which can then be whittled down to optimum number by behavioral means.

A more perfect system for intelligent regulation of clutch would require ovulation to be recognized, or even stimulated by social behavior or fantasy. Then coitus could be undertaken at times that precisely generated the required births, avoiding the wastage of unwanted infants caused by actual human behavior. But that a powerful selective pressure works against this ideal system is revealed by the curious human property of concealed ovulation.

Concealed ovulation has been explained in the past as part of the system maintaining prolonged pair bonds in primates. This suggestion was originally put forward by Zuckerman (1932) and later given wide popular currency by Morris (1967). The argument is that breeding pairs of humans and other primates are kept together by frequent sexual pleasure, in particular that the male is tied to the female for the reward of frequent coitus. The Zuckerman-Morris hypothesis thus claims that ovulation is concealed from both parties as a tactic to separate the postulated social and pair-bonding function of coitus from its reproductive function. But this hypothesis predicts that frequent coitus as a social function would be usual among primates, a prediction that is now known to be false (Jolly, 1972).

Burley (1979) has argued that females able to associate coitus at times of ovulation with the painful experience of childbirth would avoid coitus then, thus releasing an extremely powerful selection pressure for ovulation to be hidden. The Burley hypothesis not only explains hidden ovulation in humans but also suggests that the theoretically "ideal" system of conceptions chosen to yield optimum clutch would not be preserved by natural selection in a species for which giving birth was so painful and dangerous to the female. The argument may be generalized by saying that intelligent females able easily to lower their fecundity below optimum in order to spare themselves inconvenience, pain, or danger would tend to do so and thus should be selected against. This logic suggests that the use of intelligence to avoid conception, though not eliminated entirely, was curbed by natural selection in evolving

human populations. Excessive avoidance of reproduction was an instance in which CPSB reduced fitness, thus promoting selection for any trait which would remove the stimulated behavior from conscious control.

Thus the phenomenon of hidden ovulation suggests that clutch size in ancestral humans could not be regulated to an optimum by coition on demand. Two other methods of conscious regulation of clutch-size are possible; more subtle forms of contraception and the alternative of culling surplus live births.

Social practices like manipulating the age of marriage, or the practice of prolonged lactation in which children are suckled for many years, either control the length of time during which the clutch accumulates or they alter child spacing. Both, therefore, could be effective regulators of achieved fecundity and family size, and we know that they work because both have been used in recent human populations. These methods of contraception would meet the requirements of the model in that young people act under coercion, letting their reproductive practice be guided by social instruction in which the importance of the postreproductive, older female in the family unit is likely to be decisive. Depending as they do on the CPSB property, these forms of contraception could not be neutralized by natural selection.

A more direct form of control of clutch size, however, is culling of surplus live births, for which the human reproductive system seems well suited. Intermittent, regular, or constant sexual activity is characteristic of humans, for whom coition seems to be independent of environmental cues (Table 1.). When coupled with hidden ovulation, this behavior should yield births throughout the twenty-five years or so during which a healthy female is fertile, resulting in families far larger than can be reared in a family unit in any culture of which we have knowledge or which we can readily imagine to be possible with the resources available to ancestral humans. Human reproductive phenomena, therefore, seem nicely adapted to regulation of clutch-size by culling surplus live births.

Control of family size through infanticide fits the requirements of the model in that the provisions of hypotheses 4 to 6 are met completely. A decision to accept and nurse the baby is under conscious control as influenced by social coercion. Elder females, acting on their own experience of past decades, and on what has been stored in their memories of information passed down from still earlier generations by language, coerce the behavior of breeding females to adapt clutch-size to what is suited to their condition. This is a direct, though unwitting, adjusting of family size to the resource flux available for child rearing.

Thus known human properties should have let breeding females of evolving human populations keep the size of clutch to optimum bigness by means of infanticide. The mechanism, however, requires the exercise of CPSB, since it involves killing, or at least refusing to care for, an infant protected by genetically controlled behavioral responses.

Although there can never be direct evidence that infanticide was normal in early human populations, the logic suggests that they should have suffered a grievous loss of fitness without it. Infanticide has been, however, practiced very widely by extant and historic peoples, both simple hunter gatherers and the civilized (Hausfater and Hrdy, 1984). This is not evidence that the first evolving humans engaged in infanticide, but it does show that the CPSB involved is relatively simple. There is thus nothing implausible in the conclusion that a principal method of regulating clutch in the earliest human populations was culling surplus births rather than by contraception.

When reading the literature on infanticide in historical populations it is important to notice that many authors have assumed that a result, or even an intended goal, of the practice ought to be population control, as, for instance, Carr-Saunders (1922), Harris (1977), and Bates and Lees (1979). If so, this is CPSB with a vengeance in which individuals sacrifice personal fitness for the common good. I do not believe that any society has achieved that degree of altruism, and no evidence is offered by any of the authors requiring that their particular societies have done so. What all the data actually show is that birth-spacing, family size, gender mix, or apparent health of offspring are consciously manipulated by judicious culling of the baby crop. Each of these motives relate directly to the perceived advantage of the individual

female whose infant is killed, or to the advantage of those in a position to coerce her (Hausfater and Hrdy 1984). Mothers and their advisors, therefore, use their CPSB to frustrate genetic instructions that would have them nurture offspring against their perceived best interest.

All contemporary records of infanticide show that the process has the immediate result of clutch regulation, whatever the characteristics of the baby culled. Abnormal infants, or one of a twin, may be removed. In many societies female infants may be killed preferentially, either because the cost to the family of rearing females might be higher than the cost of rearing males, or (more likely) from coercion by males in circumstances of strong male to male competition (Dickmann 1984). In strongly polygynous societies it is male infants that are removed preferentially (Scrimshaw 1984). But the overall result of all these variants is that the total number of healthy children added to the family is appropriate to the resources available to that family for child-rearing. This is well-documented by the recurrent conclusion in studies of infanticide that birth-spacing is manipulated in this way, and that birth-spacing itself can be correlated to available resources (Blurton-Jones and Sibly 1978; Scrimshaw 1984). In every instance fitness is served by keeping the total family size down to manageable proportions. In none is population regulation the goal; rather the consequence of infanticide in all instances is to maximize reproductive success.

Thus it is a legitimate conclusion that evolving humans should have used infanticide as a means of clutch regulation, just as their successors have done. With culling of surplus births in place as a normal clutch-regulation procedure, the original human breeding strategy becomes a complete, understandable whole. Intelligence, coupled with a prolonged juvenile period of helpless dependency, allows females to train all of a brood to optimal niche. The members of the brood are raised synchronously to make this training practicable. Human sexual phenomena ensure a sufficient number of babies that cannot be frustrated by exercise of CPSB. Optimal family size is derived from time series data collected over generations and passed on through language as part of local culture. And a family of this size is achieved by clutch regulation through the exercise of CPSB to provide contraception and, more importantly, culling of surplus births through infanticide. Integral to the operation of this system are long lives, prolonged juvenility, hidden ovulation, menopause, and language. These genetically determined traits were all necessary to the evolution of human intelligence.

#### The model extended

The model developed so far can be collapsed into three parts:

1. The principle of niche-fixity is upheld in that the way of life is learned from role models and then fixed by traits of adult conservatism once the individual joins the breeding population.
2. Young are raised synchronously and trained to optimum niche.
3. Family size is adjusted to the resources available for child rearing under the guidance of elders.

The combined selective advantage of these traits is that individual breeding success is enhanced. Yet the traits have demographic consequences for successor human populations that are quite outside the scope of the original selection.

Humans were able to spread to fresh habitats at the perimeter of their range by gradual learning and fixing of new niche parameters. Two consequences of human life-history phenomena and intelligence made this possible. The first was that the span of child rearing was long compared with the time it would take a family to journey between countries with different resource bases. Thus a young family or group at the periphery of a home range, in which most resources were already taken up by a relatively dense human population, could gradually extend the ancestral range at a pace that should allow learning to use a changing resource base as it went.

A second consequence of intelligence that allowed expansion of range was learning to modify environments through the use of fire and with clothing. Following selection for intelligence, therefore, the first true human niche was bounded by the use of fire

and clothing, parameters that greatly extended the habitats to which people could penetrate, together with complete learning of which resources for life were provided in each new habitat. The global range that hunter-gatherer populations attained before 30,000 B.P. was a consequence of this habitat tolerance and niche-learning. No other species has attained so global a distribution, presumably because for all the rest different niches for life with different hazards and different resources must be found through speciating<sup>1</sup>.

Yet the learning of new niches implied by the geographic spread requires that the human niche can be of different sizes. Some patterns of resource should yield predictable, dense food supplies, whereas other resources in other places should be unpredictable, scattered, or less dense, resulting in narrow or broad niches accordingly (Hutchinson, 1978). A narrow niche is a specialist niche in which a species is adapted to a narrow range of resources, strict environmental limits, or both. A broad niche, by contrast, is that of a generalist species able to make use of a wide range of alternate foods in various environmental regimens. Examples of both abound in natural history.

Early humans could move from an environment requiring the specialized habits of a narrow niche to one with the broad niche mandate of resources unpredictable in time and space, or back again, with comparative ease. By reason of this our ancestors occupied virtually every habitat on earth as mere super-foragers, whether hunters, gatherers, or fishers. For more recent human populations this ability to acquire niches of different breadths has had different and drastic social consequences. People can be raised into poverty, with its requirements of few resources per head and the skills to use only those few resources. Or people can be raised to wealth, requiring that many and various resources be available for the training of each child and resulting in adults equipped with varied skills and niche requirements that demand many resources from the environment. Wealth and poverty represent large and small niches; and the result of a somewhat Faustian bargain struck when natural selection permitted the evolution of intelligent learning about how to live (Colinvaux 1982).

This ability of the human species to live in niches of different sizes has particular implications in view of the breeding strategy which is to adjust clutch-size to resources available for child-rearing. It is, therefore, evident that the size of a family should be a function of size of niche as set by the pattern of local resources used, and we may write:

**HYPOTHESIS 7 : human clutch size should be an inverse function of niche size**

If the (admittedly dangerous) assumption is made that post-agricultural peoples still regulate clutch partly in the ways of our first ancestors, then a formal test of hypothesis 7 is readily to hand. It lies in the observation known as the "demographic transition". This is the phenomenon of family size in civilized societies falling as wealth increases, which is an exact realization of the prediction of hypothesis 7. Raising children to conditions of affluence requires very many resources per child, as well as many resources to support the niche of the parents. In these circumstances the optimum clutch that the parents can expect to provide for over the minimum span of two decades is likely to be small, with the consequent effect of reducing family size. Conversely poor people need few resources to rear a child to the expectations of poverty, particularly when the child can be a net producer before being fully raised. The paradoxical result is that poor people can afford more children than can the wealthy, exactly as predicted by the hypothesis. Thus the proposed model of human

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<sup>1</sup> W.C. Rothenbuhler has suggested to me that a comparable global distribution has been achieved by honey bees. If this is true, the explanation probably is that pollen and nectar of flowers of all habitats are so similar that the one species of bee can exploit all varieties. There is then sufficient scope for behavioral variety in the bees of a colony to cope with the small range of environmental obstacles to visiting the flowers of the different habitats.

reproduction and niche-learning provides a theoretical explanation for the demographic transition.

Another expected consequence of learned niche, learned clutch, and learned or planned parental care is that infant survival should be high. Indeed, increased survival of offspring is used in the model as the principal selective advantage of learned behavior and CPSB. Deviant phenotypes are not lost but their deficiencies are made good by training so that a larger proportion of the chosen clutch survives to adulthood. This virtually ensures that in most generations more adolescents come of breeding age than are needed to replace their parents, which yields:

**HYPOTHESIS 8 :** In most human generations more offspring are raised to maturity than bred in the parental generation  
of which a corollary might be :

**HYPOTHESIS 9 :** Infant mortality is not usually sufficient to result in a population equilibrium in humans

Testing these two hypotheses is difficult. No adequate data can be found for family size or infant mortality in primeval populations, despite the increasing ingenuity being shown by anthropologists at deducing human behavior from cut-marks on bone (Binford, 1985). And interpretations of modern data are colored by the assumption that human populations must traditionally have been regulated by infant or juvenile mortalities adjusted to the birth rate in the simplistic equation of birth rate = death rate. Indeed, it is possible to wonder if any modern data sets exist that are not themselves suspect as products of sampling procedures designed in the expectation that infant mortality should normally "balance" the numbers in large families.

Yet if human populations are not curbed by mortality imposed on the young, and if they are not to grow without limit, then alternative constraints on population growth must be present at any times that equilibrium numbers persist. Only two possibilities for regulation, other than imposed mortality, exist. One is that CPSB be used to override the mechanism to select optimum clutch so that individuals sacrifice fitness for population control by choosing small families. The claim that no peoples at any time acted in this altruistic manner obviously cannot be substantiated. But if individuals mostly continue to act in the ways that maximize fitness by optimizing family size to resources, then only one mechanism for population stability remains. This is provision for a subpopulation of adults denied by social mechanisms the opportunity to breed.

**HYPOTHESIS 10:** At equilibrium, human populations should be regulated by recruitment to the breeding population

This hypothesis cannot be falsified by data on cultures that still exist which show that impediments to the breeding population are ubiquitous in human affairs. I continue to make a distinction, of course, between sex and breeding. Coitus unlikely to lead to a surviving adult being raised, even when a conception follows coitus, is not the onset of breeding. The breeding population and the child-raising population are coincident, and the child raising population receives formal recognition in all societies, often by an institution of marriage. Thus populations of crowded peoples are predicted to be regulated by constraints on marriage contracts. In crowded caste systems, or at times of economic stress, impediments to marriage ranging from provision of sufficient dowry, through delayed marriage to outright celibacy seem to be standard responses. Possibly most revealing is delayed marriage, a proceeding inherently likely to invoke a "zero class" who marry so late that they do not marry at all.

Restricting recruitment to the breeding population should develop as a natural extension of the system in which females of reproductive age have their behavior constrained by instruction from their elders. Whether to start a family at all is merely an extension of the decision made routinely of whether to accept or reject the next live birth. Furthermore the requirements for an episode of child rearing that

must last for two decades requires social tolerance of the breeding couple and their offspring by others that should not be granted if their presence posed threats to the survival of families already established.

This postulated exclusion of some individuals from the breeding population at equilibrium is comparable to the process by which birds of territorial habit can be denied the territories without which they cannot breed, a circumstance for which there is now conclusive evidence (Hensley and Cope, 1951; Klopfer, 1969; Krebs and Davies, 1978). Territoriality in song birds is in no sense behavior selected to provide population regulation, though it does have this effect. To the contrary, the traits of territoriality give fitness to individuals by boosting their reproductive success. Population regulation is a bizarre side-effect of the behavior. Likewise with humans putting impediments in the way of young couples who wish to start a family. The proceeding does not represent a conscious attempt to control population; rather it is a side-effect of behavior whose primary selective advantage is to promote individual breeding success. For ancestral humans the base behavior is to breed according to advice of collected elders, which allows for optimizing of family size, but a necessary corollary of the behavior is that when population densities are high some individuals cannot find opportunity to breed at all.

#### Concluding note

The model rejects the concept that a decisive selective advantage for intelligence can be found in the way it equipped early humans as foragers or in social encounters. The reasons for this rejection are two-fold: first that the principle of niche-fixity would be violated by excessive individualism of the kind made likely by an experimental approach to living, and second that human life-history phenomena are consistent with selection to constrain learning in adults. Like other animals that learn, humans are programmed to learn the population niche when young, after which they retain what has been learned for the rest of their lives. The principle of niche-fixity is upheld.

This is not to say there could be no advantage to the early human forager from some of the properties of intelligence. The beginnings of environmental control represented by fire, clothing, and the building of shelters, for instance, should certainly have increased the fitness of individuals who learned them. But the use of fire and shelter seem inadequate compensation for the perils of loss of niche awaiting an animal in the stage of being half-way clever.

Instead the model proposes that dawning intelligence gave such advantage to the successful rearing of children and control of reproduction that selective enhancement of the trait should have been rapid. For this selection to work, it is required that intelligence be accompanied by language to communicate between generations, by long life, by habits of instruction, and by postreproductive lives of females, all of which are traits characteristic of humans. But these traits are not necessary to an hypothesis that invokes the use of fire or shelter etc. Thus the proposed model has a predictive power that the hypothesis equating intelligence with a better forager has not.

Two separate advantages for human reproduction are provided by intelligence, the raising of all young to be as good as the best, despite different genotypes, and the regulation of family size. I expect the first of these to have yielded the largest increase in fitness and thus to have been associated with the crucial traits in the selection for intelligence. When a female can train all her young well enough for them all to grow up and enter the breeding population she makes her line nearly immune from the customary winnowing of natural selection. When this female competes for fitness with others whose young do suffer selective winnowing it seems clear that her advantage is large. This child training would not be possible without language for instruction and the postulate predicts that humans should have long lives, with many postreproductive years beyond menopause for females. Thus it seems reasonable to conclude that most probably the extra fitness yielded by child-training was the cause of the primary selection for human intelligence.

The advantage of being able to refine family size to optimal bigness under the

instructions of elders who are walking libraries of past experiences of the population should also have been important. That intelligence is required for the proper functioning of the mechanism regulating the human family is strongly suggested by the sexual properties of humans, as has been discussed. Thus it seems likely that selection for powers of child-rearing went on in parallel with selection for better clutch regulation, both depending on the traits that collectively represent intelligence.

I have constructed all the above arguments in terms of fecundity and female fitness, partly for convenience but more importantly because it is not unreasonable to expect a close bond between mother and child persisting in the more formative years after the earlier obligate relationship of nursing. But the arguments for the selective advantage of child rearing and family regulation obviously apply just as cogently to the male who has a half share in the resulting progeny. To the extent that human males shared in the instruction of the young, and in the counsels making the crucial decisions on whether to accept live births as members of the family, their behavior is consistent with the model. Thus males should remain with females as fathers training their young and sharing in reproductive decisions. This is a more satisfactory, and more humane, explanation of pair-bonding in humans than the Zuckerman-Morris hypothesis of bonds maintained by the lure of frequent coitus. The model put forward here essentially denies the naked ape thesis, suggesting instead that humans are very different animals for whom even their social lives are conditioned by most un-apelike learning.

The model suggests that rapid selection for intelligence was possible. It is likely that H. sapiens appeared within very few generations of the beginning of selection for intelligent child-rearing and family choice. If this was so, the fossil hominid line is to be thought of as the slowly changing equilibrium out of which came the punctate episode of the evolution of Homo in the late Pleistocene.

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