



Early hominids may have been weed species

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Contributed by C. Owen Lovejoy, December 11, 2017 (sent for review November 13, 2017; reviewed by Clark Spencer Larsen and Alan C. Swedlund)

Panid, gorillid, and hominid social structures appear to have diverged as dramatically as did their locomotor patterns as they emerged from a late Miocene last common ancestor (LCA). Despite their elimination of the sectorial canine complex and adoption of bipedality with its attendant removal of their ready access to the arboreal canopy, *Australopithecus* was able to easily invade novel habitats after florescence from its likely ancestral genus, *Ardipithecus* sp. Other hominoids, unable to sustain sufficient population growth, began an inexorable decline, culminating in their restriction to modern refugia. Success similar to that of earliest hominids also characterizes several species of macaques, often termed “weed species.” We here review their most salient demographic features and find that a key element is irregularly elevated female survival. It is reasonable to conclude that a similar feature characterized early hominids, most likely made possible by the adoption of social monogamy. Reduced female mortality is a more probable key to early hominid success than a reduction in birth space, which would have been physiologically more difficult.

Australopithecus | macaques | chimpanzee | hominin | primate biodemography

There is no exception to the rule that every organic being naturally increases at so high a rate that, if not destroyed, the earth would soon be covered by the progeny of a single pair.

—Charles Darwin, 1859, *On the Origin of Species by Means of Natural Selection*

Bipedality and canine reduction play pivotal roles in almost every account of human origins. Each does so because it is both unique to hominids and readily observable in the fossil record. Availability of direct evidence, however, should not be the sole arbiter of an element’s potential role in human emergence. Other factors may have played equally prominent roles, even if their contributions are less physically traceable.

One that is likely to have been unusually prominent is the relative abundance of Plio-Pleistocene hominid taxa versus the virtual absence of any fossil traces of all other hominoids. The demographic collapse of the latter, following their remarkable florescence during the mid- to late Miocene, appears to have been well established by the early Pliocene. Does this striking contrast in success contribute to a greater understanding of our origins? We contend that it does and that data now available from living primates show that just as upright walking and canine reduction were central to human origins, so also was our unique demography (*vide infra*). It cannot be simply fortuitous that a mammal so intensely specialized as were early hominids could have so effortlessly invaded novel habitats.

The Late Miocene Hominoid Fossil Record and the African Last Common Ancestor

Unlike long-held 20th-century scenarios of human evolution, new sources of morphological and contextual data now demonstrate that most current hominoid specializations emerged only after the close of the late Miocene and after divergence of the three main surviving African hominoid clades. New Miocene taxa such as *Pierolapithecus* and *Hispanopithecus* reveal a postcranium

unlike those of all living apes and one primarily adapted to above-branch pronograde (1–3). The last common ancestor (LCA) appears to have been a generalist chiefly adapted to bridging and clambering, with significant suspension and vertical climbing having since emerged separately in small populations of gorillids and panids but never having impacted hominids (4–6).

Extant hominoid social structure is also likely to have only recently evolved from a multimale–multifemale LCA with intraspecific agonism ameliorated by significant sperm competition, perhaps most similar to that in bonobos (*Pan paniscus*) and muriquis (*Brachyteles* spp.) but in sharp contrast to much more aggressive chimpanzees (*Pan troglodytes*) (7). Gorillids have most likely undergone progressive elevation of a single dominant male from an originally multimale ancestral structure, encouraged by smaller, more easily defended territories promoted by increasingly intensive processing of nonpatchy terrestrial herbaceous vegetation.

These revelations drive two downstream pivotal questions: Why have apes become so ecogeographically constrained while hominids have simultaneously become so ubiquitous? With brains only half the size of our own, earliest *Homo* had occupied the entire Old World by 2 Mya (8, 9). Its presumptive ancestors, with relative brain sizes essentially equal to those of living panids and gorillids, had spread over much of Africa by 3–4 Mya. However, apes at the same time were essentially becoming extinct despite their continued occupation of the most ecologically stable ecozones in Africa (7). While taxonomic assessments remain controversial, none detract from the general agreement that the early hominid invasion of novel habitats from the South African veldts to East African lake margins coincided with the first emergence of *Australopithecus*. Hominid bipedality is certainly distinctive but of its own accord lacks explanatory power sufficient to account for this degree of vigorous habitat expansion, and stone tools are only half the age of

Significance

Earliest hominids demonstrate major differences from fundamental behaviors typical of other primates. These included upright walking, a reduction in canine dimorphism, and unusual demographic success. All three were likely parts of a comprehensive adaptive complex that was also unlike that of any other primate and likely reflect a novel social structure. When primate “weed species,” such as some macaques, are examined for those key behavioral features most responsible for their unusual great demographic success, an irregular but robust elevation of female survivorship emerges as key. It is likely that a similar adaptation characterized earliest hominids such as *Australopithecus*.

Author contributions: R.S.M. designed research; R.S.M., M.E.C., and C.O.L. performed research; R.S.M., M.E.C., and C.O.L. analyzed data; and R.S.M., M.E.C., and C.O.L. wrote the paper.

Reviewers: C.S.L., The Ohio State University; and A.C.S., University of Massachusetts, Amherst.

Conflict of interest statement: R.S.M. (author) and A.C.S. (reviewer) shared authorship of an encyclopedia entry during the past 48 mo.

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This article contains supporting information online at www.pnas.org/lookup/suppl/doi:10.1073/pnas.1719669115/-DCSupplemental.

the hominid “epidemic.” What adaptive agency fueled this remarkable biological phenomenon?

Apes Versus Monkeys

During the late middle Miocene, the folivore–frugivore continuum that apes had mastered for millions of years failed to spare them from novel competition from newly radiated cercopithecoid clades. Fortunately for those seeking to explicate early human evolution, descendants of both groups are extant, and their contrasting demographic patterns can provide insight into both the simultaneous decay of Plio-Pleistocene apes and the expansion of forest cercopithecoine monkeys (e.g., guenons, mangabeys). Bearing immediately on such comparisons is the “contrast between adaptable, opportunistic, wide-ranging species, the tramps [or “weedy” species], and the successful specialists in their narrow niches” (ref. 10, p. 43). Along those lines, Ripley (11) argued that some “weed” primates—small macaques, small langurs, and humans particularly—are facultatively r-selected. She reasoned that the most capable colonizers were those that could adaptively increase breeding rates whenever invading novel habitats. However, we have now intensively reviewed recent primate biodemographic data and have found that “adaptive” fertility does not appear to play such a role. Rather, recent catarrhine data suggest that the dominant factor in this change is not fertility but instead mortality.

The fossil record shows that apes have been transformed from relatively small-bodied, agile, skilled arborealists to generally larger bodied, longer lived specialists (4–6). This trajectory resulted in their evolutionary progression from “r” to “K” and most likely exposed them to ecological competition with cercopithecoine opportunists that relied largely on the same adaptive strategies abandoned by late Miocene apes. There is an obvious advantage to effective mothering that accompanies protracted longevity in K-selected species. However, the isolation of modal mortality structures employed by the ape’s r-selected competitors does not account for their success in a simple way. The r–K distinction within primates is a continuum, not a dichotomy. African-savanna and occasional gallery-forest vervets (*Chloropithecus aethiops*) mature faster, breed more, and have shorter lifespans than do other closely related cercopithecoines, such as the swamp-forested De Brazza’s monkeys (*Cercopithecus neglectus*) (12) and the forest-dwelling blue monkeys (*Cercopithecus mitis*) (13). All are successful species and widely distributed in East and Central Africa. However, they appear to have radiated in different ways.

Vervets have large day ranges that can be expanded in times of food shortage and are found in more varied and cyclic environments (14). It is useful to characterize the numerous vervet subspecies as slightly more r-selected than the undifferentiated De Brazza’s monkey. However, one of the greatest catarrhine contrasts on the r–K spectrum is between Old World monkeys and the great apes that occupy Miocene “refugia.” This contrast also provides an instructive model about the nature of human demographic origins, and one group of cercopithecoine monkeys is particularly revealing.

Hominids and Macaques: The Ultimate Weeds?

The most demographically successful Pleistocene primates have been *Australopithecus* and its descendant *Homo*, a clade that emerged around 3.5 Mya and rapidly spread from Africa to Eurasia, as well as *Macaca*, which diverged from African papionins about 7 Mya, spreading over much of the Old World (4–6). Even today its members have the widest geographic range of any primate save *Homo*. A few of the 20 or so species of macaques are best studied, and their biology, ecology, genetics, and social structures are now well-known.

Macaques are all semiterrestrial, ranging in habitat from forests to grasslands, equatorial to temperate regions, and grasslands to swamps. Species range widely and without regard to phylogeny on the frugivorous–folivorous continuum but favor fruit when available.

Four macaque species are particularly successful in areas used by humans. These are *Macaca mulatta* and *fascicularis* (from the *fascicularis* species complex) and *Macaca sinica* and *radiata* (the Sri Lankan toque monkeys and Indian bonnet macaques, both from the *sinica* lineage). Richard et al. (15) have designated all four as “weed species,” owing to their preference for riverine secondary forests, which were favored across tropical Asia during thousands of years of swidden agriculture. While those authors attribute their success to certain feeding talents, their capacity to invade and hold disturbed habitats by means of extremely high fertility rates is more distinctive and can serve as a model for their late Miocene radiations. Moreover, these species also tend to succeed in eozones that often parallel those of early hominids, especially gallery forests.

Macaque social structures have a common theme, with minor variations (16). Adult females are philopatric and maintain kin-bonded matrilineal. Males almost always disperse, repeatedly transferring from one troop to another at and after maturity. Males are thereby not closely related.

Two species of the *fascicularis* group, rhesus and long-tailed macaques, are the most successful and widespread of all non-human primates. The *sinica* group supplies the other two weed species—the bonnets of the Indian mainland (*M. radiata*) and the toques on the island of Sri Lanka (*M. sinica*). Each thrives in both wild and urban environments.

“Formal” Biodemography of Four Macaque Species

Two types of biodemographic data can be used to measure population growth rates. Census-based annual growth rates of rhesus macaques are remarkable for any primate species, even in human settings. Southwick et al. (17) have reported annual growth rates of rhesus in the tropical Nanwan Nature Reserve in China of 12.7% (1965–1984), which later slowed to 8.9% (1984–1987). Another team (18) observed population growth over two decades for rhesus monkeys in northern India (Aligarh). Couched in questions about biosocial regulation of population numbers, these census studies were extensive, and appropriately based on the dynamics of nonmigrating females, revealing several instances of severe decline (likely due to trapping for biomedical purposes) as well as specific growth peaks between 10% and 16% per annum. The other measures of growth rate are intrinsic, which for rhesus monkeys require us to turn to studies from which we can estimate life-table and fertility functions—that is, those analyses based on the estimation of “female monkey-years.”

We present a summary of such demographic parameters of these two species groups in Table 1, whose content requires some explication. Rhesus (*M. mulatta*) data (Table S1) can be gleaned from a captive population (the California Primate Research Center, CPRC) and a managed colony in the Caribbean (Cayo Santiago, CS). These have similar proportions of the female birth cohort surviving to the beginning of reproduction and nearly identical future life expectancies at that age. Both colonies are indeed weedy and have intrinsic annual growth rates of 0.06 and 0.09, respectively; these growth rates translate into a doubling of these populations every 8–12 y. However, these data are difficult to accord with those from the Nanwan and Aligarh monkey booms without positing considerable mortality reductions compared with the CS and CPRC levels (Table 1, rows 1 and 2).

A second species, closely related to *M. mulatta* (19, 20), is *M. fascicularis*, the long-tailed, crab-eating, or cynomolgus macaque. This species is of special interest because it is widespread across southeast Asia, regularly exploiting marginal habitats (21). Life table and fertility functions have been observed for a wild population during a 12-y period at Ketambe, Sumatra, Indonesia (22) (Table S2). Although the Ketambe females have only slightly greater female survival at age 5 than do their rhesus counterparts, they have twice the life expectancies at that age. Still, they achieve

Table 1. Mortality, fertility, and growth in macaque populations

Macaque population	ℓ_5	e_5	T	GRR	R_0	r
<i>Fascicularis</i> group						
(1) <i>M. mulatta</i> , CS (managed colony)	0.63	8.1	7.8	3.4	1.6	0.06
(2) <i>M. mulatta</i> , CPRC (captive)	0.67	8.4	7.5	3.7	2.0	0.09
(3) <i>M. fascicularis</i> , Sumatra (wild)	0.68	16.8	12.6	5.5	3.1	0.09
(4) CPRC <i>M. mulatta</i> fertility; wild <i>M. fascicularis</i> mortality	0.68	16.8	7.9	3.7	2.4	0.11
<i>Sinica</i> group						
(5) CPRC <i>M. radiata</i> fertility; CS <i>M. mulatta</i> mortality	0.63	8.1	8.9	5.8+	2.2+	0.09
(6) <i>M. sinica</i> , Sri Lanka (wild)	0.15	16.4	14.7	8.5	0.9	-0.01
(7) <i>M. sinica</i> fertility (LA-corrected); <i>M. fascicularis</i> mortality	0.68	16.8	12.8	8.1	4.0	0.11
(8) <i>M. sinica</i> fertility (LA-corrected); "Cercopithecine" mortality	0.80	14.5	12.5	7.3	3.6	0.10

Sources, abbreviations, and notes: (1) van Schaik and Isler (2012) (42); (2) Sade et al. (1976) (43), but see Smith (1982) (28); (3) Smith (1982) (28); (5) Silk (1988) (25): fertility after maternal age 15 y not well sampled, graduated; (6) Dittus (1975) (29); (7) Silk (1990) (26): LA, lactational amenorrhea; (8) Altmann (1980) (44), Gage and Dyke (1993) (31).

an intrinsic rate of no more than 9% per annum (Table 1, row 3)—that is, a value identical to that of the CPRC captives. However, artificially combining the “best of both worlds,” long-tailed adult longevity and CPRC rhesus early fertility, yields an annual intrinsic rate exceeding 10% (Table 1, row 4). The true long-tailed weed species capacity is ably demonstrated by the fact that a small founder population of only 10–15 (i.e., N_c) (23) was introduced into the small African island of Mauritius at the beginning of the 18th century and quickly exploded into a high-density population. Today, Mauritius represents an apparently inexhaustible supply of these primates for research laboratories around the world (24).

Generation statistics do not reflect one of the most powerful elements of annual growth; that is, absent from Table 1 is the fact that rhesus females begin reproducing in their 4th y (i.e., between ages 3.0 and 4.0 y), while long-tails do not begin until their 6th. More than 75% of the CPRC females survive into their 4th y, and nearly 80% of the CS females survive to begin reproduction. By comparison, only 67% of the long-tails survive to their 6th y. Female rhesus reproduction is all but completed by the 15th y, whereas surviving long-tailed macaque females produce almost half their daughters after this age. The single measure that best reflects this great difference between the two species is T , the average generation length, which as a divisor converts the logarithm of the net reproductive rate (R_0) into the annual intrinsic rate of growth under stable population assumptions (*SI Stable Population Theory*). CPRC and CS rhesus have average generation lengths of less than 8 y; long-tailed macaques have more than 12 y. However, the higher fertility, better surviving *M. fascicularis* increase yearly in numbers no more rapidly than do the earlier-to-breed *M. mulatta*.

Silk (25, 26) has summarized much of captive bonnet fertility, but we still lack data on wild or even provisioned–managed populations. Female bonnet macaque fertility rates are greater than those of the *fascicularis* group (Table S1). Captive-colony observations suggest that female bonnet macaques (*M. radiata*) age and become debilitated on a schedule similar to rhesus females, but the sample size is small (27). There are no bonnet life tables available at this time. However, a rhesus table (28) can be coupled with a low-end estimate of the bonnet gross reproductive function (25). This produces weedy net reproductive and intrinsic growth rates (Table 1, row 5).

Dittus (29) has reported observations of the closely related toque macaques (*M. sinica*) that inhabit semideciduous forests surrounding ancient temples. Their diet is largely frugivorous along with leaves and insects that supply necessary protein (30). These toques raid crops when opportune and seem to suffer low-to-moderate amounts of human and other predation. However, subadult mortality is artificially extreme because of droughts and a recent devastating “100-y hurricane” that produced food privation

during the 4-y Dittus field study. A striking result seen in the toque female life table is the survivorship level at the beginning of reproduction—only 15% of the female birth cohort survives to 5 y (Table 1, row 6). Infant females suffer more than 50% mortality, most in the first half year (29), and the remainder of prereproductive female mortality is so high that life expectancy actually increases through the first quinquennium of life. In fact, the earliest parts of the survivorship and life expectancy functions almost suggest a type III mortality model, which is obviously artificial and not sustainable for a mammal.

The social implications of these data for understanding human evolution are more than instructive. Quite simply, prereproductive toque females often die because they tend to be the least dominant members of their troop. Like all of the other toques, they spend most of their waking hours foraging for nutritional items; however, their prizes are often stolen from them by larger, older, and more dominant males, sometimes directly from their cheek pouches. Female survival rates sharply improve at the beginning of reproduction, and this continues through the first 10 y of fertility. Mortality begins to rise again at around age 15, even before the late fertility peak is achieved (29).

In terms of animal years of observation, the Dittus study (Table 1, row 6) provides the best estimation of fertility performance for any feral cercopithecine monkey species available to date (Table S2). This function differs from human archetypal fertility in that the peak rates are relatively later in the age span, the whole curve is flatter, and there seems to be no postreproductive period for toque females. The gross reproductive rate (GRR) is the highest known for any anthropoid. However, survivorship is such that even in the presence of such a large troop GRR, female survival is so poor that the net reproductive rate (R_0) is only 0.9; that is, in a biodemographic sense, each toque mother does not even replace herself with a whole daughter (Table 1, row 6). Of course, any number less than 1.0 is not sustainable, and in this model, there is an intrinsic annual decline ($r = -0.01$).

No extant species of macaque is a perfect proxy for stem cercopithecoids, but most share sufficiently similar biodemographic parameters to allow modeling a likely general primitive state. Predicted survivorship of female long-tailed macaques after age 5 is virtually identical to that of toques ($e_5 = 16.4$ vs. 16.8 y; Table 1, 6 and 7). Estimating ages and census proportions is difficult and problematic when a field duration is less than 12 (22) or even 4 y (29). Nevertheless, the equality of the adult portions of these two life tables suggest their mutual reliability. On the other hand, we found that female cohort episodes differ greatly between these two species before age 5—that is, in the prereproductive years (total mortality = 85%, *sinica*; compared with 32%, *fascicularis*). Therefore, we have combined the *M. fascicularis* life table with the *M. sinica* fertility function, reduced by 5% to reflect increased infant

survival, lactation amenorrhea, and birth intervals (Table 1, row 7). We have also merged the “model cercopithecine” mortality (data from Japanese macaques, yellow baboons, and especially rhesus macaques, virtually all captive; Table S2), estimated by Gage and Dyke (31), and combining these papionins with *M. sinica* fertility, incorporating an even larger lactation correction for increased infant survival. These two mortality models are very different—compare 7 and 8 in Table 1. The long-tailed model (Table 1, row 7) addresses only the gap in female subadult survival, while the cercopithecine model (Table 1, row 8) increases this correction but reduces the survivorship of mothers. While the mortality functions have different shapes, the results are similar: very high net reproductive rates and Malthusian coefficients at or greater than 10%.

In the case of the remarkable toque data, it is difficult to imagine a fertility function much higher than the one measured during the Dittus study, which was a time of severe nutritional stress. On the other hand, provisioning and captivity may well provide a model of the other extreme of “boom-and-bust” monkey biodemographic cycles. Rather than a hypothesis of facultative increase in fertility rates during times of plenty, the more obvious link between environment and growth is an increase in survivorship of females to and/or through the reproductive years. Had the observed survivorship of toque females at the start of reproduction (15%) been increased to, say, just 50%, the toque troops would have grown at substantial rates during the study years. We argue that the biology of female monkey fertility is more resistant to the environment than many have come to believe. Instead, it is the lessening of macaque prereproductive mortality, propelling larger proportions of the female birth cohort into the reproductive years, which results in high intrinsic population growth. This demographic picture of secondarily r-selected cercopithecoids is almost certainly likely to have been fundamental to their success in the Neogene, and it offers a crucial understanding of early hominid demography and its remarkable contrast to that of apes.

The Decline of Forest Apes

For the purposes of comparing the life histories of weed macaques to those of chimpanzees, we look to summary works (Table S3) on their mortality (32) and fertility (33) to permit stable-population estimates of key comparative measures of biodemography and natural selection: average generation length, net reproductive rate, and annual intrinsic rate of population increase. These sources involve smaller samples, longer life spans, obligate female mobility, and less variable ecological conditions than do the macaque studies. All of these conditions are attributable to the ecogeographic decline of panids since the end of the Miocene.

The largest number of chimpanzees in continuous observation is from the Gombe Stream Reserve in Tanzania, and the various subgroups of this population and its field workers have for more than 50 y produced a wealth of behavioral, biological, and ecological insight into humans’ closest evolutionary relative. The next largest cohort of chimpanzees is at Tai Forest, Ivory Coast and has been under observation since 1982. Smaller numbers of chimpanzees at Kibale Forest National Park (Uganda), Mahale Mountains National Park (Tanzania), and Bossou (Guinea) also

served in the construction of the best available composite life table of the free-living chimpanzee (32). In a comprehensive study, Emery Thompson et al. (33) evaluated age-specific fertility data from the aforementioned six free-ranging populations to determine the reproductive role of the oldest female chimpanzees (Table S3).

Despite myriad sampling problems, these surveys reveal a clear and remarkable story of chimpanzee life history and biodemography (Table 2). Survivorship of female wild chimpanzees at age 5 (but see Table S3) is equal to or less than that of *fascicularis* group macaques—that is, 60–64%. Even more important is that chimpanzee females begin reproduction nearly a full decade later than the macaques reported here and that starting at age 15, only 41% (Table 2, row 1) and 55% (Table 2, row 2) of chimpanzee females survive to reproduce at all.

GRRs of all weed macaques (Table 1) are larger than those of all chimpanzee models (Table 2), yet even these understate the contrasts. The composite chimpanzee demographic profile with by far the largest samples (Table 2, row 1) is summarized by a net reproductive value (R_0) less than 1.0, indicating intrinsic decline. When the Gombe samples (with better female prereproductive survivorship) are considered alone (Table 2, row 2), the result is no better than demographic stationarity. Only when the Gombe mortality function is combined with the fertility function estimated from virtually all chimpanzee populations ever observed (slightly higher early fertility and lower late fertility; Table 2, row 3) is a model produced that yields a positive intrinsic rate of growth—albeit one that is still an order of magnitude beneath some of our macaque models (Table 1).

Critically important is the fact that the entire maternal fertility period in macaques is compressed to, at most, half of that of chimpanzees (Tables S1–S3). A single measure that reflects this macaque advantage is average generation length (T), which is the mean number of years between the birth of mothers and their offspring. This figure is less than 15 in island toques and long-tails and less than 9 in continental bonnet and rhesus monkeys. By contrast, T is uniformly between 22 and 24 y in the models of free-ranging chimpanzees (Table 2), which is very similar to the value of T for human noncontracepting populations (34). More important than the generation’s total number of offspring is the average age of the mothers when they give birth. That is, the difference in maternal age distributions in *years* shows the full contrast between weed macaques and chimpanzees. Growth and development, reproduction, and senescence are so protracted in the latter that generational fertility measures actually make only a small part of the point.

Keyfitz and Flieger (35) developed a method for calculating T intrinsic to a stable population defined by the age-specific mortality (L_x) and fertility (m_x) functions with surprisingly few iterations (*SI Stable Population Theory*). It is based on the Lotka equation and clarified for primatologists by Smith (28). [The concept of a female’s reproductive value, derived by R. A. Fisher in 1929 also from the Lotka continuous form (36), is also useful in the context of species comparisons but is not applied here.] T converts R_0 to the annual intrinsic rate of growth (r), or the Malthusian parameter, which is the ultimate measure of demographic growth and therefore the sum of effects of natural selection. Viewed in

Table 2. Mortality, fertility, and growth in chimpanzee populations

Chimpanzee population	ℓ_{15}	\bar{e}_{15}	T	GRR	R_0	r
(1) Five-site composite mortality; six-site composite fertility	0.41	15.1	22.4	3.5	0.8	−0.011
(2) Gombe mortality; Gombe fertility	0.55	17.8	23.6	3.4	1.0	0.000
(3) Gombe mortality; Five-site composite fertility	0.55	17.8	22.0	3.3*	1.2	0.009
(4) Breeding facilities mortality; Composite fertility	0.68	26.3	24.3	3.5	1.8	0.025

Sources and notes: (1) Hill et al. (2001) (32), Emery Thompson et al. (2007) (33); (2) Emery Thompson et al. (2007) (33); (4) Dyke et al. (1995) (37): the total GRR for the three breeding facilities is 3.1.

*Compared with (1): Gombe female chimpanzees (3) do not live quite long enough to birth the last 0.2 daughters.

these terms, the monkey–ape contrast is in full display. All demographic models of wild chimpanzees produce intrinsic growth rates within a percent of stationary conditions (Table 2). Chimpanzee communities simply cannot rebound from periodic declines or die-offs as can weed macaques. It seems that all four weed species are capable of almost 10% growth per annum, and rhesus census data suggest values that are potentially even higher (17, 18). Thus, all weed macaques appear to be able to double their population numbers in 8 y under favorable conditions, an important characteristic for a colonizing, or weedy, primate species.

Captive-chimpanzee survivorship does not accurately reflect that of wild chimpanzees (32). In particular, prereproductive mortality is much higher among wild populations for a number of reasons. We therefore added one additional mortality study (37) to the composite fertility function (33) (Table 2, row 4). This model artificially increases both prereproductive survivorship and adult longevity by large amounts. However, the population's intrinsic rate of growth is still well below macaque values, in most cases by an order of magnitude. Moreover, the observed GRR of these established breeding colonies (see footnote in Table 2) is no greater than that of wild, nonprovisioned, chimpanzees. These data firmly establish that the notion of adaptive fertility (see ref. 11) fails to apply to hominoids and that the primary reason for chimpanzee population growth success (or failure) is external mortality.

Discussion

Some time ago we attempted to provide one solution to the “riddle” of the extraordinary demographic success of early hominids and its dramatic contrast with the failure of apes to sustain themselves even in relatively stable refugia. We argued that subadult survivorship would have been hampered by very prolonged periods of subadult dependency (5–7, 38).

We suggested that a decrease in birth space, made possible by auxiliary male contribution to the reproduction process (e.g., male provisioning with serial monogamy), might have proved a key agent for early hominid success. Indeed, some major reproductive breakthrough was clearly a requirement in light of other changes that were appearing in the early hominid record, especially those associated with a substantial reduction in climbing ability with the introduction of myriad lower limb changes (e.g., hamstring gracilization, high distal-femoral valgus, loss of the grasping great toe, rigidification of the foot) that were required for habitual upright walking. It is highly unlikely that these changes were sufficient to enable hominids to effect robust invasions of new habitats. Some other characters must have been responsible for their apparent demographic “revolution.” The elements of demographic success and failure discussed above suggest that the most effective route toward reproductive success must have been a dramatic reduction in subadult female mortality. However, there are no analogous social behaviors or mechanisms in extant cercopithecoids and/or nonhuman hominoids that, if adopted by early hominids, could account for such reductions (7, 39).

It is also worthy of note that there is a profound disconnect between human reproductive physiology and any direct enhancement of fertility that was likely in early hominids. Human reproductive mechanisms are strikingly inert. On face value, permanently enlarged mammae signal constant lactational amenorrhea and thereby discourage intercourse. Unlike the vivid announcement of ovulation by panids and cercopithecines or the special drive seen in female gorillids at the peak of fertility, humans lack either. The unique “simple penis” of humans lacks mechanoreceptors likely to speed ejaculation for successful intercourse (40, 41). Human sperm quality is poor, the refractory period for males high, and our sperm midpiece is relatively small. It seems somewhat ironic that the virtually unique demographic success of hominids is coupled with perhaps one of the weakest battery of breeding mechanisms available to most other primates (for review, see ref. 7).

However, the lesson of the “weed macaques” is that occasional marked reduction in subadult female mortality may have

been the engine of early hominid success. Recall the very high prereproductive mortality of wild *M. sinica* ($l_5 = 0.15$) and the moderately high measure of the same for wild chimpanzees ($l_{15} < 0.55$; Table 2). Correcting for this mortality, our models show macaque Malthusian parameters of at least 10% (Table 1). Turning our attention to early hominids, we ask: what novel behavioral mechanism might have reversed such mortality-inducing differences and thus have been responsible for a revolutionary demographic advance? What social shift might have greatly reduced mortality in young females? A reduction in female-female competition and of the intensity of both male and female dominance hierarchies are likely possibilities in light of what we have learned from toque macaques. What novel feature of early hominid behavior could have produced such reductions? And yet there would appear to be a dearth of candidate social behaviors practiced by any known cercopithecoid or hominoid that might have played such a role.

One possibility is made likely by a prominent and unique aspect of early hominid anatomy—dramatic reduction and eventual elimination of the sectorial canine complex. Once early hominids became increasingly restricted to nonarboreal sources with adaptations to upright walking, there must have been an expansion of their core areas and intensive food searches. However, such a strategy would have exposed young (as well as fully adult) females to even *higher* levels of extrinsic mortality due to predation. Replacement of such behavior by a male, whose reward was likely simply the maintenance of copulatory vigilance with a single (or a few) female(s), would have correspondingly enhanced his reproductive success—even lacking eventually all of the “secondary sexual mechanisms” listed earlier. In short, enhancement of female survivorship by limiting excessive exposure to predation during feeding would have effected a substantial demographic advantage.

Such a change certainly looms as a strong and novel agent of demographic success because it signals reduction of intragroup competition and potential reduction in hierarchical relationships in both sexes. No other known social behavioral pattern seen in other anthropoids would seem capable of the reduction in female mortality, especially if considered within the context of intensified parenting and reduced exposure to perilous terrestrial environments that would have been made possible by male provisioning, the practice of which would also tend to substantially reduce dominance hierarchies. Moreover, the eventual acquisition of tool making must have been a profoundly social phenomenon in the sense that it required at least the rudiments of a “tradition” in the classic anthropological sense, something that would have been unlikely to have occurred absent stable male-female bonding within the larger social context. All of these features are made possible only by the adoption of a unique social structure, heretofore unknown for any other primate—*social monogamy*. The ameliorative effects of regular pair-bonding within a social group could have so increased allo-cooperation and reduced debilitating competition, especially for newly immigrated maturing females, that female survivorship would likely be enhanced both before and after sexual maturity (for review, see refs. 7 and 39).

Summary

In retrospect panid, gorillid, and hominid social structures appear to have diverged as dramatically as their locomotor patterns since the LCA, and a unique social “system” that must have emerged among earliest hominids likely played the key role in providing them a very probable substantial reduction in female mortality. It is therefore unlikely to be a simple coincidence that bipedality, accelerated demographic success, loss of access to the arboreal canopy, and elimination of the sectorial canine complex all emerged in concert during earliest human evolution, and it is equally unlikely that all of these elements were not integral parts of some major transformation in basal hominid social strategy that would thereafter lead to their unparalleled demographic success.

1. Moyà-Solà S, Köhler M, Alba DM, Casanovas-Vilar I, Galindo J (2004) *Pierolapithecus catalaunicus*, a new middle Miocene great ape from Spain. *Science* 306:1339–1345.
2. Hammond AS, Alba DM, Almécija S, Moyà-Solà S (2013) Middle Miocene *Pierolapithecus* provides a first glimpse into early hominid pelvic morphology. *J Hum Evol* 64:658–666.
3. Moyà-Solà S, Köhler M (1996) A *Dryopithecus* skeleton and the origins of great-ape locomotion. *Nature* 379:156–159.
4. Lovejoy CO, Suwa G, Simpson SW, Matternes JH, White TD (2009) The great divides: *Ardipithecus ramidus* reveals the postcrania of our last common ancestors with African apes. *Science* 326:73.
5. White TD, et al. (2009) *Ardipithecus ramidus* and the paleobiology of early hominids. *Science* 326:75–86.
6. White TD, Lovejoy CO, Asfaw B, Carlson JP, Suwa G (2015) Neither chimpanzee nor human, *Ardipithecus* reveals the surprising ancestry of both. *Proc Natl Acad Sci USA* 112:4877–4884.
7. Lovejoy CO (2009) Reexamining human origins in light of *Ardipithecus ramidus*. *Science* 326:74e1–74e8.
8. Lordkipanidze D, et al. (2013) A complete skull from Dmanisi, Georgia, and the evolutionary biology of early Homo. *Science* 342:326–331.
9. Lordkipanidze D, et al. (2007) Postcranial evidence from early Homo from Dmanisi, Georgia. *Nature* 449:305–310.
10. Jolly A (1985) *The Evolution of Primate Behavior* (Macmillan, New York), 2nd Ed.
11. Ripley S (1980) *Infanticide in Langurs and Man: Adaptive Advantage or Social Pathology? Biosocial Mechanisms of Population Regulation*, eds Cohen MN, Malpass RS, Klein HG (Yale Univ Press, New Haven, CT), pp 349–390.
12. Rowell T (1979) How would we know if social organization were not adaptive? *Primate Ecology and Human Origins*, eds Bernstein IS, Smith EO (Garland, New York), pp 1–22.
13. Cords M, Chowdhury S (2010) Life history of *Cercopithecus mitis stuhlmanni* in the Kakamega forest, Kenya. *Int J Primatol* 31:433–455.
14. Napier JR, Napier PH (1967) *A Handbook of Living Primates* (Academic, New York).
15. Richard AF, Goldstein SJ, Dewar RE (1989) Weed macaques: The evolutionary implications of macaque feeding ecology. *Int J Primatol* 10:569–594.
16. Thierry B (2011) The macaques: A double-layered social organization. *Primates in Perspective*, eds Campbell CJ, Fuentes A, MacKinnon KC, Bearder SK, Stumpf RM (Oxford Univ Press, New York), pp 229–241.
17. Southwick CH, Zhang Y, Jiang H, Liu Z, Qu W (1996) Population ecology of rhesus macaques in tropical and temperate habitats in China. *Evolution and Ecology of Macaque Societies*, eds Fa JE, Lindburg DG (Cambridge Univ Press, Cambridge, UK), pp 95–105.
18. Southwick CH, Richie T, Taylor H, Teas HJ, Siddiqi MF (1980) Rhesus monkey populations in India and Nepal: Patterns of growth, decline, and natural regulation. *Biosocial Mechanisms of Population Regulation*, eds Cohen MN, Malpass RS, Klein HG (Yale Univ Press, New Haven, CT), pp 151–170.
19. Tosi AJ, Morales JC, Melnick DJ (2002) Y-chromosome and mitochondrial markers in *Macaca fascicularis* indicate introgression with Indochinese *M. mulatta* and a biogeographic barrier in the Isthmus of Kra. *Int J Primatol* 23:161–178.
20. Roos C, Zinner D (2015) Diversity and evolutionary history of macaques with special focus on *Macaca mulatta* and *Macaca fascicularis*. *The Nonhuman Primate in Nonclinical Drug Development and Safety Assessment*, eds Bluemel J, Korte S, Schenk E, Weinbauer GF (Academic, Waltham, MA), pp 3–16.
21. Gumert MD, Fuentes A, Jones-Engel L, eds (2011) *Monkeys on the Edge: Ecology and Management of Long-Tailed Macaques and Their Interface with Humans* (Cambridge Univ Press, New York).
22. van Noordwijk MA, van Schaik CP (1999) The effects of dominance rank and group size on female lifetime reproductive success in wild long-tailed macaques, *Macaca fascicularis*. *Primates* 40:105–130.
23. Bonhomme M, Blancher A, Cuartero S, Chikhi L, Crouau-Roy B (2008) Origin and number of founders in an introduced insular primate: Estimation from nuclear genetic data. *Mol Ecol* 17:1009–1019.
24. Satkoski Trask J, George D, Houghton P, Kanthaswamy S, Smith DG (2013) Population and landscape genetics of an introduced species (*M. fascicularis*) on the island of Mauritius. *PLoS One* 8:e53001.
25. Silk JB (1988) Social mechanisms of population regulation in a captive group of bonnet macaques (*Macaca radiata*). *Am J Primatol* 14:111–124.
26. Silk JB (1990) Sources of variation in interbirth intervals among captive bonnet macaques (*Macaca radiata*). *Am J Phys Anthropol* 82:213–230.
27. Jensen GD, Blanton FL, Gribble DH (1980) Older monkeys' (*Macaca radiata*) response to new group formation: Behavior, reproduction and mortality. *Exp Gerontol* 15: 399–406.
28. Smith DG (1982) A comparison of the demographic structure and growth of free-ranging and captive groups of rhesus monkeys (*Macaca mulatta*). *Primates* 23:24–30.
29. Dittus WPJ (1975) Population dynamics of the toque monkey, *Macaca sinica*. *Socioecology and Psychology of Primates*, ed Tuttle RH (Mouton Publishers, The Hague), pp 125–151.
30. Hladik CM (1981) Diet and the evolution of feeding strategies among forest primates. *Omnivorous Primates*, eds Harding RSO, Teleki G (Columbia Univ Press, New York), pp 215–254.
31. Gage TB, Dyke B (1993) Model life table for the larger Old World monkeys: A revision. *Am J Primatol* 29:287–290.
32. Hill K, et al. (2001) Mortality rates among wild chimpanzees. *J Hum Evol* 40:437–450.
33. Emery Thompson M, et al. (2007) Aging and fertility patterns in wild chimpanzees provide insights into the evolution of menopause. *Curr Biol* 17:2150–2156.
34. Hill K, Hurtado AM (1996) *Ache Life History* (Aldine DeGruyter, New York).
35. Keyfitz N, Flieger W (1971) *Population, Facts and Methods of Demography* (W.H. Freeman & Co., San Francisco).
36. Fisher RA (1929) *The Genetical Theory of Natural Selection* (Dover Publications, New York), 2nd Ed.
37. Dyke B, Gage TB, Alford PL, Swenson B, Williams-Blangero S (1995) Model life table for captive chimpanzees. *Am J Primatol* 37:25–37.
38. Lovejoy CO (1981) The origin of man. *Science* 211:341–350.
39. Raghanti MA, et al. A neurochemical hypothesis for the origin of hominids. *Proc Natl Acad Sci USA* 115:E1108–E1116.
40. Reno PL, et al. (2013) A penile spine/vibrissa enhancer sequence is missing in modern and extinct humans but is retained in multiple primates with penile spines and sensory vibrissae. *PLoS One* 8:e84258.
41. Reno PL (2014) Genetic and developmental basis for parallel evolution and its significance for hominoid evolution. *Evol Anthropol* 23:188–200.
42. van Schaik CP, Isler K (2012) Life-history evolution. *The Evolution of Primate Societies*, eds Mitani JC, Call J, Kappeler PM, Palombit RA, Silk JB (University of Chicago Press, Chicago), 1st Ed, pp 220–244.
43. Sade DS, et al. (1976) Population dynamics in relation to social structure on Cayo Santiago. *Yearb Phys Anthropol* 20:253–262.
44. Altmann J (1980) *Baboon Mothers and Infants* (Harvard Univ Press, Cambridge, MA), 1st Ed.