日本人類学会進化人類分科会

ニュースレター

目次

第29回シンポジウム

「資源をめぐる葛藤とその解決法の進化史」

オーガナイザー：山極壽一(京都大学大学院理学研究科)

ディスカッサント：　竹ノ下祐二（中部学院大学）、河合香吏（東京外国語大学 AA 研）

日時：　2012年 11月 2日（金）17時20分から19時20分まで

場所：　慶應義塾大学日吉キャンパス　C 会場

山極壽一（京都大学大学院理学研究科）
　　「資源をめぐる葛藤の進化史的背景」

藤田志歩（鹿児島大学）
　　「ストレスホルモンの解析と霊長類の葛藤」

中務真人（京都大学大学院理学研究科）
　　「化石霊長類群集における競争とニッチ分割」

木村大治（京都大学大学院アジア・アフリカ地域研究研究科）
　　「アフリカの狩猟採集民と農耕民の森林資源をめぐる葛藤と解決」

討論
総会

「大型類人猿の生活史戦略と人類進化」

7 月 6 日(金) ウインク愛知　1004 会議室
オーガナイザー：山極壽一(京都大学大学院理学研究科)
　　　　　　　　古市　剛史(京都大学霊長類研究所)
　　　　　　　　中務真人(京都大学大学院理学研究科)

　山極壽一（京都大学大学院理学研究科）
　「Life history strategies of the great apes」」

　Jay KELLY（アリゾナ州立大学)
　「Life history inference in the early hominins Australopithecus and Paranthropus」

Life history strategies of the great apes

山極壽一

京都大学大学院理学研究科

Primates show slow life history traits, such as small litter size, long gestation, long lactation, and long life span, in spite of striking contrasts in habitats, diet, mobility and range size between them (Harvey et al., 1987; Read & Harvey, 1989; Ross, 1998). Recent arguments have proposed determinant factors of slow life history in primates, such as large brain size (Allman et al., 1993; Martin, 1996), high risk of juvenile mortality (Janson & van Schaik, 1993) and arboreal life style (Eisenberg, 1981; Martin, 1995), but no single factor seem to fully explain it (Harvey & Purvis, 1999; van Schaik & Deaner, 2002).

Ecological factors may influence the life history traits of primates in various ways (Kappeler et al., 2003). The low growth rate of primates may be caused by a negative association between mortality rates and growth rates, and the juveniles' vulnerability to food shortage and predation may shape their life history traits (Janson & van Schaik, 1993). Primates may be adapted to the low mortality rates prevalent in their ancestral habitat (tropical forests), since other arboreal mammals such as bats (Jones & MacLarnon, 2001) also have low mortality rates. Primates living in the more unpredictable habitats have higher birth rates and earlier age at first reproduction (Ross, 1998). The apes that are strictly distributed in and around the tropical forests have slow life history traits, while old world monkeys living in variable habitats have relatively rapid life history traits. Large intra-specific variations are also found in some life history traits. Female vervet

monkeys may respond to limited access to food resources by delaying reproduction (Cheney et al., 1988). Female Japanese macaques and savanna baboons with high ranks tend to mature earlier than females with low ranks (Altmann et al., 1988; Gouzoules et al., 1982; Takahata et al., 1999). These observations may suggest that life history traits of primates may have evolved as a species-specific strategy as well as the immediate responses to environment changes.

Social structure and social behavior are also important for life history traits. Among mammals, primates have a unique social feature in that the two sexes live together even outside the breeding season. This may result in diversity of social structure and may characterize the fast-slow continuum in relation to social systems. Female gregariousness, social relationships, or alloparental care of dependent infants may also affect life history traits such as postnatal growth rate, weaning age and inter-birth interval (Fairbanks, 1990; Stanford, 1992). Male reproductive strategies may constitute a strong selective force on life history traits. Infanticide by males promotes prolonged male-female association (van Schaik, 2000), complex male-infant relationships (Paul et al., 2000), patterns of female movements between groups (Steenbeck, 2000; Yamagiwa & Kahekwa, 2001), and female reproductive biology (Watts, 2000; van Noordwijk & van Schaik, 2000). Recent findings show large variations in social structure and behavior between species and within species (Barton et al., 1996;

Henzi & Barrett, 2003; Doran et al., 2002; Yamagiwa et al., 2003). Life history traits are also easy to change, relatively independently, via selection (Kappeler et al., 2003). However, it is still unclear how such social variation is linked with life history variation.

The social structures of the great apes are highly differentiated. Both male and female orangutans usually live alone and overlap their home range partially with neighboring individuals of the same sex (Galdikas, 1984; Delgado & van Schaik, 2000; van Schaik, 1999). A male's large range includes multiple small ranges of females, although "unflanged male," mature but with undeveloped external adult features, occasionally roam widely (van Schaik et al., 2004). Gorillas form a cohesive group consisting of a mature male and several females with their offspring (Schaller, 1963; Jones & Sabater Pi, 1971; Fossey, 1983; Yamagiwa, 1983). They do not show territoriality, and their home ranges extensively overlap with those of neighboring groups (Schaller, 1963; Yamagiwa et al., 1996; Parnell, 2002). Chimpanzees form a large group including multiple males and females, but they frequently change partners to associate with and range in small parties (Goodall, 1968; Nishida, 1968; Boesch & Boesch-Achermann, 2000). Inter-group relationships are antagonistic and are sometimes characterized by overt aggression, even including killing individuals of neighboring groups during encounters (Goodall et al., 1979; Nishida et al., 1985; Watts et al., 2006).

Despite such sharp differences in social structure, females of the great apes have the common feature of starting reproduction after leaving their natal groups. A comparison of life history parameters in female great apes indicates that orangutans have the slowest life history.

|	Pongo	Gorilla	Pan
Female body weight (kg)	37	80	40
Gestation length (day)	264	258	228
Length of menstrual cycle (day)	30	32	37
Length of estrus per cycle	2-3	1-3	7-17
Age at first reproduction (Year)	15.6	10.4	13.7
Captive	10.6	9.4	10.5
Inter-birth interval (year)	8.1	4.3	5.8
Captive	5.2	4.2	3.2

Table 1. Comparison of female reproductive features among great apes

Both species of orangutans (*Pongo abelii* and *P. pygmaeus*) show the highest age at first reproduction (15.4 and 15.7 years on average, respectively) and the longest inter-birth interval (9.3 and 7.7 years on average, respectively) among the apes. Gorillas (*Gorilla beringei beringei* and *G.b. graueri*) show the lowest age at first reproduction (10.1 and 10.6 years, respectively) and the shortest inter-birth interval (3.9 and 4.6 years, respectively). Both species of chimpanzees are intermediate between orangutans and gorillas. The previous studies argued that ecological factors, such as frugivorous diet and arboreal lifestyle, promoted slow life history among extant apes (Doran et al., 2002; van Schaik & Deaner, 2002; Wich et al., 2004). However, recent studies reported frugivorous diet and arboreal foraging of western gorillas (Remis, 1997; Rogers et al., 2004). Although the more frugivorous orangutans (*Pongo abelii*) at Ketambe show slower life history than the less frugivorous orangutans (*Pongo pygmaeus*) at Tanjung Putting, the more frugivorous bonobos (*Pan paniscus*) show relatively faster life history than the less frugivorous chimpanzees (*Pan troglodytes*).

Social factors, rather than ecological factors, may influence the life history parameters of female apes. Among them, their solitary nature and male reproductive tactics may have great influences on the fast-slow continuum in the life history of female

apes. Female orangutans, who usually spend a solitary life, show the slowest life history. Maturing females need to establish their own home range and relationships with reproductive mates after separation from their mothers. They need a longer time to attain these tasks than female chimpanzees and gorillas, who transfer into other groups immediately after emigration. Solitary travel for weeks or months by female chimpanzees or gorillas has rarely been seen (Wrangham, 1979; Nishida, 1979; Goodall, 1986; Boesch & Boesch-Achermann, 2000; Watts, 2003; Stokes et al., 2003; Yamagiwa et al., 2003). Female chimpanzees and gorillas may easily find mates for reproduction in the group they join and thus may not need to establish their own ranging areas. Instead, they need to establish social relationships with unrelated conspecifics within the new group. Immigrant females usually get harassed by resident females in both chimpanzees and gorillas (Goodall, 1986; Idani, 1991; Furuichi, 1997; Watts, 1991, 1994; Harcourt & Stewart, 2007). Female gorillas get support from the leading males, who frequently intervene in conflicts among females (Watts, 1997; Harcourt & Stewart, 2007). The leading male monopolizes most of the copulations with fertile females and takes intensive care of the offspring before and after weaning (Fossey, 1979; Fletcher, 2001; Stewart, 2001). These social features may facilitate weaning at the earlier age, shorter inter-birth interval, and female reproduction at an earlier age for gorillas than for chimpanzees. By contrast, female chimpanzees and bonobos copulate with multiple males and take care of infants by themselves (Tutin, 1979; Goodall, 1986; Kano, 1992). Female chimpanzees tend to associate or interact with other adults less frequently than males, and mothers with dependent infants rarely join males (Wrangham, 1979; Nishida, 1979;

Boesch & Boesch-Achermann, 2000). Immigrant female bonobos first establish affiliative relationships with resident females through socio-sexual behavior (Idani, 1991; Kano, 1992; Furuichi, 1997; Hohmann et al., 1999). Although group life may facilitate female chimpanzees in starting or resuming reproduction earlier than do female orangutans, more complex social relationships within a group and unassisted caretaking may prevent them from having a fast life history.
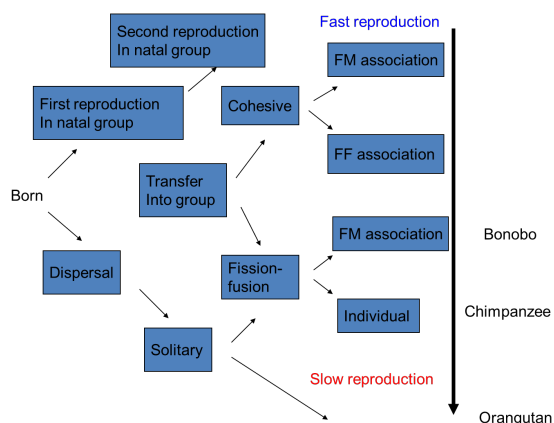
Figure 1. Costs of female transfer and fast-slow continuum of life history

In summary, male mating tactics may influence the life history of the great apes in different ways. Female dispersal and independent reproduction from related conspecifics may enable them to form various social structures and flexible life history traits according to male mating strategies. Ecological factors basically shape the gregariousness of females in female-dispersal species, but they can choose from a wide variety of feeding strategies, from individual dispersal to moving in cohesive groups. Males also take various mating tactics according to female movement and association patterns, which in turn also vary with male associations and mating strategies. Although the influences of these ecological and social factors on life history of great apes are different between genera, between

species, and between populations, the solitary nature may urge females to choose a slower life history, while stable associations between males and females may promote a faster life history. Frugivorous orangutans and chimpanzees may suffer more costs of female dispersal through decreased foraging efficiency than folivorous gorillas, and chimpanzees with fission-fusion grouping may suffer more social stress than gorillas in highly cohesive groups. Such differences may generally shape the fast-slow continuum of life history in female-dispersal primate species.

REFERENCES

Allman JM, McLaughlin T, Hakeem A (1993) Brain weight and life-span in primate species. Proc Natl Acad Sci USA 90: 118-122.

Altmann J, Hausfater G, Altmann SA (1988) Determinants of reproductive success in savanna baboons. In: Clutton-brock TH (ed), Reproductive success, Chicago, The University of Chicago Press, pp. 403-418.

Barton RA, Byrne RW, Whiten A (1996) Ecology, feeding competition, and social structure in baboons. Bahav Ecol Sociobiol 38: 321-329.

Boesch C, Boesch-Achermann H (2000) The chimpanzees of Tai Forest. Cambridge University Press, Cambridge.

Cheney DL, Seyfarth RM, Andleman S, Lee PC (1988) Reproductive success in vervet monkeys. In: Clutton-brock TH (ed), Reproductive success, Chicago, The University of Chicago Press, pp.

Delgado R, van Schaik CP (2000) The behavioral ecology and conservation of the orangutan (*Pongo pygmaeus*): a tale of two islands. Evol Anthropol 9: 201-218.

Doran DM, Jungers WL, Sugiyama Y, Fleagle JG,

Heesy CP (2002) Multivariate and phylogenetic approaches to understanding chimpanzee and bonobo behavioral diversity. In: Boesch C, Hohmann G, Marchant LF (eds), Behavioural Diversity in Chimpanzees and Bonobos, Cambridge, Cambridge University Press, pp.14-34.

Eisenberg JF (1981) The mammalian radiations: An analysis of trends in evolution, adaptation, and behavior. Chicago University Press, Chicago.

Fairbanks LA (1990) Reciprocal benefits of allomothering for female vervet monkeys. Anim Behav 40: 553-562.

Fletcher A (2001) Development of infant independence from the mother in wild mountain gorillas. In: Robbins MM, Sicotte P, Stewart KJ (eds), Mountain gorillas: three decades of research at Karisoke. Cambridge University Press, London, pp. 153-182.

Fossey D (1979) Development of the mountain gorilla (Gorilla gorilla beringei): the first thirty-six months. I n: Hamburg DA, McCown ER (eds), The great apes, Benjamin/Cummings, Menlo Park, pp. 138-184.

Fossey D (1983) Gorillas in the Mist. Boston, MA: Houghton Mifflin.

Furuichi T (1997) Agonistic interactions and matrifocal dominance rank of wild bonobos (*Pan paniscus*) at Wamba. Int J Primatol 18: 855-875.

Galdikas BMF (1984) Adult female sociality among wild orangutans at Tanjung Putting Reserve. In: Small MF (ed), Female primates: studies by women primatologists, Alan R Liss, New York, pp. 217-235.

Goodall, J. (1968) The behavior of free-living chimpanzees in the Gombe Stream Reserve.

Anim Behav Mono 1**:** 161-331.

Goodall J (1986) The Chimpanzees of Gombe. Belknap, Cambridge.

Goodall J, Bandora A, Bergmann E, Busse C, Matama H, Mpongo E, Pierce A, Riss D (1979) Intercommunity interactions in the chimpanzee population of the Gombe National Park. In: Hamburg DA, McCown ER (eds), The Great Apes, California, Benjamin/Cummings, Menlo Park, pp. 13-53.

Gouzoules H, Gouzoules S, Fedigan LM (1982) Behavioral dom9inance and reproductive success in female Japanese monkeys (*Macaca fuscata*) Anim Behav 30: 1138-1190.

Harcourt AH, Stewart KJ (2007) Gorilla Society: Conflict, Compromise and Cooperation Between the Sexes. The University of Chicago Press, Chicago.

Harvey PH, Martin RD, Clutton-Brock TH (1987) Life histories in comparative perspective. In: Smuts BB, Cheney DL, Seyfarth RM, Wrangham RW, Struhsaker TT (eds), Primate Societies, University of Chicago Press, Chicago, pp. 181-196.

Harvey PH, Purvis A (1999) Understanding the ecological and evolutionary reasons for life history variation: Mammals as a case study. In McGlade J (ed), Advanced ecological theory: Principles and applications, Blackwell, Oxford, pp. 232-248.

Henzi P, Barrett L (2003) Evolutionary ecology, sexual conflict, and behavioral differentiation among baboon populations. Evol Anthropol 12: 217-230.

Hohmann G, Gerloff U, Tautz D, Fruth B (1999) Social bonds and genetic ties: kinship, association, and affiliation in a community of bonobos (*Pan paniscus*). Behaviour 136: 1219-1235.

Idani G (1991) Social relationships between immigrant and resident bonobo (*Pan paniscus*) females at Wamba. Folia Primatol 57: 83-95.

Janson CH, van Schaik CP (1993) Ecological risk aversion in juvenile primates: Slow and steady wins the race. In: Pereira ME, Fairbanks LA (eds), Juvenile primates, development and behavior. Oxford University Press, Oxford, pp. 57-74.

Jones C, Sabater Pi J (1971) Comparative ecology of *Gorilla gorilla* (Savage and Wyman) and *Pan troglodytes* (Blumenbach) in Rio Muni, West Africa. Bibliotheca Primatologica 13: 1-96.

Jones KE, MacLarnon A (2001) Bat life histories: Testing models of mammalian life history evolution. Evol Ecol Res 3: 465-476.

Kano T (1992) The Last Ape: Pygmy Chimpanzee Behavior and Ecology. Stanford, Stanford University Press.

Kappeler PM, Pereira ME, van Schaik CP (2003) Primate life histories and socioecology. In: Kappeler PM, Pereira ME (eds), Primate life histories and socioecology, Chicago University Press, Chicago, pp. 1-23.

Martin RD (1995) Phylogenetic aspects of primate reproduction: The context of advanced maternal care. In: Pryce CR, Martin RD, Skuse D (eds), Motherhood in human and nonhuman primates, Karger, Basel, pp. 16-26.

Martin RD (1996) Scaling of the mammalian brain: The maternal energy hypothesis. News Physiol Sci 11: 149-156.

Nishida T (1968) The social group of wild chim-

panzees in the Mahali Mountains. Primates 9: 167-224.

Nishida T (1979) The social structure of chimpanzees of Mahale Mountains. In: Hamburg DA, McCown ER (eds), The great Apes, Benjamin/Cummings, Menlo Park, pp. 73-121.

Nishida T, Hiraiwa-Hasegawa M, Hasegawa T, Takahata Y (1985) Group extinction and female transfer in wild chimpanzees in the Mahale Mountains. Z Tierpsychol 67: 284-301.

Paul A, Preuchoft S, van Schaik CP (2000) The other side of the coin: infanticide and the evolution of affiliative male-infant interactions in Old World primates. In: Van Schaik CP, Janson CH (eds), Infanticide by males and its implications, Cambridge University Press, Cambridge, pp. 269-292.

Parnell RJ (2002) Group size and structure in western lowland gorillas (*Gorilla gorilla gorilla*) at Mbeli Bai, Republic of Congo. Amer J Primatol 56: 193-206.

Read AF, Harvey PH (1989) Life history differences among the eutherian radiations. J Zool 219: 329-353.

Remis MJ (1997) Western lowland gorillas (*Gorilla gorilla gorilla*) as seasonal frugivores: Use of variable resources. Am J Primatol 43: 87-109.

Rogers ME, Abernethy K, Bermejo M, Cipolletta C, Doran D, McFarland K, Nishihara T, Remis M, Tutin CEG (2004) Western gorilla diet : a synthesis from six sites. Am J Primatol 64: 173-192.

Ross C (1998) Primate life histories. Evol Anthropol 6: 54-63.

Schaller, G.B. (1963). The Mountain Gorilla: Ecology and Behavior. University of Chicago Press, Chicago.

Stanford CB (1992) Costs and benefits of allomothering in wild capped langurs (*Presbytes pileata*). Behav Ecol Sociobiol 30: 29-34.

Steenbeek R (2000) Infanticide by males and female choice in wild Thomas's langurs. In: Van Schaik CP, Janson CH (eds), Infanticide by males and its implications, Cambridge University Press, Cambridge, pp. 153-177.

Stewart KJ (2001) Social relationships of immature gorillas and silverbacks. In: Robbins MM, Sicotte P, Stewart KJ (eds), Mountain gorillas: three decades of research at Karisoke. Cambridge University Press, London, pp. 183-214.

Stokes EJ, Parnell RJ, Olejniczak C (2003) Female dispersal and reproductive success in wild western lowland gorillas (*Gorilla gorilla gorilla*). Behav Ecol Sociobiol 54: 329-339.

Takahata Y, Huffmann MA, Suzuki S, Koyama N, Yamagiwa J (1999) Why dominants do not consistently attain high mating and reproductive success: a review of longitudinal Japanese macaque studies. Primates 40: 143-158.

Tutin CEG (1979) Mating patterns and reproductive strategies in a community of wild chimpanzees (*Pan troglodytes schweinfurthii*). Behav Ecol Sociobiol 6: 29-38.

Van Noordwijk MA, van Schaik CP (2000) Reproductive patterns in eutherian mammals: adaptations against infanticide? In: Van Schaik CP, Janson CH (eds), Infanticide by males and its implications, Cambridge University Press, Cambridge, pp. 322- 360.

Van Schaik CP (1999) The socioecology of fis-

sion-fusion sociality in orangutans. Primates 40: 73-90.

Van Schaik CP (2000) Infanticide by male primates: the sexual selection hypothesis revisited. In: Van Schaik CP, Janson CH (eds), Infanticide by males and its implications, Cambridge University Press, Cambridge, pp. 27-60.

Van Schaik CP, Deaner RO (2002) Life history and cognitive evolution in primates. In: de Waal FBM, Tyack PL (eds), Animal social complexity, Harvard University Press, Cambridge, MA.

Van Schaik CP, Preuschoft S, Watts DP (2004) Great ape social systems. In: Russon AE, Begun DR (eds), The Evolution of Thought: Evolutionary origins of great ape intelligence, Cambridge, Cambridge University Press, pp. 190-209.

Watts DP (1991) Harassment of immigrant female mountain gorillas by resident females. Ethology 89: 135-153.

Watts DP (1994) Agonistic relationships between female mountain gorillas (Gorilla gorilla beringei). Behav Ecol Sociobiol 34: 347-358.

Watts DP (1997) Agonistic interventions in wild mountain gorilla groups. Behaviour 134: 23-57.

Watts DP (2000) Causes and consequences of variation in male mountain gorilla life histories and group membership. In: Kappeler P (ed), Primate males, Cambridge University Press, Cambridge, pp 169-179.

Watts DP (2003) Gorilla social relationships: a comparative overview. In: Taylor AB, Goldsmith ML (eds), Gorilla biology: a multidisciplinary perspective, Cambridge University Press, Cambridge, pp. 302-327.

Watts DP, Muller M, Amsler S, Mbabazi G, Mitani JC (2006) Lethal intergroup aggression by chimpanzees in the Kibale National Park, Uganda. Amer J Primatol 68: 161-180.

Wich SA, Utami-Atmoko SS, Mitra Setia T, Rijksen HD, Schurmann C, van Hooff JARAM, van Schaik CP (2004) Life history of wild Sumatran orangutans (*Pongo abelii*). J Hum Evol 47: 385-398.

Wrangham RW (1979) Sex differences in chimpanzee dispersion. In: The Great Apes, Hamburg DA, McCown ER (eds), The Benjamin/Cummings, Menlo Park, Californis, pp. 481-489.

Yamagiwa J (1983) Diachronic changes in two eastern lowland gorilla groups (Gorilla gorilla graueri) in the Mt. Kahuzi region, Zaire. Primates 24: 174-183.

Yamagiwa J, Maruhashi T, Yumoto T, Mwanza N (1996) Dietary and ranging overlap in sympatric gorillas and chimpanzees in Kahuzi-Biega National Park, Zaire. In: McGrew WC, Marchant LF, Nishida T (eds) Great Ape Societies. Cambridge University Press, Cambridge, pp 82-98.

Yamagiwa J, Kahekwa J (2001) Dispersal patterns, group structure and reproductive parameters of eastern lowland gorillas at Kahuzi in the absence of infanticide. In: Robbins MM, Sicotte P, Stewart KJ (eds), Mountain gorillas: three decades of research at Karisoke. Cambridge University Press, London, pp 89-122.

Yamagiwa J, Kahekwa J, Basabose AK (2003) Intra-specific variation in social organization of gorillas: implications for their social evolution. Primates 44: 359-369.

Life-history inference In the early hominins *Australopithecus* and *Paranthropus*

Jay Kelley

Institute of Human Origins, Arizona State University

For primates as a whole, age at M1 emergence has been demonstrated to be a reliable proxy for the general pace of life history. New ages at M1 emergence for several wild great ape individuals (~3.7-4.6 years) show a particularly close correspondence to key life-history attributes related to lifetime reproductive output, more so than body mass or adult cranial capacity. If these new ages approximate the respective species means, then age at M1 emergence would appear to be a highly reliable predictor of life history within Hominidae, including fossil members of the clade.

Estimated ages at M1 emergence were calculated for four species of the early hominin genera *Australopithecus* and *Paranthropus* using data on adult average cranial capacity, as well as previously estimated ages at death in several infant and juvenile individuals that died during or soon after M1 eruption (Bromage & Dean, 1985; Dean, 1987; Dean et al., 1993; Lacruz et al., 1995). The latter were based partly on the preserved growth records in the teeth of these individuals combined with data on tooth formation in extant apes.

Species	Specimen	M_1 eruption stage	Estimated age at death (yrs)	Estimated age at M_1 emergence (yrs)[a]
Australopithecus afarensis	LH 2	Recently into occlusion	3.25	2.9
Australopithecus africanus	Sts 24	Recently into occlusion with slight wear	3.30	2.9
Australopithecus africanus	Taung 1	Recently into occlusion with very slight wear	3.73-3.93	3.3-3.5
Paranthropus robustus	SK 62	Cusp tips just below alveolar margin	3.35-3.48	3.8-3.9
Paranthropus robustus	SK 63	In occlusion with wear facets	3.4-3.7	2.8-3.1
Paranthropus boisei	KNM-ER 1820	Mesial cusp tips above level of dP_4 cervix	2.5-3.1	2.7-3.3

[a] Based on age at death estimates, adjusted for stage of eruption.

Table 1. Estimated ages at death and M1 emergence in six early hominin individuals

The two methods generally produced different results. Predicted M1 emergence ages based on cranial capacity were in the range of 3.7-3.8 years using either an all-anthropoid or gorilla model, or 4.3-4.4 years using a chimpanzee model. Those based on ages at death in the early hominin indi-

viduals had an overall range (lowest minimum to highest maximum estimates for all individuals) of 2.7-3.9 years, with a range of species means of approximately 3.0-3.4 years (Table 1).

Four of the six individuals, however, had mean estimates of only about 3.0 years. Most interesting, unless early hominins are modeled as chimpanzees in the age at M1 emergence/cranial capacity regression, the ranges from both methods are below, or barely overlap, the range of M1 emergence ages of the free-living great ape individuals (3.7-4.6 years).

What stands out in these results is that most of the estimates of age at M1 emergence derived from ages at death in the early hominin individuals are so much earlier than the expected ages based on cranial capacity, and, for the most part, also so much earlier than those determined for the extant great ape individuals. However, in extant great apes and humans, cranial capacity is neither a particularly precise nor accurate predictor of age at M1 emergence, nor is it strongly concordant with the timing of key life-history attributes. Equally important is that age of M1 emergence does appear to be a very reliable predictor of life history in extant hominids.

The critical issue, therefore, is the accuracy of the age at death estimates in the fossil hominins, which largely determines the accuracy of the estimates of age at M1 emergence. If they are reasonably accurate, then the life histories of *Australopithecus* and *Paranthropus* species would likely have been considerably faster than in any of the extant great apes. Alternatively, there could have been selection for accelerated dental development and therefore early M1 emergence, as in indriids for example compared to other lemurs, perhaps associated with relatively early weaning. Again as in indriids, other life history parameters might have been relatively slower and more or less commensurate with cranial capacities, which were nearly identical

to those of gorillas. Finally, it is possible that the ages at death in most or all of the early hominin juveniles have been systematically underestimated, with consequent underestimation of ages at M1 emergence. An examination of molar crown and root formation in early hominins, extant great apes and humans suggests that this may indeed be the case unless root growth in the early hominins was more rapid even than in *Gorilla*, which, perhaps along with *Pongo,* has the fastest root growth among extant great apes and humans. Estimates of M1 crown formation times in *Australopithecus* and *Paranthropus* mostly fall in the range of about 2.4-2.7 years. Even with root extension rates as fast as in *Gorilla*, M1 emergence any earlier than about 3.5-3.7 years of age would therefore be highly unlikely. If the ages at death in the early hominin individuals have in fact been underestimated, then their life histories would likely have been slower than presently appears to be the case and probably more in line with those of the extant great apes, as suggested by their cranial capacities.

Until recently, none of the above alternatives could be dismissed and each could be argued with reference to growth and ecology in extant primates. Means now exist, however, to determine – without recourse to the partially destructive methods otherwise needed to reveal all the dental growth information required to calculate reliable and precise ages at death – if the ages at death in the early hominins examined here have been underestimated. Together, confocal microscopy and X-ray synchrotron microtomography can faithfully render many of the details of dental incremental growth that previously had to be estimated for specimens that could not be sectioned. A project has now been initiated by researchers in France and the U.S. to re-examine ages at death in a number of fossil hominins using these techniques.

REFERENCES

Bromage, T. G. & Dean, M. C. (1985). Re-evaluation of the age at death of immature fossil hominids. *Nature* 317, 525–527.

Dean, M. C, Beynon, A. D, Thackeray, J. F. & Macho, G. A. (1993). Histological reconstruction of dental development and age at death of a juvenile *Paranthropus robustus* specimen, SK 63, from Swartkrans, South Africa. *Am. J. Phys. Anthropol.* 91, 401–419.

Dean, M. C. (1987). Growth layers and incremental markings in hard tissues: A review of the literature and some preliminary observations about enamel structure in *Paranthropus boisei. J. Hum. Evol.* 16, 157–172.

Lacruz, R. S., Ramirez Rozzi, F. & Bromage, T. G. (2005). Dental enamel hypoplasia, age at death, and weaning in the Taung child. *S. Afr. J. Sci.* 101, 567–569.