Grandmother Hypothesis (GMH)

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References

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Background ∼ One of the greatest puzzle in evolutionary biology — Why do only human females among any organism survive longer time after menopause?

- ◦ Williams (1957): "stopping-early hypothesis" Midlife menopause is due to changes in the optimal allocation of reproductive effort for older women. That is, the better maternal care is (by aging), the more the survival probability of offspring is. (It is a tradeoff. By the difference of suffering proportion in whole population, selection pressure is stronger in young ages than in later ages. Thus, even if a gene enhancing fitness in young ages has deletorious effect in later ages, it will be favored by selection.)
- † Refutations: If the benefits of extended maternal care favored stopping-early, many other species such as chimpanzees, langurs, macaques and baboons should do so, but they don't (e.g. Pavelka and Fedigan, 1999: Arashiyama female macaques experience the end of reproductive life in average age 25, very close to the lifespan).
- ◦ Avoiding mortality risk from the late-career offspring, to gain survival benefit for her dependents. In other words, tradeoffs between investments in current offspring and production of additional offspring.
- † Refutations: Benefits of extended care are not large enough to compensate for reduced fertility.
- ◦ Instead of asking why stop reproduction early, asking why live so long after stopping; comparisons (using life history traits) with other great apes (based on Charnov's (1993) life history invariants) showed human age-specific fertility decline is not relatively early (Hawkes *et al.*, 1998). Human riddle is not early reproductive senescence but somatic longevity!!
  - ◦ Long postcycling survival must have an origin in primate life history. Life history traits (length of lifespan, size and age at first reproduction) correlate each other. In general, longer lifespan animals have later ages at maturity: this correlation has long considered as the result of natural selection on optimal allocation of resources between somatic growth and reproductive investment; under the high risk of mortality, the larger an organism is, the lower the mortality before reproduction is.
  - ◦ Charnov's idea: the shape of tradeoff between mortality risk and other life history traits might be invariant across transformations of body size and philogeny. The model assumes stationary population. He devided mortality into two. Early mortality is density-dependent. After that, continuously declining to a constant (M) before maturation. Under this situation, the relationships between (1) α and M^{-1}, (2) $\mathbf{b}$ and α, (3) δ are invariant across mammals (See the Table 0 for the meanings of variables).
  - ◦ Hawkes *et al.* (1998) tested the following 3 predictions about human life histories. 1) If the entire adult life span in humans is devoted to the production of descendants, age of maturity should be adjusted to it, and human αM should not differ from other pongids, 2) If the feature that postcycling females contribute to their daughters' fertility favors long lifespans, $\mathbf{b}$ for α should be higher in humans than in a grandmotherless primate, 3) High birth rate is possible because grandmothers' energy contributions allow their daughters to wean baby early, thus in relatively low weight.
  - ◦ Hawkes *et al.* suggested that mutations to slow aging can accumulate in lineages where grandmothers promote the survival and reproduction of offspring likely to bear those mutations. As the result, αM for humans, chimps, gorillas, and orangutans were 0.44, 0.45, 0.46, and 0.46, respectively. $\alpha\mathbf{b}$ for average 3 human populations, chimps, gorillas, and orangutans were 2.05, 0.70, 0.79, and 0.52, resprctively. Human δ was same as gorillas, and lower than chimps and orangutans.

Table 0. Important life history traits.

Item	Description
α	age of maturity (or time from weaning to first conception)
$\mathbf{b}$	annual birth rate
M	average adult instantaneous mortality rate (M^{-1} is average adult lifespan)
T_{MAX}	maximum life span, with relationship $\mathrm{M}^{-1} = 0.4\mathrm{T}_{MAX} - 0.1$
δ	the ratio of offspring weight at weaning (the size that an offspring must reach before the mother moves to next reproduction) to mother's body weight

Aims of this study

1) Review the general theory and the specific model underlying GMH (summarized above).
2) Extend the comparisons for 4 species by Hawkes *et al.* to 16 primate species.

Method

- Datasets for 16 primates were obtained from published papers about nonprovisioned wild populations. *Homo sapiens* was represented by Ache people, tropical foragers of South America.
- Variables used were, age at first birth (=age at maturity, α), average interbirth interval (IBI, cannot be used to estimate weaning age, but to calculate actual birth rate), adult female weight, age at weaning, and female weight at weaning.
  - Using IBIs which preceding infants survived to calculate $\mathbf{b}$ can avoid overstatement of human birth rate.
  - α is defined as the time from weaning to first birth (same as Purvis and Harvey, 1995), instead of age at first birth (Charnov, 1993) or time from weaning to first conception (Hawkes *et al.*, 1998).
- To estimate expected human birth rate, the regression equation of actual primate $\mathbf{b}$ excluding human data on α was used.
- The regression of weaned weight (W_0) on adult weight (W_α) provides an estimate of δ over the primate dataset.
- M^{-1} is estimated as $M^{-1} = 0.4T_{MAX} - 0.1$. The equation was obtained by the regression for 16 non-primate species, M^{-1} (Millar and Zammuto, 1983) and T_{MAX} (Eisenberg, 1981, observation in zoo) were highly correlated (r=0.95) (see the legend to Fig. 5.6 from Charnov, 1993). (Estimating M from actual life tables is favorable but no data.)
- Regression was done by SPSS 6.1. All variables were basically log-transformed. Regression used for the dataset with interrelationships (phylogenetic relationships) is not ideal, and the bias can be removed by assuming true phylogenetic tree. But because the true phylogenetic tree about primates is still uncertain, simple regression has been done.

Results

- 14 primate species including humans provided an estimate $(\alpha M)^{-1} = 1.45$, within the confidence intervals of Charnov's estimate from 26 mammalian species (1.30-1.54). Fig.1 shows the regression of α on 1/M, where Ache is not outlier. The proposal of GMH that α is adjusted to entire life span is supported.
- Table 1 shows that the actual birth rates of 4 human populations are 2-5 times higher than predicted from other primate invariance. When Ache is included in the regression of $\mathbf{b}$ on α, it becomes a positive outlier (Fig.2). This also support GMH prediction.
- Table 2 shows the invariant values calculated in this study and 3 other studies (Charnov, 1993; Hawkes *et al.*, 1998; Purvis and Harvey, 1995). Different definition of α did not affect the relationship between $\mathbf{b}$ and α, coefficient close to -1, meaning optimum tradeoffs between the two traits.
- Fig.3 shows δ for humans, chimps and gorillas are lower than 0.33 but within 95% confidence interval of the regression equation for 16 primates. The regression coefficient is 0.99. Even in multiple regression model where, besides adult body weight, investment time (gestation time plus weaning age) is included as an independent variable, all variation of weaning weight was explained by adult body weight. Partial residual plot (Fig.4) shows that Ache is not unique. Weaning as early and light as gorrilas.

Discussion

- The result supported the result by Hawkes *et al.* (1998).
- Hadza hunter gatherer in Africa provided the case of higher return rates by mothers and offsprings foraging together than separately, suggesting the possible selection for the evolution of somatic longevity by mother-infant food sharing, and the case of higher return rates by mothers and grandmothers than juveniles, suggesting the contribution of grandmothers to offsprings' survival, and the case of care-taking effort by grandmothers to grandchildren making mothers' productivity larger (a series of papers by Hawkes *et al.*).
- Competing ("male provisioning hypothesis"): If females forage locally, males forage more broadly, which makes offspring survivorship increasing and birth spacing decreasing, in monogamous society. For this, males must favor mating over parenting effort. This hypothesis must consider interaction betweeem females and male life histories. GMH considers only females. It cannot be comparable.
- Competing ("embodied capital model"): In addition to male provisioning, reduction in mortality risks, through intergenerational resource flows and the contribution of the long period of juvenile learning and development to adult foraging, reproductive, and social performance, increases longevity and delays maturation. GMH considers long juvenile as a consequence, not a cause of longevity.
- GMH provides parsimonous explanation for both increased postmenopausal longevity and delayed maturity. Grandmothers provisioning and subsequent increased birth rate may contribute to 2 other unique features of human evolution: (1) to overcome geographic and ecological barriers to dispersal and (2) population growth necessary to occupy widely separated habitats. It's ultimate explanation.

Nakazawa's point of view

- Basically the author confirmed the conclusion by Hawkes *et al.* by testing larger datasets. GMH is relatively plausible.
- But, as the author recognized, using regression as the method to consider invariant relationships for phylogenetically related data points may include substantial bias. After obtaining reliable true phylogenetic tree for primates, GMH must be tested again.