Mortality Risk/Human Life History Traits

Life History Theory

* The most basic tenant of life history theory, which logically follows from the laws of thermodynamics, is the principle of allocation: energy used for one purpose cannot be used for another.
  + Natural selection on the timing of life events, such as growth, maturation, reproduction, and death, depends on the ecology of energy production and mortality hazards (i.e. Stearns 1992; Charnov 1993)
  + Extrinsic adult mortality may be the most important initial variable in limiting the feasible set of life history parameters that maximize the fitness of an organism (Charnov 1991; Harvey and Nee 1991).
* Charnov and Berrigan (1993) claim that tradeoffs between life history traits make certain allometric relationships invariant at the species level. Humans have especially slow life histories compared to other primates and other mammals.
  + Human life history is characterized by: an exceptionally long lifespan, and extended period of juvenile dependence, support of reproduction by older post-reproductive individuals, and male support of reproduction through the provisioning of females and their offspring. (Kaplan 1997; Kaplan et al. 1999)
  + Kaplan et al. (1999) suggest that these human life history characteristics and extreme intelligence are co-evolved responses to a dietary shift toward foods that are high quality, nutrient-dense, and difficult to acquire.
* Tradeoffs
  + Current vs. Future Reproduction (Fertility timing)
    - Principle of allocation: current investment in reproduction will entail a future cost in survival or fertility.
    - True impact of future costs is determined by the extrinsic mortality curve and growth rate of the population (Hill 1993)
      * When survival is low, future costs are unlikely to be paid by most individuals, favoring current investment in reproduction.
      * When population growth is rapid, future reproduction will contribute a lower proportion to the gene pool, favoring current investment in reproduction.
    - This tradeoff is thought to be the major reason lifespans are not infinite.
      * Higher number of offspring was associated with increased risk of early mortality for both mothers and fathers but significantly greater for mothers. (Mace 2000; Penn and Smith 2007)
  + Production vs. Reproduction (Growth)
    - Physiological and morphological sexual maturity is tightly linked to age of first birth in most organisms, but humans show a lag between these events. Adult pelvic widening, menarche, and even copulation generally precede birth by several years. (Wood 1994)
    - Growth ceases at adulthood and the production energy is then channeled into reproduction (Charnov and Berrigan 1993).
    - The optimal age of maturity is when the proportional change in reproductive value, which increases with age, exactly equals the proportional change in juvenile survivorship, which decreases with age.
    - Increased mortality around the age of maturity has been associated with earlier sexual maturity (i.e. Wilson and Daly 1997).
  + Quantity vs. Quality (Mating behavior and parental investment)
    - Principle of allocation: each additional offspring necessarily reduces average investment per offspring.
    - The optimal investment per offspring is reached at the investment level where the proportional decrease in number of offspring produced is equal to the proportional increase in survival of offspring to adulthood. (Harpending et al. 1990)
      * Optimal investment per offspring is independent of parental income (Smith and Fretwell 1974). All parents should produce offspring of the same quality, but parents with more resources should produce more offspring. But! What about the modern demographic transition?
    - A multigenerational model of fertility and fitness that allows for investment in own embodied capital (fixed costs of offspring production and investment that affects survival) and the embodied capital of offspring (adult income of offspring) (Kaplan 1996). This eliminates the expectation that parents of varying income levels will produce offspring of equal quality.
      * Offspring can also contribute to their own embodied capital and the embodied capital of grandoffspring.
      * This tradeoff is optimized to maximize the number of grandoffspring.

Senescence – progressive increase in age-specific mortality rates (Kirkwood and Shanley 2010)

* Mutation accumulation theory: At older ages, the force of selection is too weak to oppose the accumulation of germ-line mutations with late-acting deleterious effects. (Medwar 1952)
* Antagonistic pleiotropy: Genes with beneficial effects early in life will be favored by natural selection even if these genes have negative effects at later ages. (Williams 1957)
* Maintaining the soma for survival requires constant effort that comes at the expense of reproduction, so somatic maintenance inevitably fails.
  + Disposable soma hypothesis: The primary role of soma is to support the germline’s evolutionary significant role in reproduction. (Kirkwood 1977; Kirkwood and Rose 1991)
* Gompertz mortality curve predicts an exponential increase in age-specific mortality across adulthood. It gives a fair fit to mortality data across a variety of taxa (Finch 1990).
  + Heterogeneity in frailty explains the association between lower mortality and a steeper increase in death risk across adulthood (i.e. faster rate of demographic aging) (Vaupel et al. 1979, 1998). Older age groups are a subset of younger ones that are biased toward less frail individuals. However, when background mortality is low, mortality selection is weaker, and more of the frail survive longer.
  + The same logic can be applied to heterogeneity in fertility (Hawkes et al. 2010).
* Intergenerational transfers, in addition to fertility, are the strongest predictors for demographic aging rates in human populations (Lee 2003, 2008).

Menopause and post reproductive lifespan

* Kin selection and inclusive fitness (Hamilton1966)
  + No parental care: The only effect of living longer is the increase in total fertility due to the additional fertility realized at later ages.
  + With parental care (or any form of kin assistance): the value of living longer depends on contributions made to kin during the post-reproductive period.
* Kaplan et al 2010: A shift toward a diet of high-quality, nutrient-dense, and difficult-to-acquire foods requires an extended learning phase to develop the necessary skills. Juveniles must rely on provisioning from other group members. The human foraging niche favors old age production and kin investment for both sexes. Therefore, for both sexes, fitness is maximized by reproductive cessation and allocation of remaining resources to mortality reduction, physical maintenance, and intergenerational transfers.
  + Hawkes et al. 1997, 1998: Grandmother Hypothesis
    - Extended post-reproductive lifespan, rather than early termination of fertility, is the derived trait of humans (Hawkes et al. 1998). Limited oocyte supply along with a consistent rate of atresia will necessarily result in menopause in any long-lived female mammal. It is the length of human post-reproductive lifespan that needs an evolutionary explanation.
  + Male Provisioning (e.g. Hill 1993; Gurven and Kaplan 2006)
    - Male contribution to group nutrition through hunting may account for around 80% of the calories, making males a significant contributor to child surivival.
  + Pooled energy budgets of humans allow childbearing females to have offspring more rapidly than primates of similar body size. (Kramer and Ellison 2009)
  + With increasing human fertility, the number of collateral and descendant lineal relatives for each individual increases, while the number of ascendant lineal relatives is unaffected. It seems logical to conclude that energetic contributions from collateral and descendant lineal relatives become increasingly important. Therefore, it is unlikely that grandparental contributions would continue to create the selective pressures necessary for extended lifespan. (Ellison 2010)
    - Ellison (2010) suggests that it is the extended life span of humans that allowed for the emergence of indirect reproductive effort among post-repoductive individuals.
    - My opinion: While I agree with Ellison’s conclusion, I think his logic is flawed. Grandparents make up a smaller proportion of relatives, but may contribute proportionally or absolutely more than each individual ascendant or collateral relative, who may be allocating more effort to their own fitness.
      * See Kaplan (1994): Wealth in families tends to flow down the generations, not up.

Short Interbirth Interval and Cooperative Breeding

* The human interbirth interval of about 3 years in natural fertility populations is out of line with that of other great apes of similar body size. Orangutans have an interbirth interval of about 8 years and the chimpanzees’ is 4-5 years. (Galdikas and Wood 1990)
* Cooperative Breeding – social system in which nonmaternal individuals help support offspring who are not their own.
  + Selective pressures for distinctively human cognitive and emotional capacities arose from our evolution as cooperative breeding apes (Hrdy 1999).
  + The prosociality required for shared intentionality is absent in chimpanzees, but present in cooperatively breeding primates. Chimpanzees exhibit many of the important cognitive preconditions for “uniquely human” mental capacities to evolve, but they lack the psychological preconditions. In humans, the cognitive component evolved due to common descent from ape ancestors, and the motivational component due to convergent evolution of traits typical of most cooperative breeders. (Burkart et al. 2009)
* Compared to men, women have relatively low variance in fertility, so improving the survival of a woman’s children may be the most effect way for relatives to increase her reproductive success (Strassmann and Gillespie 2002).
* Sear and Mace (2008): In a review of 45 studies from a variety of mostly natural fertility populations, the authors found at least one non-maternal relative who improved the survival rates of children in almost all studies. Help from kin may be a universal feature of human child rearing, but who helps is dependent on different ecological conditions.

Parent-Offspring Conflict

* Parents and offspring are not genetically identical, so their relationship cannot be viewed as a purely cooperative interaction (Trivers 1974).
* The selective forces acting on fetal genes may oppose those acting on maternal genes, creating a genetic conflict between mother and fetus (Haig 1993).
* Natural selection will favor offspring that increase parental investment and mothers that limit excess transfers to offspring.