



How to explain the unusually late age at skill competence among humans

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ABSTRACT

Humans stand out among primates and other mammals in reaching adult-level foraging skills very late in development, well after the onset of reproduction. The aim of this paper is to place this unusual human skill development into a broader comparative context. Among birds and mammals in general, duration of immaturity, indexed by age at first reproduction (AFR), and adult brain size have undergone correlated evolution. This pattern is consistent with two causal processes: AFR is either limited by the time needed to learn adult-level skills (needing to learn) or by the energy needed to grow brain and body to full size (energetic constraints). We tested predictions arising from these two hypotheses with data retrieved from the published literature for 57 mammal and bird species. First, most mammals reach adult-level foraging skills well before the developmental period is completed, implying that energy constraints determine the age at first reproduction, whereas most birds reach adult-level foraging skills around the time of maturity, suggesting time needed for skill acquisition determines the onset of reproduction. Second, within mammals we found that with increasing niche complexity, the age of adult-level skill competence moves closer to the age at first reproduction. Third, when looking at how adult-level skills can be reached later, we found that gregariousness, slow conservative development and post-weaning provisioning allow mammals to reach their skills later. Finally, in species with intense sharing of resources (such as cooperative hunters) competence in foraging skills may even reach peak values after age of first reproduction. We conclude that the human pattern of skill acquisition could arise because our hominin ancestors added cooperative breeding and hunting to the slow development they had as great apes with increasingly complex niches. This result provides a broad biological foundation for the embodied capital model.

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Introduction

Human children take many years to learn how to forage efficiently. Among human foragers, women reach peak foraging efficiency in their mid-20s, i.e., well after the age at first reproduction (AFR) of around 19 for women, whereas men reach theirs even later, in their 30s or 40s (Hill and Kaplan, 1999; Gurven et al., 2006; Kaplan et al., 2007). Some components, for instance strength and athleticism (e.g., ability to hit a target: Blurton-Jones and Marlowe, 2002), reach their peak values soon after AFR, but human foraging, especially hunting, requires experience-based knowledge of detailed processing techniques and prey behavior. Moreover, there is no reason to assume that hunters and gatherers do not maximize their returns during foraging trips, supporting the interpretation that the experience required for successful gathering, and hunting

in particular, takes years to accumulate. The embodied capital hypothesis (Hill and Kaplan, 1999; Kaplan et al., 2000, 2007) argues that the late acquisition of peak foraging efficiency in humans reflects the coevolution of our complex foraging niche and our unique provisioning system. Thus, the exceptionally late acquisition of efficient skills can be linked to the skill intensity of the foraging niche, and is made possible by massive intergenerational transfers of food from adults to immatures.

Humans are therefore unusual in two distinct ways (Hill and Kaplan, 1999). First, we reach adult-level skill competence well after weaning, whereas most mammals do so around or soon after weaning (see also Janson and van Schaik, 1993). This raises the general question, under which conditions does selection favor or allow an increase in the age at which adult-level skills are reached relative to the timing of weaning. Second, we reach skill competence not just late, but well beyond the age at first reproduction. This is unexpected, because animals that are less efficient than reproducing adults are not expected to be able to sustain the additional effort of reproduction. Almost certainly, therefore, skill acquisition after the onset of reproduction requires extensive food

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sharing or net provisioning, which raises the broader question about the role of provisioning in the evolution of highly complex foraging niches.

The aim of this paper is to place human skill development into a broader comparative context, by examining whether variation in the timing of the acquisition of adult-level skills across a broad array of birds and mammals is caused by (i) the time needed to learn the skills, or (ii) the energy allocated (and thus time needed) to complete full somatic growth and differentiation. Once we have identified the conditions in which time needed to learn skills limit the attainment of maturity, we can explore whether the human pattern arose through a process or a combination of processes also found in other taxa, or instead reflects processes unique to human evolution. This comparative analysis will allow us to dissect the embodied capital hypothesis into two major components, one focusing on the coevolution between the complexity of foraging skills (and thus brain size) and life history, and the other on the role of resource pooling and provisioning.

In this paper, we therefore first ask for birds and mammals in general, which factors determine the age at which adult-level foraging skills are reached. We will assume that this point is reached before, or at most around, the age at which reproduction begins, but will later discuss exceptions to this general rule as well. For birds and mammals (Fig. 1), age at first reproduction is determined by brain size, and not, as might be expected, by body size. Humans follow the primate trend in this respect. However, this correlation is consistent with two distinct processes. First, AFR may be set by the time needed to grow and differentiate the adult brain,

which develops before full body size is achieved. Second, AFR may be set by the time to learn the requisite skills. In other words, we can ask whether it is time (skill learning) or energy (growth and differentiation) that generally limits the duration of the immature period among birds and mammals. We can differentiate between these two possibilities by asking, within any given species, at what age adult-level foraging skills (denoted here as Age at Skill Competence, or ASC) are reached relative to the onset of reproduction (AFR). The focus is on ecological skills, in particular foraging, because they are known to be directly related to fitness (Stephens and Krebs, 1986), whereas social skills, including parenting, are best practiced while performing them, and are not improved by delaying reproduction (Silk, 1999). Once we have a general answer, we can explore the third possibility: that ASC is reached after AFR. We expect this to depend on provisioning or food sharing among adults, because weaned mammals or fledged birds, let alone reproducing ones, must under normal conditions be able to sustain themselves.

The needing to learn hypothesis (Ross and Jones, 1999) claims that the interspecific correlation between brain size and AFR arises because of the increasingly long time larger-brained species need to acquire skills and knowledge essential for adult survival and reproduction (rather than time needed to reach the requisite size and strength). This is so because some of the essential skills are expected to develop gradually during immaturity. Thus, as the maturing individual must learn more and more complex skills, one expects AFR to increase accordingly (Ross and Jones, 1999). The same idea has often been invoked for humans (Dobzhansky, 1962),

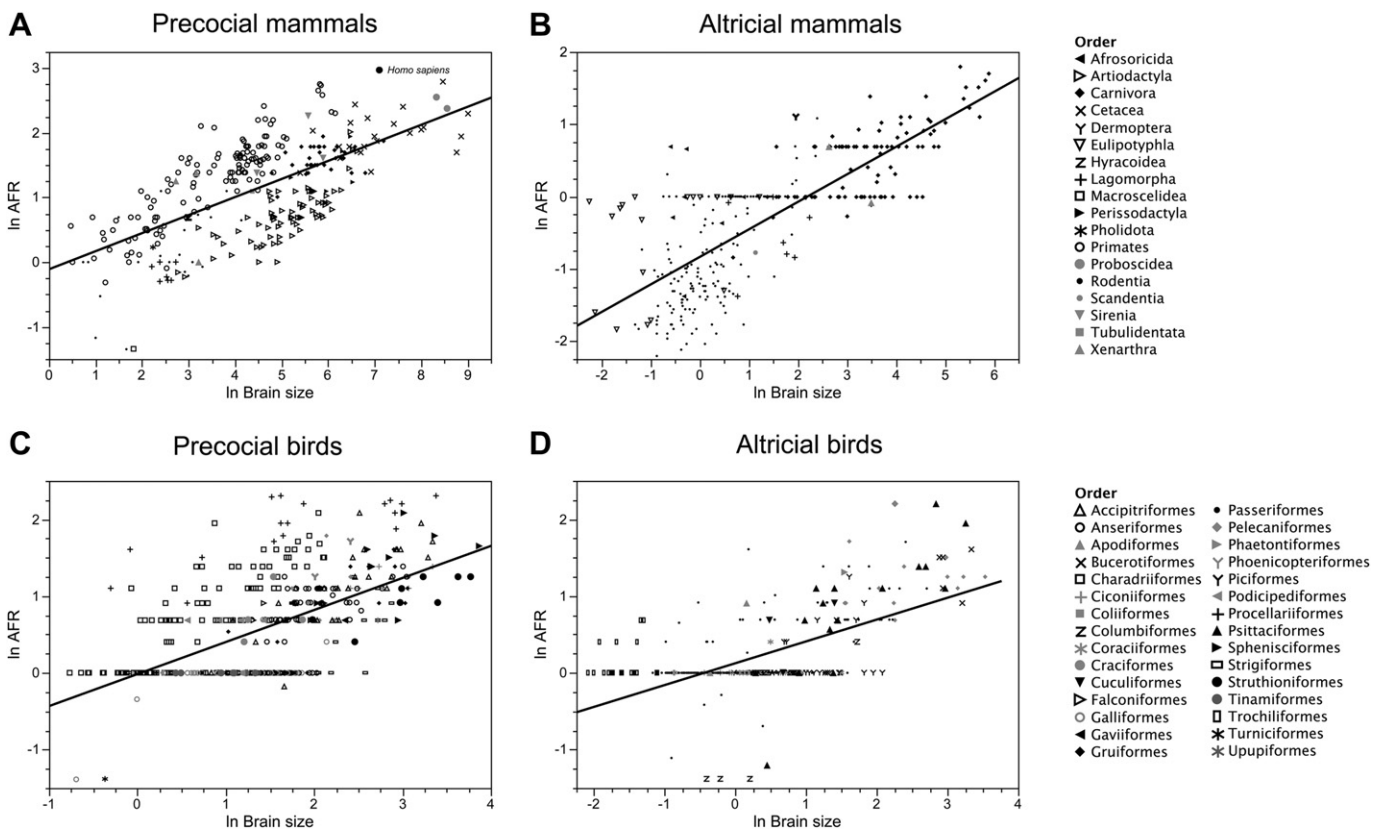


Figure 1. Age at first reproduction (AFR) versus brain size in mammals and birds, depicting non-phylogenetic least-squares regression lines. Humans were not included in the calculations, but are shown for comparison. The analysis was phylogenetic generalized least-squares regression (PGLS) with ln AFR as the response variable, ln brain size and ln female body mass as effects: A) precocial mammals ($N = 301$ species, brain: $\beta = 0.26$, $p < 0.001$, body: $\beta = 0.03$, $p = 0.542$), B) altricial mammals ($N = 312$, brain: $\beta = 0.25$, $p = 0.030$, body: $\beta = 0.05$, $p = 0.506$), C) precocial, semiprecocial and semialtricial birds ($N = 419$, brain: $\beta = 0.25$, $p = 0.008$, body: $\beta = 0.13$, $p = 0.018$), and D) altricial birds ($N = 392$, brain: $\beta = 0.21$, $p = 0.019$, body: $\beta = 0.09$, $p = 0.143$).

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