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# From rainforests to savannas and back: The impact of abiotic factors on non-human primate and hominin life histories

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## ABSTRACT

The small stature of modern human hunter–gatherers, and the developmental mechanisms by which this morphology is obtained, has been the subject of intense debate. Similarly, the causes for the unique modern human life history, which combines high reproductive rates with extended growth and long lifespans, have remained elusive. Here I explore the possible influence of some abiotic factors (temperature, rainfall, evapotranspiration) on life histories in non-human primates (gestation length, inter-birth interval, longevity) and enquire whether there exist commonalities that could shed light on the evolution of hominin life histories and its variation among *Homo sapiens*. After accounting for the effects of brain size and phylogeny, life history variables showed only moderate trends with abiotic variables. In contrast, the results were statistically highly significant when multivariate statistics and path analyses were employed, particularly for gestation length. Life histories apparently respond to actual annual evapotranspiration (AET) and annual precipitation, and their effects are contrasted; a habitat openness/aridity index was found a poor predictor however. This points towards a complex relationship between abiotic variables and primate biology. Rather than responding to any one environmental variable, it is tentatively concluded that primate energetics will respond to both, primary productivity of the habitat and environmental predictability (seasonality), which will then –in turn–modulate the pace with which primates reproduce and grow up. Against this backdrop the “unique” modern human life history pattern is, in fact, unsurprising: it probably has its origin in the ecological setting in which hominins evolved.

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## 1. Introduction

Anthropologists have long been fascinated by the adaptations that characterise modern hunter–gatherers living in tropical forests: these populations have very short statures and are collectively referred to as pygmies (Africa) and/or negritos (Asia). Evolutionary changes towards reduced height occurred several times in parallel and through different genetic mechanisms (Meazza et al., 2011; Jarvis et al., 2012; Perry et al., 2014). Small size is considered adaptive as it confers thermoregulatory advantages in hot humid climates and aids movement in densely vegetated habitats (Diamond, 1991; Minetti et al., 1994; Perry and Dominy, 2009). Similar adaptive strategies and physiological constraints almost certainly underlie the generally smaller sizes of mammals living in topical rainforests and make large mammals in such habitats vulnerable to extinction (Fritz et al., 2009; Ting et al., 2012). However, pygmies also live in cold mountainous areas (Bailey et al.,

1989), as well as in dry open habitats. Although it is possible that such populations retained their physique from an ancestral rainforest population, it is nonetheless reasonable to infer that factors other than thermoregulation and locomotion should also be entertained when explaining the pygmy phenotype (Diamond, 1991). Such factors, and the developmental mechanisms for achieving short statures in general, are likely to be found in hypotheses that are firmly rooted in life history theory (Southwood, 1988; Stearns, 1992; Charnov, 1993) and which complement, rather than replace, physiological and adaptationist explanations.

Life history hypotheses invoke *inter alia* resource availability and mortality risk as drivers of differential growth and, as a consequence, size. Resource limitation may indeed constitute a limiting factor on growth and development of some pygmy populations (Hart and Hart, 1986) but this is not universally the case, e.g. for the Aché in Paraguay who were shown to have adequate nutrient supply throughout the year (Hill et al., 1984). Similarly, propositions that the small size of pygmies may simply be a by-product of accelerated life histories due to high extrinsic and intrinsic mortality risks (Migliano et al., 2007) do not hold up to scrutiny across all pygmy populations

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(Curven and Kaplan, 2007). For example, in their longitudinal study of the Baka from Cameroon Ramirez Rozzi et al. (2015) found differences in the rates of growth between these (and other) rainforest hunter–gatherers and agriculturalists, but not in the timing of menarche or in the age of first reproduction. Therefore, the small size of West and Central African pygmies is apparently the result of changes in growth rates, either pre- or postnatally (Ramirez Rozzi et al., 2015), rather than early growth cessation. What is intriguing is that such a pattern of slower growth mirrors observations made in other primates under comparable conditions, i.e. where resources are unpredictable or seasonally abundant (Macho and Lee-Thorp, 2014). In fact, across primates the “risk aversion hypothesis” for slow growth (Janson and van Schaik, 1993) has found ample support and has even been implicated for an understanding of modern human life history evolution (e.g., Lee, 2012). Of course, direct comparisons between modern humans (or archaic hominins) and other primates are limited: modern humans will always modify, and respond to, their respective environments in more complex ways than non-human primates: they have advanced cognitive abilities and material culture, as well as unique cooperative behaviours with extremely high levels of allocare (Hawkes et al., 1998; O’Connell et al., 1999; Isler and van Schaik, 2012, 2014). Nonetheless, although behavioural flexibility and sociality will undoubtedly mitigate the effects of environmental factors on starvation and mortality, modern hunter–gatherers, like non-human primates and other mammals, are subject to comparable physiological, developmental and phylogenetic constraints. With this in mind, the parallels in life history strategies found between modern humans and other primates are not only unsurprising, but could also be informative, particularly for an understanding of the evolutionary processes that contributed to the evolution of the unique life history patterns of modern humans. To this end, the present contribution explores the relationship between abiotic factors and life history traits across primates with a view of providing a baseline against which variation in trait expression among modern humans can be better interpreted and against which other, i.e. specific selection pressures, can be appraised. Hence, it aims to create a general framework within which hominin life history evolution can be understood, bearing in mind the repeated habitat shifts undertaken by hominins during their evolutionary history.

During the late Miocene/early Pliocene hominins evolved from an essentially arboreal, frugivorous ape to a savannah-dwelling terrestrial omnivore: they abandoned tropical rainforests for more open environments (White et al., 2009; Reed et al., 2013). Archaeological evidence suggests that *Homo* returned to tropical rainforests at least 45 000 years ago (Roberts and Petraglia, 2015), whilst new evidence indicates a much earlier occupation of rainforests, at least in Southeast Asia (van den Bergh et al., 2016). Other morphological and behavioural changes aside (e.g., increased brain size, cultural innovations etc.), hominin life histories are likely to have responded to the transition from hot, humid and relatively closed habitat (i.e., from the Last Common Ancestor with chimpanzees) to drier, hot and more open habitats (i.e., early Plio-Pleistocene hominins) and, subsequently, when they spread to drier and more temperate habitats (i.e., after the emergence of *Homo ergaster*). Pleistocene reoccupation of hot/humid habitats, i.e. rainforests, would then have led to a reversal and/or novel adaptations in life history strategies. The ability to plastically alter life histories is commonly regarded a hallmark of our lineage (Kuzawa and Bragg, 2012) that will undoubtedly have facilitated hominin evolutionary success against the backdrop of increased environmental fluctuations and aridification throughout history (Potts, 1998; Potts and Faith, 2015). What is often overlooked in such arguments however is the fact that nonhuman primates similarly pace crucial stages of their development in accord with abiotic factors, resource

availability and predation (e.g., Wich et al., 2004; Brockman and van Schaik, 2005; Breuer et al., 2009; Stoinski et al., 2013). Therefore, life history plasticity may be a plesiomorphic (ancestral), rather than apomorphic (derived), trait (Macho and Lee-Thorp, 2014). If this is the case, some commonalities between life history traits and abiotic factors should be evident among primates. To determine whether this is the case is the aim of this study. It investigates the effects of temperature, rainfall and evapotranspiration on gestation length, longevity and interbirth interval, taking into account the effects of differences in brain size, phylogeny and, to a certain extent, diet. The results obtained for non-human primates are then discussed against what is known about hominin life history evolution.

## 2. Materials and methods

Female primate endocranial volumes ( $ECV_{\text{female}}$ ) were taken from Macho (2015a). Life history data, i.e. gestation length, interbirth interval and longevity, and environmental data, i.e. average annual precipitation, temperature and evapotranspiration were taken from Kamilar and Cooper (2013) (see Table S1). A simple openness/aridity index (AET/PET) was also calculated (Bremond et al., 2005); a high value denotes a closed habitat, whilst a low value indicates an open/arid habitat. Inclusion of more detailed data, either for environment (e.g., minimum/maximum temperature and rainfall etc.) or for life histories (e.g., age at first reproduction) would have resulted in a severe reduction of sample sizes. This was considered undesirable and only the larger dataset was therefore analysed further. All data were log-transformed prior to analyses and two sets of data were used: (a) the entire dataset and (b) cercopithecines and hominoids combined. Although the latter are a subgroup of the former and some similarities are therefore expected, separate analysis was deemed to better inform hominin evolution. Not only are cercopithecines and hominoids more closely related to each other, but they also share a number of key biological features like large body masses and increased encephalisation with concomitant cognitive abilities and behavioural flexibility (Reader et al., 2011). They are all ecological generalists and many tend towards terrestriality. In addition, the abiotic conditions encountered by this group alone span those encountered by the entire range of primates (Fig. 1). Their widespread distribution is indicative of this group’s evolutionary success in coping with a variety of environmental conditions and their ability to inhabit different climate zones. Cercopithecines/hominoids are therefore a good proxy for appraising the effects of abiotic factors on hominin life history evolution. Because of their derived life histories and exceptional levels of encephalisation, modern humans were not included in any of the analyses; inclusion would cause undue leverage. Finally, traditional comparative studies suffer from mixed datasets, whereby not all variables are available for all species. To avoid biases due to mixed datasets, only species were included for whom all variables were available; this reduced total sample size to  $n = 53$  (Table S1).

Although brain size and body mass are highly correlated across primates (Isler et al., 2008), brains are phylogenetically more constrained (Kamilar and Cooper, 2013) and are generally considered the pacemaker of development (Harvey and Clutton-Brock, 1985). Furthermore, a correlation exists between neonatal brain size and adult brain size, on the one hand, and neonatal brain size and gestation length, on the other (DeSilva, 2011). Hence, the residuals of life history data on  $ECV_{\text{female}}$  were calculated for all life history variables, using Phylogenetic Generalised Least Squares Analyses (PGLS) (Garamszegi, 2014). These residuals were then analysed further. Relative gestation, interbirth interval and longevity were first regressed against climatic data using Ordinary Least Squares regressions (OLS) (Fig. 2). Bearing in mind that primates may have evolved into specific ecological niches, a phylogenetic relationship

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