



HUMAN EVOLUTIONARY DEMOGRAPHY

EDITED BY
OSKAR BURGER, RONALD LEE AND REBECCA SEAR



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Oskar Burger, Ron Lee and Rebecca Sear (eds), *Human Evolutionary Demography*. Cambridge, UK: Open Book Publishers, 2024, <https://doi.org/10.11647/OBP.0251>

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ISBN Paperback: 978-1-80064-170-9

ISBN Hardback: 978-1-80064-171-6

ISBN Digital (PDF): 978-1-80064-172-3

ISBN Digital (HTML): 978-1-80064-682-7

ISBN Digital (EPUB): 978-1-80064-173-0

DOI: 10.11647/OBP.0251

Cover image: Ryota Nagasaka. Street Photography, April 20, 2020, https://unsplash.com/photos/w_5TUm7Xa00

Cover design: Jeevanjot Kaur Nagpal

5. Controversies and Unfinished Business in Hadza Demography and Evolutionary Ecology

Nicholas Blurton Jones

Demographic study of eastern Hadza hunter-gatherers between 1985 and 2000 showed a stable population with relatively normal parameters and quite a high rate of increase. Aspects discussed here are: population models and small remote populations; environmental keys to evolutionary demography of sub-Saharan savanna hunter-gatherers; grandmothers and longevity; men as helpers; whether economic and reproductive interests influence which norms invade, spread and endure.

Introduction

Hadza are a population of about 1000 people living in the Eyasi basin in northern Tanzania. They have successfully maintained their identity and their way of life as hunters and gatherers into the twenty-first century. Fieldwork among Hadza in the twenty-first century may tell the story of changes and continuities in the character and contexts of Hadza life (Marlowe 2010, Apicella et al 2012, Marlowe & Berbesque 2012, Berbesque et al 2016, Crittenden 2013, Wood & Marlowe 2013). Researchers may be able to use changes in Hadza circumstances as ‘natural experiments’ that improve our understanding of adaptation to the savanna environment in which much of human evolution took place.

My field research was confined to the twentieth century, in a collaboration with Kristen Hawkes and James F. O’Connell of the University of Utah. Pilot visits were made in 1982 and 1984, and I made a series of repeated censuses between 1985 and 2000. In 1986 and in 1989 I observed Hadza children’s foraging (1989, 1997), supplementing the extensive field work by Hawkes & O’Connell in 1985–86, and in 1988 on adult foraging efficiency and time use (O’Connell et al 1988a, 1990, Hawkes et al 1989, 1997). Throughout this period, encroachment by neighbours with other economies was evident; tourists began to visit the Hadza from about 1995 and the related effects became apparent. All of this research stemmed from previous unpublished fieldwork by Lars Smith in 1974–77, and before that by James Woodburn beginning in 1959. Woodburn was the first anthropologist to write about the Hadza in English, introducing them to academic anthropology, especially in Woodburn (1968a, b), still the best introduction to the Hadza hunting and gathering life. Much of what has followed has simply added more quantification to his ethnographic summaries.

In 2016 I published a lengthy account of the fifteen years of intermittent fieldwork on Hadza demography between 1985 and 2000 (Blurton Jones 2016 ‘BJ2016’). After a chapter on the

geography and resources of the Eyasi basin, and an effort to unearth the history of “outside” influences upon the area, detailed discussion of methods of age estimation and levels of in- or out-migration, the account included details of the demographic analyses. In the second part of the book, I used individual variation in the demographic measures to test for demographic effects of helpers, looking at fertility and mortality in relation to the availability of fathers, mothers and grandmothers, and siblings. These analyses were linked to our previous work on ecology and behavior, and to Marlowe’s fieldwork which began while he was my PhD student in 1995 and continued until ill health forced his early retirement in 2014. In my analyses I gave close attention to the possibility that family differences in vigour or access to resources might generate false associations between helpers and helped. I was also especially mindful of Hill & Hurtado’s (1996) suggestion that helpers might distribute their help in ways that obscure their effect. My 2005 and 2006 papers imply that older Hadza women, living wherever their help would maximize their own fitness, may do exactly as Hill & Hurtado suggested.

Here I summarize some of the new data and issues that might reward further attention in the Hadza or other populations, or provoke exploration in related fields. These include 1) use of population models in studies of small, remote populations; 2) the richness of the environment, and under-appreciated aspects of savanna foods; 3) issues in the study of grand-mothering and reproductive competition; 4) male reproductive strategies and the difficulty of finding father effects in the Hadza data; 5) differences between expert hunters and others, and 6) a note on behavioural ecologists’ continued invasion of the social sciences.

Population Models and Small Remote Populations

In her ground-breaking study of !Kung hunter-gatherer demography, Howell (1979) made extensive use of stable population models. If fertility and mortality remain constant for a few decades they result in a stable age structure, one in which the proportion of people in any age group remains the same, even if the population is increasing or decreasing. “Stable” refers to this constancy of age structure and is distinguished from a “stationary” population, one that neither increases nor decreases. The stable population assumption has been used to derive, from large numbers of carefully studied populations, tables of age structure under different regimes of fertility and mortality. These tables, such as Coale & Demeny 1983, allow one to relatively quickly match observations to a population regime and then extrapolate many measures that can be read off the tables and compared to field observations. These can be invaluable for a quick check on the plausibility of fragmentary data and historical accounts. However, stable population models have limitations. As the world industrializes, and changes come to the most remote locations, we can expect, and many observe, quite sudden changes in fertility, mortality and migration which disrupt the use of stable population theory. Demographers actively seek remedies (Stott 2016).

Like Hill & Hurtado (1996), I aimed to make my demographic analysis independent of the values in any set of stable population tables and thus allow the Hadza to be as unusual as the data warranted. Two kinds of dependence have been discussed. While Gage (1988) implies that hunter-gatherer (HG) or other small remote populations could fail to fit any known model population, Hill & Hurtado were particularly concerned to keep their age estimates independent of model assumptions. I made no use of published models to make age estimates, nor to extrapolate unmeasured demographic parameters for the Hadza. Thus I allowed the Hadza

population to be different from, for instance, the 326 populations used to derive the Coale & Demeny (1983) models. My raw data were census and anthropometry lists; reproductive history interviews of 227 women (91 % of women aged 15–50) which provided essential data on births, relative ages and deaths of infants and small children and close relatives; “where are they now” interviews with small groups of adults in many locations (valuable for determining deaths of adults); and history interviews with a few older adults.

Like people in many isolated rural societies, Hadza do not keep records nor (until sometime early in the twenty-first century) know the year. Thus, during our observations, the great majority had no accurate knowledge of their ages. Estimating age was thus a major task of both fieldwork and data processing, as it has been among !Kung and Ache and other such populations. Diekmann et al (2017) describe a method that gives measures of error in estimates of individual ages derived from matching age ranks to known ages. My method is described at length in Chapter 4 of my book and in its supplementary information (www.cambridge.org/Hadza, click on Resources, Supplementary Materials). I used a combination of previous data, interviews about historical landmark events, such as the departure of six men to join the Kings African Rifles at the beginning of World War Two, and a major earthquake in May 1964, age rankings by the subjects, or by parents concerning their children. During our visits data were gathered on new births and deaths, both by observations and interview. Together with the ages of the youngest babies recorded during pilot visits and Lars Smith’s 1977 census, and three children recognized in partial genealogies in Dorothea Bleek’s notebooks from her 1930 field visit to Hadza (Cape Town University Library, Bleek archive) we compiled a list of people of “known” ages. The age estimations involved more information than the simple regression of age rank on known age in Blurton Jones et al (1992). The results survived a variety of checks described in BJ2016. The ages of old people are the most contested; some researchers still are not acquainted with Howell (1979) and Hill & Hurtado’s (1996) evidence that so-called “primitive life” is not especially short. While all directly observed hunter-gatherers, like all directly observed human populations, show quite high life expectancy at age 45 (>20 more years, Blurton Jones et al. 2002, Gurven & Kaplan 2007), it is still commonly asserted that, during pre-history, few if any people lived past age 45. Indications to the contrary, such as Walker et al 1988, Mollesen et al 1993 and others are discussed in BJ2016 SM 8.7.

Dyson (1977) estimated Hadza fertility and mortality from data gathered during the 1966–67 International Biological Program visits led by Nigel Barnicot and James Woodburn. My data showed that fertility and mortality had changed very little between 1967 and my study period. Thus I was able to use the stable population assumptions to derive predictions from a simple population simulation. The simulations allowed input levels of fertility, mortality and migration to be as observed, or to be experimentally manipulated. The simulation can generate predicted age structure and other measures that were shown to stabilize rapidly and thus could be compared with the observations. The most valuable predictions are those tested by data gathered independently from the original fertility and mortality. Examples were rate of increase from the population register, age structure from anthropometry sessions and age at death (a measure independent of the risk group that has a crucial influence on age-specific mortality).

Hadza emerged as fairly typical of a high-mortality rural population. With TFR 6.1, life expectancy at birth 32.7 (and 39.2 at age 20, and 21.3 at age 45) for sexes combined, much like other hunter-gatherers (see Blurton Jones et al 2002, Gurven et al 2007), their demographic

parameters differed little from those of Europe before the late 1700s. Dyson's and my analyses imply quite rapidly increasing populations, measured as the intrinsic rate of natural increase r , during the second half of the twentieth century at between 0.0139 and 0.0162. Hadza mortality was intermediate between !Kung ($e_0 = c.30$) and Ache ($e_0 = 37.8$ male, 37.1 female). Confidence intervals acquired from resampling gave a 95% confidence range for Hadza fertility. Ache fertility lies above the high end of this range, and !Kung below the lower end.

Comparing my results with results from Coale & Demeny (1983) tables (BJ 2016: 183) showed nothing unusual, except for a larger difference between male and female mortality than shown in their best matching model. This suggests to me that reference to existing tables could be a safe and economical way to make use of brief field visits or fragmentary and uncertain historical data. An analogous approach could be valuable for demographic study of higher primates (Gage 1998). As Howell has pointed out, if the researcher suspects that a population shows some unusual feature, this should be visible as a departure from model tables which can be used as a null hypothesis. Given the varied census effort, the extreme mobility of Hadza, and their habit of not infrequent name changes, I did not explore the use of two-census methods used successfully on other populations by Gage et al (1988). However, more detailed analyses of fertility, mortality and reproductive strategies require much more detail than can be obtained in a quick census. Especially important are data on individuals, including even partial longitudinal data. Most of the successful recent demographic and life history studies of small remote populations have employed repeat visits, reproductive history interviews, anthropometry, and more (examples include Howell 1979, 2010, Hill & Hurtado 1996, Early & Headland 1998, Borgerghoff-Mulder 1992, 2009, Winking & Gurven 2011).

Rapid increase, and the potential for rapid increase among hunter-gatherers was discussed by Hill & Hurtado 1996, Keckler 1997, Boone 2002, and before them by Birdsell 1968, Hassan 1978 and Carr-Saunders 1922. Keckler proposed that rapid increase followed by crashes may have been representative of many hunter-gatherer populations. In my Chapter 11 I explore this in relation to Hadza increase, the fragmentary indications of Hadza fertility response to drought or abundance and the lack of evidence of significant density dependent regulation. In relation to seasonal movements, and secular changes in rainfall, we get a picture of a more populous, interactive and turbulent past than the traditional picture of hunter-gatherers as small isolated bands wandering alone under perpetual threat of extinction.

Environmental Keys to Evolutionary Demography of Warm-Climate Hunter-Gatherers

The sub-Saharan savanna figures prominently in discussions of human origins and in the archaeological record. In Africa, tropical forests receded and grasslands (which include bushland and wooded grassland — open grass plains are exceptional, Belsky 1990) expanded during crucial periods in human evolution. Many of us think the nature of savanna resources ultimately determined key features of our species.

One of the benefits of toiling along behind high-endurance !Kung and Hadza may be an improved appreciation of this habitat from a forager's viewpoint. Foremost, after the critical issue of water, is the rarity and unpredictability of catches of the spectacular large mammals of today's savanna, which include some (or their taxonomic kin) that dominate the archaeological record. The relationship of ungulate biomass to rainfall allows calibration of the likelihood of

bygone times with both fewer and sometimes more frequent catches in Hadza country (Coe et al 1976, O'Connell et al 1988, Blurton Jones 2016 Fig 2.3). Given year-to-year variation in rainfall (a range not unlike longer-term variation in annual averages) Hadza have experienced times with 30% less, and 30% more rainfall with approximately matched variation in large ungulate biomass between 1700 and 4800 kg/sq km.

The field observer quickly learns about the nature of the plant foods consumed daily. Because of the way savanna plants adapted to the extreme seasonal variation in rainfall, there are abundant calories available in the sub-Saharan savanna if you are able to recognize, acquire and process them (Hawkes et al 1997, Kaplan 1997). Notable “staple” food plants are many different storage organs (tubers) and durable fruits and nuts such as Baobab (*Adansonia*), Mongongo (*Ricinodendron*), Marula (*Birrea*) available for long segments of the dry season and into the wet season. Widely distributed are the inconspicuous fruits of the several *Grewia* species, which Lee showed cover a lengthy season in the Kalahari. In Hadzaland Baobab trees grow in extensive “patches” in locations as evident in Obst's 1915 map as they are today.

The abundance can be truly astonishing. Lee (1979) documents the abundance of Mongongo nuts in a grove and data on food value and processing, Wiessner (2014, fig. 2) shows the wide distribution of groves. Eastern Hadza country harbors abundant tubers (Vincent 1985), extremely abundant (we have air counts) Baobab trees. Baobab pith and seeds yields 3.81 kcal/g thus an easily gathered 10 kg totals 38,100 kcal to be processed at leisure in camp. There are no mongongos but there are Marula nuts west of Lake Eyasi where Berbesque recorded them being used by Hadza children (personal communication 1916). Peters (1987) maps the wide distribution of Mongongo, Marula and Baobab in the sub-Saharan savanna. Day-to-day variation in the amounts an individual acquires can be quite large. In this and other features the savanna plant foods resemble on a smaller scale the rare catch of a hunter, encouraging transfers from those who got more that day to those who got less.

The seasons can starkly illustrate a difference between plant food use in the forest by our nearest living non-human primate relatives, and in the savanna by hunter-gatherers. Early-wet-season fruit sets a context for foraging not unlike that of a forest-living frugivore. As two individuals stand side by side at a fruit tree there is little incentive for anything other than continued picking of what is right there in front of you, and little either can do to enhance the other's picking rate. The dry season (and much of the wet season when short fruiting seasons are over or yet to begin) presents a different picture. The abundant and nutritionally rewarding foods in the savanna come in large packages. Some are difficult to acquire but with luck can result in a large pile that can quickly be made ready to eat (e.g. roasted tubers). Others are easier to acquire but require longer processing (e.g. Baobab pods and seeds, or Mongongo nuts). At the same time, the haul may make a splendid target for a free-loader. This may contribute to the tendency for humans to regard other humans as resources (Draper 1989), together with the apparently greater ease of joining human groups than that observed among many other primates. The potential for sharing or free-loading on savanna plant foods needs to receive more detailed attention.

The most rewarding resources (deep tubers, mongongos, Baobab) are difficult for children to acquire or process, perhaps sometimes due to their lack of strength — body weight is as good a predictor of return rate as age (Blurton Jones et al 1997), and the skills appear rapidly learned (Blurton Jones & Marlowe 2002). Even Hadza children obtain only about half their daily calorie

requirements before about age 15 (Blurton-Jones et al. 1989,1997, Crittenden et al. 2013); !Kung children are even more restricted (Blurton Jones et al 1994). This difficulty of childhood access to savanna foods provides a simple ecological reason for the lengthy dependence of pre-adult humans, and the overlapping “stacked” family of dependents that results (Gurven & Walker 2006, with consequences for the mother illustrated in Blurton Jones & Sibly 1978 fig 2). Occupying savanna offered massive resources but at the cost of economically dependent juveniles. This provides an opportunity of fitness reward to adult helpers who can transfer some of their haul to related children.

Grandmothers and Longevity

In this section I summarize the new data on Hadza grandmothers. I have neither the space nor the competence to review all the current models of the evolution of grandmothers.

All known contemporary and historical (i.e. with written records) human populations show a lengthy post-fertile life and we may treat this as a product of evolution and seek explanations from natural selection. Post-fertile life is best measured as “PrR” (Levitis et al 2013). This is the proportion of years lived from first reproduction, that are lived post-reproductively (in life table notation, L_x from the age when 95% of fertility is completed divided by L_x from the age when the first 5% of fertility is achieved). Although requiring data on age-specific fertility and mortality, this avoids the debatable use of maximum observed age. Ellis et al (2017) show that on this measure post-reproductive life-spans are rare among mammals. Levitis et al Table 1 shows that human PrR substantially exceed those of other primates. The PrR measure is also high among several Cetaceans (Croft et al 2016, Ellis et al 2018, Foster et al. 2012).

Field experience among Hadza impelled Hawkes to attend to grandmothers as providers and to think about the evolutionary challenge of their existence (Hawkes et al 1989, 1997, 1998, 2018). The importance of grandmothers as helpers, or potential helpers in societies of many types (Sear & Mace 2008) should not be overlooked. Grandmothers may be under-appreciated by those who work in public health in the developing world. We should note that, while twenty-first-century gerontologists work in a world of 80-, 90- and 100-year-olds, grandmothers throughout most of the world are active women in their late 40s, 50s, 60s and early 70s.

Hawkes’ “Grandmother Hypothesis” (“GMH”) is a well-developed attempt to account for the origin of grandmothers by natural selection. We can begin with the contrast between the ecology of weanling great apes, able to feed themselves upon weaning (e.g. Bray et al 2018), and the ecology of dry-season savanna foods — they are abundant, and adults can acquire large quantities but children cannot. An older woman (OF) less burdened by a suckling and a series of still-young dependent weanlings can produce a surplus. Giving some of it to her adult daughter (YF) may enhance the daughter’s reproductive success, thus contributing to OF’s fitness. Selection might favor an OF who lives a little longer and remains a little more vigorous. In early formulations, Hawkes left the ancestral age-specific fertility as a conserved character. In recent computer modeling, Hawkes and colleagues (Chan et al 2016, Kim et al 2018) have shown that under the realistic conditions of the model, where age at last birth is allowed to evolve, it remains at the ancestral level while lifespan increases.

In Hawkes et al 1998 (see Hawkes et al 2018 for a summary) more consequences are drawn from Charnov’s (1993) model of mammalian life history evolution. Increased longevity implies lower adult mortality. This is expected to lead to a later age at first reproduction and longer

growing period, just as observed (and without reference to the belief that it takes twenty years to learn to become a hunter-gatherer). Again, following Charnov's framework we should expect the prolonged period of growth to lead to a larger body size. Humans are indeed larger than their closest relatives. In O'Connell et al (1999) we included an increase in size in our argument that grandmothing might be linked to the origin of *Homo* and the larger body size of *H. erectus*. Adhering closely to the view of life history evolution presented by Charnov (1993), and in an exegesis by Hawkes (2006), Hawkes et al (1998) proposed that the combined productivity of OF and YF should enable a greater rate of production of offspring. Human fertility rates are indeed much higher than great ape fertility (Walker et al 2008), and inter-birth intervals correspondingly shorter.

Hawkes continues to expand the human traits that may have followed, such as the adaptations of infants and children in the "stacked family" to intense competition for helpers and increased payoffs for attending to and predicting the behaviour of other individuals, and an influence upon adult sex ratios and the competitive situation of males (Coxworth et al 2015). Thus a relatively simple coherent consequence of selection could be held responsible for a number of features of human uniqueness. None of the unique features of our species have lacked their particular alternative explanations. Few of the alternatives appear as coherent or comprehensive as GMH, though some share the same ecological argument for the dependency of weanlings and pre-adults. All could benefit from more empirical support.

Hawkes et al (1997) showed a positive effect of Hadza grandmother foraging time on the growth of weaned children, and Blurton Jones et al. 2005, 2006 reported that older Hadza women lived where one would predict if their help enhanced their own fitness. But we have had to wait a long time to assemble the evidence of their demographic effect (BJ2016 Chapter 18). Hill & Hurtado (1996) warned us that helpers can obscure their own effects by, for instance, directing more help to those most in need (which often may offer the greatest benefit to the helper's fitness). Since dead grandmothers cannot help anyone, and, among Hadza, the paternal grandmother seemed as likely as the maternal grandmother to live with a child, in BJ2016 Chapter 18.4 I compared children who had a living grandmother with those who had neither grandmother alive. Children under 5 are more likely to survive if they have a living grandmother than if they do not. Either grandmother seems to provide a benefit. The effect remains significant if the first year of life is excluded. The effect is strongest on children of the youngest mothers. The effect is large, $\beta = 0.5017$, $p = 0.010$, with Odds Ratio 1.65 (95% range: 1.13–2.41). The odds of survival with a grandmother are more than one and a half times greater than the odds of survival with no grandmother. This effect gives $l_{15} = 0.63$ with a grandmother alive and 0.45 with neither alive, a striking demographic difference.

Several alternative explanations for the apparent effect of grandmothers on child survival were examined in BJ2016 Chapter 18.5. 1) Associations between a living grandmother and child survival could simply reflect familial differences in vigour/frailty. Multilevel logistic regressions that controlled for grandmother identity did not remove the impact of grandmother presence. 2) Epidemics are known to carry off the very old and very young. This could create associations between a living grandmother and child survival, but would generate some synchrony between the deaths of grandmothers and children. The data did not support this. 3) Adult Hadza women who had lost their mother during childhood tended to be shorter and lighter, and, in other populations, smaller women have been reported to have less child rearing success than larger

(e.g. Monden & Smits 2009). Controlling for mother weight or height did not remove the “grandmother effect”.

The Hadza grandmother effect seemed to be robust, resisting several alternative explanations. We assume the effect is primarily due to the large amount of food that Hadza grandmothers acquire (Hawkes et al 1989, 1997) and can be seen daily to share with younger kin. Although we have noticed the occasional strikingly warm relationship between grandfather and grandchild, grandfathers (not all are still married to the grandmother) seemed to show little effect on child survival.

Hawkes’ “Grandmother Hypothesis” (“GMH”) includes the proposition that the help given by grandmothers allowed a shortening of inter-birth intervals (IBI) below the lengthy IBI of higher primates. Hadza IBI, at 2.8 years, are close to the hunter-gatherer mean of 3.0 years (Walker et al 2008, Marlowe 2010). I could see no significant difference in closed, non-replacement IBI between Hadza women who had a living mother or mother-in-law (“senior helper”) and those who had neither. But there was a striking and statistically significant difference in the length of successful IBI, intervals that added a surviving child to the family (BJ 2016 fig. 18.6). The median successful interval for women with a senior helper was 3.0 years, for those without, 3.67 years (the means were 3.2 and 4.8). These data support the view that a helper can allow shorter IBI to pay off in increased reproductive success (RS). The l_{15} without grandmother roughly corresponds to rate of increase in r of about 0.004 (doubling in 173 years) or an r of about 0.15 with grandmother (doubling in 47 years). Were grandmothers responsible for explosive human population growth rates evolving from the teetering population dynamics of our closest primate kin?

In BJ2016 Chapter 19 I tried to use the Hadza data to address Cant & Johnson’s (2008), and Johnstone & Cant’s (2010) (C&J) important suggestion that conflict between the generations may have played a significant part in the evolution of menopause and post-reproductive life. One essential feature of both Hawkes’s GMH and C&J’s suggestion is that the resources acquired by the grandmother are limited and, if used for the grandmother’s continued reproduction, cannot be used for her daughter or daughter-in-law’s reproduction. In the case of food collected by the grandmother, the resource is clearly divisible and depreciable in Clutton-Brock’s (1991) terminology. Other forms of care, baby-sitting, or remembering where to find water in a rare extreme drought, may not share this feature and thus entail no allocation between mother and daughter’s reproduction. They are non-depreciable; I think of them as “umbrella care”: you could shelter five Hadza-sized children under a large umbrella as effectively as you could shelter one, and for the same cost. For instance, the effects of some aspects of ‘baby-sitting’, often envisaged as the main task for grandmothers by those unfamiliar with the vigour of Hadza grandmothers and their !Kung counterparts, do not diminish as the recipients of help become more numerous. Vigilance may be valuable, but in a bush camp the effort of watching over one toddler (with no door to disappear through) may not detract from the ability to watch over another, including your own. Likewise, the “library function” of old individuals provides a non-depreciable good; it benefits all who follow and costs the grandmother the same regardless of the number of beneficiaries, nor need it interfere with her own reproduction.

C&J examine conflict between the reproduction of an older female OF (mother or mother-in-law) and younger female YF (daughter or daughter-in-law). They describe different resolutions of contests over the grandmother’s resources that can arise from different dispersal patterns,

which affect the relatedness between co-resident OF and YF and the fitness interests of each. Two settings contrast with the usual mammalian pattern in which young give way to old. When a group is enduring, with a mating system in which males mate during excursions outside their home group, the older should give way to the younger in reproductive competition. They suggest that this accounts for the post-reproductive life observed in Orca females (Olesiuk et al 2005, Croft et al 2016). The second setting that promotes the old giving way to the young is female dispersal. Since older literature (and some contended modern literature) claims that female dispersal characterizes hunter-gatherer and higher-primate populations, C&J suggest that this may be a key to the evolution of human menopause and post-fertile life. Female dispersal produces an asymmetry in potential competition over resources gathered by OF. Under female dispersal, while the offspring of YF are related to OF through OF's sons, the future offspring of OF are unrelated to YF and bring YF no fitness benefit. YF should contest more vigorously and prevail. OF is expected to give way, doing better to direct her resources to her son's wife's children and forgo further child-bearing.

The logic is enticing and, together with the special features of human forager resources, would account for the scarcity of post-reproductive life among mammals, where male dispersal is widely observed. There are data from patrilocal farming societies that show negative relationships between the reproduction of OF and YF, especially daughters-in-law (Strassman & Garrard 2011) and they can be used to support the importance of competition. In the Hadza data I was unable to find consistent support for negative relationships between reproduction of any category of OF and YF, either in fertility or child survival. In contrast, positive associations between OF and daughter's reproduction were both striking and significant, perhaps a challenge to our claims about allocation of resources between mother and daughter.

In discussing C&J I pointed first to the frequency with which the composition of Hadza camps changes. Moving away has been described as a solution to conflicts among hunter-gatherers. I also suggested that the breadth of Hadza food sharing, characteristic of most known hunter-gatherers (arguably a consequence of the character of savanna foods) may have overshadowed or even reversed any underlying competition between mother and adult daughter. Reduction in day-to-day variance of food intake may be a significant feature of female cooperation among foragers. Hadza serial monogamy, resulting in many families of half-sisters, may offer a potential addition to the competition models of C&J (see also Moya & Sear 2014).

The contest approach sometimes appears to differ from Hawkes' GMH by taking human lifespan as a given, and then to aim to account for a reduced age at last birth. This view would arise if one measures life span and life events not in years but as percentages of an unvarying given life span, which equates the human 70 years with a chimpanzee's 45 years (BJ2016 SI 19.2). Taking life span as a given leaves us seeking no adaptive reason for the excess of human life spans over those of other great apes.

Ancestral human dispersal patterns may be difficult to determine (Vigilant & Langergraber 2011, Koenig & Borries 2012). The original view in anthropology was heavily dependent on interviews with men about kinship terms and marriage rules (nowadays interesting to human behavioral ecologists as efforts to promote men's interests in controlling sexual access to females (Rodseth 2012), a little-discussed instance of male cooperation). The relationship of these rules to actual distribution and movement of people was rarely reported. If we take recent hunter-gatherers, and observational statistical studies as representative, we see a variety of residence

and dispersal patterns, centering on bilocal (Alvarez 2004, Hill et al 2011, Marlowe 2004a). One comment: if chimpanzees are taken to represent an ancestral female dispersal, then the brevity of post-fertile life among chimpanzees emphasizes that we should not lose sight of the importance of the transfer of divisible, depreciable resources among hunter-gatherers. The services that post-reproductive Cetaceans provide for their younger kin are as yet not totally clear. Effects on survival, strongest upon sons, are shown, as well as some evidence about the support of sons in conflicts (Foster et al 2012), leadership (Brent et al 2015) and food sharing (Wright et al 2016).

Finally, we should acknowledge that positive grandmother effects have been demonstrated in only one other hunter-gatherer population: the Ache, among whom Hill & Hurtado (1991) showed effects but reported that they did not outweigh a high hypothesized rate of continued child-bearing. Howell (2010) found negative associations of co-resident !Kung grandmother and paternal grandfather with early childhood body-mass index, perhaps not the best measure to use with 1 to 5 year olds — but her descriptions suggest the value of parents to a young couple.

Another competing view of grandparenting and the evolution of human life histories is presented in the chapter by Kaplan. Usually referred to as the “Embodied capital” theory (Kaplan et al 2000) it emphasizes the economic contributions of older men as well as older women, and the accumulation of skills during the pre-adult period. A number of writers promote an idea that links the value of learning to prolonged childhood, and that of a longer adult life to recoup the benefits, often linking this to evolutionary changes in brain size. Many variants of this view can be found, its latest re-incarnation is Pretelli et al (2022), but I think they greatly underestimate the speed with which hunter-gatherer children can learn subsistence skills.

Men as Helpers: Looking for Father Effects

Investigators of human evolution and behaviour have long believed that humans live in pairs because men contribute to the household income. Supporting evidence from hunter-gatherers is surprisingly thin. In their extensive and careful review of the literature on natural-fertility societies, Sear & Mace (2008) found little evidence that fathers’ presence increased the survival or growth rates of their children. Obst (1912) regarded Hadza men as exemplary fathers, to be contrasted with their neighbours. In the field I, and doubtless others, have seen warm and attentive interactions between Hadza men and their children. Yet in my Chapter 15 on marriage and Chapter 21 on men as helpers I found only sparse support for significant effects of paternal provisioning. Although the samples are large, as large as for grandmothers, the analysis is far from simple, and may merely illustrate the difficulty of non-experimental research.

Direct observation could measure men’s transfer of resources to their wives. Marlowe (2010: table 8.5) approximated this with the amounts of food brought back to camp per day by married Hadza men. He found that men with infants brought home more than men with older children or no children, or step-children. He suggested this was an indication of the importance of men’s provisioning. But if we want to look at actual consequences, we must collect a larger sample than is possible in direct observation studies. Then we need some proxy measures that reflect the transfer of resources from husband to wife. Neither number of marriages, nor number of divorces seemed important given the serial monogamy that is common among Hadza.

I used two proxy measures. Firstly, in Chapter 21 on fathers as helpers, I used father absence. For each year of a woman or a child's life, I checked whether the father was recorded as still married to her or not. The probability of a divorced father being in the same camp as his children was very low (BJ2016 Fig 21.1). If the father was still married to mother, then the probability of child death was lower, but not significantly so, with $p = 0.330$ and the 95% confidence interval for the odds ratio ranging from 0.48 to 1.28 (i.e. roughly from half the chance of a death when the father is present to substantially more deaths when he is present (OR = 1 when there is exactly no effect)). With 191 child deaths out of 695 children and 3869 child-years of data, and the father absent in one third of the child-years, this was not strong support for a helper effect of the father on the survival of children. But there were small, positive, statistically significant effects of a father's presence on the growth of children aged 5–12.

A second proxy measure (in Chapter 15 on marriage) for the evidence of an effect of men's provisioning (BJ 2016 fig 15.8a & b, and table 15.3) was the percent of adult life (20 to 40 for women, 25 to 50 for men) in a marriage ("pctmarr"). This measure was used on the assumption that transfer of resources, to be effective, would be a continuous series of events. The husband was assumed to bring food home and make some available daily, weekly and preferentially to his wife. Then the more time that a woman had a husband during her child-bearing years, the more resources she would have received. Correlations with fertility would be expected either if intercourse was more frequent within marriage or if fertility was enhanced by the supply of resources from the husband. So the positive correlations of a women's time in a marriage with their number of living children (in table 15.3 panel A, not significant in panel B) and with her fertility (number of births, in both panels of table 15.3) are not unequivocal support for an advantage from resource transfers. Success at keeping children alive ("sssurv") should provide clearer evidence of the fitness-enhancing effect of resource transfers. But there is not a significant relationship between pctmarr and sssurv among Hadza women ($b = 0.6025$, $p = 0.236$, adjusted R-squared = 0.4%, $N = 116$ women). While the beta is large, the p value was far from significant and R-squared is trivially small, "pctmarr" accounted for virtually none of the variance in "sssurv". The women seemed to gain no child survival from the presence of a husband.

Borgerhoff Mulder (2017) raised two important points about this analysis; firstly, a potential confounding factor. The women who were seldom alone would tend to have shorter average IBI than those who spent a smaller percent of their adult life in a marriage ("pctmarr"). I had shown (BJ2016 ch. 17) that among Hadza, as among many others, short IBI were associated with lower offspring survival. The confound was not difficult to test. Adding each woman's mean IBI to the regression models did not change the picture. While mean IBI was positively associated with child survival ($b = 0.4302$, $p = 0.000$), controlling for its effect did not reveal a hitherto hidden benefit of pctmarr on child survival. Pctmarr remained non-significant ($b = 0.1337$, $p = 0.659$).

Given the frequency of divorce and remarriage among Hadza, we could ask whether the result was distorted by step-fathers, who Marlowe 2010 observed to bring home less food (Marlowe 2010:215). Regression of "sssurv" on the number of divorces weakly suggests the potential confound may be realistic ($b = -0.1473$, $p = 0.056$, with adjusted R-sqd 2.0%). But adding the number of divorces to the original regression model failed to generate a significant positive effect of time in a marriage upon the proportion of the woman's children that she kept

alive (ssurv = No of divorces $b = -0.1456$ ($p = 0.063$) + pctmarr $b = 0.0493$ ($p = 0.878$)). The adjusted R-sqd at 1.3%. remained trivially small.

In other circumstances, different measures of marriage may be more meaningful. Among the Pimbwe, the number of sequential marriages is a predictor of women's RS but not men's (Borgerhoff Mulder 2009). The best proxy for male transfer of resources may be different in different populations or contexts. If we look at a wider range of populations, recalling Richard Lee's (1968) demonstration of the latitudinal variation in proportions of meat or plant foods in foragers' diets, we will include many in which there is clearly greater opportunity for men to control resources and for women to have less independent access to resources than among !Kung or Hadza. In such contexts, a woman's best way to gain access to resources may be to associate with one or a few men who gain sexual access for differential allocation of resources. This is surely today a common feature of marriage but perhaps it was not the original form.

Unlike post-reproductive women, men of any age, no matter how much they could help their wife and children, have competing routes to increased fitness. Age-specific fertility of Hadza men continues well above zero into their 60s (BJ 2016 fig 7.7). In some populations, especially those with strongly maintained monogamous marriages, men's reproduction closely tracks their marital status and the age of their wives (Tuljapurkar et al 2007, Vinicius et al 2014). Such populations also tend to have lower variance in male RS (Schacht et al. 2014, Betzig 2012). But in other populations, Hadza included, men sometimes desert their wives, embark on a new marriage to a younger woman and raise a second family of children, almost doubling their RS. That only a few succeed, and many fail, does not show weaker selective gains to the successful.

Winking & Gurven (2011) added a fifth population, Tsimane, to Blurton Jones et al (2000) and Hurtado & Hill (1992) and carefully extended the comparison to cover a man's entire reproductive career. They found that "the fertility costs due to greater offspring mortality are overcome by only minor differences in the ages of first and second spouses." While they discuss some influences on the opportunity for men to remarry a younger spouse, they give little emphasis to Hurtado & Hill's (1992) "fertilities per male" (mean TFR x N of adult women / N of adult men). Perhaps we should attend to this measure as an indicator of the level of male-male competition and the pay-off for mate guarding, Schacht & Bell (2016), and as a reflection of the competitive situation in which males exist. Mate guarding is one alternative idea about the origin of marriage (Sear & Mace 2008, Hawkes et al 1995, Coxworth et al 2015, Loo et al 2017, Lukas & Clutton-Brock 2013, Opie et al 2013, Chapais 2013). We might wonder how some men succeed in the competition.

Hunting Big Game

During the 1980s fieldwork we were struck by the preponderance of large animals taken by Hadza, and the rapidity with which most of the meat disappeared to other men's huts. Experimental follows of men paid to pursue only small game showed, we argued in Hawkes et al (1991), that exclusive pursuit of small game would be the evolutionarily stable strategy (ESS) for men who foraged only for the benefit of their own children's weekly supply of meat. We have argued with Wood & Marlowe (2013, 2014) and others about this. There are several strands to the argument; most are covered at one point or another in Hawkes' papers, and I will not address them here.

Finding little indication of direct reciprocation of meat shares (Hawkes et al. 2001a), Hawkes (1990 and subsequently) proposed that some form of social consequence maintained the pursuit of big game. Hawkes labeled the process “Show-off”, as conspicuously misleading a term as my “Tolerated theft” (1987). Both catchy labels have led readers astray. Tolerated theft is just a statement of the simplest economics of potential conflicts over food acquired in large packages with high temporal variance. Hadza hunters do not show off; they maintain a modest demeanor as described among !Kung by Lee (1969) and Wiessner (2014), and among Hadza and others by Woodburn 1979), nor do they fit the image of ceaseless “womanizers” given by one science writer.

Smith & Bliege Bird (2000) and Hawkes & Bliege Bird (2002) later proposed that Hadza men’s pursuit of large game, and other risky pursuits, are examples of Zahavi’s handicap principle (elaborated and its theoretical basis tested by Grafen 1990, Biernaskie 2014). Because of the exertion and risk of hunting large animals, in competition with lions and hyenas and perhaps at some cost to one’s wife and children, and because of the availability of the meat being impossible to hide from camp members (given the easy visibility of smoke and vultures), hunters ensure that their qualities are known to many. More recently, Bliege Bird et al. (2012) have discussed “the hierarchy of virtue”: competition for a reputation as the most altruistic (a large experimental literature covers such reputations); and Hawkes has emphasized the information that other men may take from a man’s success at big-game hunting that may lead to concessions over access to mates. Perhaps we should become more explicit in our hypotheses about the audience’s interests in the signal, and the consequences of their interest for the signaler. We might also look more closely at how the show-off proposals compare and contrast with ideas about social selection (West-Eberhard 1983, Nesse 2007, Barclay 2013).

To pursue the “show-off” idea, Marlowe and I independently asked women to nominate men who they regard as good hunters (“who often hit large animals”) (“GH”). In separate small samples we find the abundance of nominations correlate positively with observed hunting success. We also find that GH have greater RS than other men (which is not uncommon, von Rueden & Jaeggi 2016). My analyses leave some mysteries. I did not find the wives of GH more fertile once their age is taken into account, and I found their children were significantly more likely to die (95% range of the odds ratio was 1.06–1.35, and BJ2016 fig. 21.2), even after one accounts for the wife’s age as a continuous variable, or a wife’s membership of the least successful age group (under-19-year-olds) (BJ2016Table 21.2). In my data, GH gain most of their excess RS by spending less time unmarried and by remarrying younger women (as Marlowe 2010 also reports) and raising a second family (a history not unknown in industrial societies).

The GH are a minority and, if we remove them from the sample, among “ordinary Joe’s” (who all profess to hunt almost daily, with very little success, and who nonetheless collect shares from any large kill) we see a marginally significant positive effect of the father’s presence in the household on their children’s survival, although it is not possible to totally exclude a confound with the tendency for marriages to break up after the death of a child.

Thus Hadza men can follow alternative strategies. In addition to GH and Ordinary Joe there were seven men who worked for money from outside sources, “wage earners”, who had two wives with several children surviving and growing well, and six intriguing “Cads” who, despite having children by a large number of women, had no greater RS than average. The variety of strategies illustrates that a simple dichotomy into “parenting effort” versus “mating effort”

is only a beginning. Each can take many forms. “Mating effort” especially includes a range of possibilities such as mate guarding and other strategies of competition, including “show-off” or pursuit of status. If there are alternative strategies open to men then we might expect mechanisms to have evolved that enable them to select an appropriate strategy. The process should take account of their own abilities and experience, the strategies adopted by their competitors and the availability of opportunities.

Do Economic and Reproductive Interests Influence which Norms Invade, Spread and Endure?

While GH achieve superior RS, their wives, it seems, do not. If we had found that wives of GH had higher RS we might have been tempted to stop the investigation, because the result seemed to fit so well the received wisdom that men hunt to feed their wives and children. We could avoid that temptation by, for instance, wondering whether GH get higher quality wives (Hawkes et al 2001b). In the sample of 323 marriages, controlled for the woman’s age, wives of GH are slightly more likely to have been nominated as hard workers by other women ($b = 1.999$, $p = 0.019$). But another temptation, long ago discarded, is reappearing: the temptation to announce a “norm” and turn away. Let me discuss a hypothetical example.

Marlowe (2004b, 2010 fig 7.4) reports that 55% of Hadza women said they preferred to marry a good hunter. Why? To eat more meat? But note that we have shown no benefit of the meat bonanzas to the wife or young children of a good hunter. Instead, the wives are more likely to have to put up with his affairs, eventually more likely to be deserted in favour of a younger woman, and their small children will suffer a lower chance of survival. Perhaps it is just a “norm” among Hadza that women should marry a good hunter. In the uneasy relationship between simple “old-school” behavioural ecology and cultural transmission theory, and isolation from the broader history of the social sciences, some nowadays apparently find the use of the “norm” as an explanation tempting. But there may be gains from stubbornly pursuing the behavioural ecology paradigm. Do individual economic and reproductive interests influence which norms invade, spread and endure?

The idea of a norm is not useless; for instance, it brings to mind the possibility that people keep telling young women that they should marry a good hunter. These people could be self-interestedly increasing their chance of a share in the bonanzas. If the mother of two daughters persuaded both to marry a GH, she might eat meat more often. If she persuaded her sister to persuade her daughter, and her son, overhearing the exhortations, noted the likely benefits of becoming a good hunter, the older women would have a chance of eating meat at least weekly, perhaps almost daily. By her redistributions, the older woman might benefit a wide array of young kin with a greater meat intake, and this might, barely conceivably, outweigh the losses to each daughter.

So there may be reasons for some people to promote the “norm”. But why should the young women fall for the propaganda? We should have asked them, although some of the youngest seemed not to know who the good hunters were (Blurton Jones 2016:272). I did ask a few women whether they would have a problem acquiring food if their husband went away for a while “on safari”. Fifteen out of the eighteen said they would have no problem.

Like the older women, if the young woman could persuade her sister or cousin to marry a good hunter, she may share the supposed benefit of a more even supply of meat. If all

these women were successful in their efforts at “farming men” then we might expect to see aggregations of GH. But my Hadza field assistant said that if you were the only good hunter in camp, people came to expect too much of you. On the other hand, if there were many, you were no longer anyone special. It was best to be one of a few. Wood (2006) interviewed thirty-four Hadza men on their preference for joining a camp with skilled hunters or with poor hunters. Twenty-six preferred to join a camp of skilled hunters; only eight preferred a camp with less meat. The camp composition data may give some answers, and show whether the wife of a GH gains a different social position from others. Although at present we cannot see her gains in RS, she may more often have older related helpers in her camp than comparable women married to less successful hunters, or other social advantages which (as in other species) may translate in the longer term to fitness advantages. Perhaps the father’s status affects her older children (Scelza 2010), even after the GH has moved on to another marriage. If sons of GH become GH there could be a runaway effect of female preference for GH.

So in challenging the tempting “excuse” of a “norm”, neither ignoring it nor taking it as an explanation, we were led to potentially answerable questions. They centre around the shared or conflicting interests of individuals or classes of individuals. Why would anyone make propaganda, promote a norm, if the targets want to perform the desired behaviour anyway? It might be a useful rule of thumb to believe that when we are tempted to postulate a “norm” and close the investigation, we should instead look for conflicts of interest. This research strategy is not as new as the temptation. It has obvious links to research on adaptation in animal communication (Davies et al. 2012), an illustrious precedent in the work of Alexander (1979) and his students on kinship systems, and some vigorous history in the social sciences (Harris 1968, Bicchieri 2006).

Acknowledgements

The work summarized here was funded by grants from NSF and UCLA and others listed in our publications. It was conducted under permits from Tanzania’s COSTECH and UCLA’s HSPC. It owes everything to the friendly patience of many, many Hadza.

References¹

- Alexander, Richard D. 1979. *Darwinism and Human Affairs* (Seattle: University of Washington Press).
- Alvarez, Helen P. 2004. ‘Residence groups among hunter-gatherers: a view of the claims and evidence for patrilocal bands’, in *Kinship and Behavior in Primates*, ed. by B. Chapais and C. M. Berman (New York: Oxford University Press).
- Apicella, Coren L., Frank W. Marlowe, James H. Fowler, and Nicholas A. Christakis. 2012. ‘Social networks and cooperation in hunter-gatherers’, *Nature*, 481.7382: pp. 497–501. <https://doi.org/10.1038/nature10736>
- Barclay, P. 2013. ‘Strategies for cooperation in biological markets, especially for humans’, *Evolution and Human Behavior*, 34.3: pp. 164–75. <https://doi.org/10.1016/j.evolhumbehav.2013.02.002>
- Belsky, A. Joy. 1990. ‘Tree/grass ratios in East African savannas: a comparison of existing models’, *Journal of Biogeography*, 17.4/5: pp. 483–89. <https://doi.org/10.2307/2845380>

¹ Note this chapter has been posted on the Open Science Framework website since 29/06/2019, after it was accepted for publication, so the references will reflect when the chapter was written and not the OBP publication date.

- Berbesque, J. Colette, Brian M. Wood, Alyssa N. Crittenden, Audax Mabulla, and Frank W. Marlowe. 2016. 'Eat first, share later: Hadza hunter-gatherer men consume more while foraging than in central places', *Evolution and Human Behavior*, 37.4: pp. 281–86. <http://doi.org/10.1016/j.evolhumbehav.2016.01.003>
- Betzig, Laura. 2012. 'Means, variances, and ranges in reproductive success: comparative evidence', *Evolution and Human Behavior*, 33.4: pp. 309–17. <http://doi.org/10.1016/j.evolhumbehav.2011.10.008>
- Bicchieri, Christina. 2006. *The Grammar of Society: The Nature and Dynamics of Social Norms* (Cambridge: Cambridge University Press).
- Biernaske, Jay M., Alan Grafen, and Jennifer Perry. 2014. 'The evolution of index signals to avoid the cost of dishonesty', *Proceedings of the Royal Society B*, 281.1790: pp. 20140876. <https://doi.org/10.1098/rspb.2014.0876>
- Birdsell, Joseph, B. 1968. 'Some predictions for the Pleistocene based on equilibrium systems among recent hunter-gatherers', in *Man the Hunter*, ed. by R. B. Lee and I. DeVore (Chicago: Aldine).
- Bliege Bird, Rebecca, Brooke Scelza, Douglas W. Bird, and Eric Alden Smith. 2012. 'The hierarchy of virtue: mutualism, altruism and signaling in Martu women's cooperative hunting', *Evolution and Human Behavior*, 33.1: pp. 64–78. <http://doi.org/10.1016/j.evolhumbehav.2011.05.007>
- Blurton Jones, Nicholas. 2016. *Demography and Evolutionary Ecology of Hadza Hunter-Gatherers, Cambridge Studies in Biological and Evolutionary Anthropology* (Cambridge: Cambridge University Press). <http://doi.org/10.1017/cbo9781107707030>
- Blurton Jones, Nicholas G. 1987. 'Tolerated theft, suggestions about the ecology and evolution of sharing, hoarding and scrounging', *Social Science Information*, 26.1: pp. 31–54. <https://doi.org/10.1177/053901887026001002>
- Blurton Jones, N.G. 2006. 'Contemporary hunter-gatherers and human life history evolution', in *The Evolution of Human Life History*, ed. by K. Hawkes and R. R. Paine (Santa Fe, Oxford: School of American Research Press, James Currey).
- Blurton Jones, N.G., K. Hawkes, and P. Draper. 1994a. 'Foraging returns of !Kung adults and children: why didn't !Kung children forage?', *Journal of Anthropological Research*, 50.3: pp. 217–48. <https://doi.org/10.1086/jar.50.3.3630178>
- Blurton Jones, N.G., K. Hawkes, and J.F. O'Connell. 1989. 'Modelling and measuring costs of children in two foraging societies', in *Comparative Socioecology*, ed. by V. Standen and R. A. Foley (Oxford: Blackwell Scientific).
- Blurton Jones, N. G., K. Hawkes, and J.F. O'Connell. 1997. 'Why do Hadza children forage?', in *Genetic, Ethological and Evolutionary Perspectives on Human Development*, ed. by N. L. Segal, G. E. Weisfeld and C. C. Weisfeld (Washington DC: American Psychological Association).
- Blurton Jones, N.G., Kristen Hawkes, and J.F. O'Connell. 2002. 'Antiquity of postreproductive life: Are there modern impacts on hunter-gatherer postreproductive life spans?', *American Journal of Human Biology*, 14.2: pp. 184–205. <http://doi.org/10.1002/ajhb.10038>
- Blurton Jones, Nicholas G., Kristen Hawkes, and James F. O'Connell. 2005. 'Hadza grandmothers as helpers: residence data', in *Grandmotherhood. The Evolutionary Significance of the Second Half of Female Life*, ed. by E. Voland, A. Chasiotis and W. Schiefenhovel (New Brunswick, NJ: Rutgers University Press).
- Blurton Jones, N.G., and F.W. Marlowe. 2002. 'Selection for delayed maturity: does it take 20 years to learn to hunt and gather?', *Human Nature*, 13.2: pp. 199–238. <https://doi.org/10.1007/s12110-002-1008-3>
- Blurton Jones, Nicholas.G., Frank.W. Marlowe, Kristen Hawkes, and James F. O'Connell. 2000. 'Paternal investment and hunter-gatherer divorce rates', in *Adaptation and Human Behavior: An Anthropological Perspective*, ed. by L. Cronk, W. Irons and N. Chagnon (New York: Aldine de Gruyter). <http://doi.org/10.4324/9781351329200-6>
- Blurton Jones, N.G., and R.M. Sibly. 1978. 'Testing adaptiveness of culturally determined behaviour: Do bushman women maximise their reproductive success by spacing births widely and foraging seldom?', in *Human Behaviour and Adaptation: Society for Study of Human Biology Symposium No 18*, ed. by N. Blurton Jones and V. Reynolds (London: Taylor & Francis).

- Blurton Jones, N.G., L.C. Smith, J.F. O'Connell, K. Hawkes, and C.L. Kamuzora. 1992. 'Demography of the Hadza, an increasing and high density population of savanna foragers', *American Journal of Physical Anthropology*, 89.2: pp. 159–81. <https://doi.org/10.1002/ajpa.1330890204>
- Boone, James L. 2002. 'Subsistence strategies and early human population history; An evolutionary ecological perspective', *World Archaeology*, 34.1: pp. 6–25. <http://doi.org/10.1080/00438240220134232>
- Borgerhoff Mulder, Monique. 1992. 'Demography of pastoralists: preliminary data on the Datoga of Tanzania', *Human Ecology*, 20.4: pp. 383–405. <https://doi.org/10.1007/bf00890427>
- Borgerhoff Mulder, Monique. 2009. 'Tradeoffs and sexual conflict over women's fertility preferences in Mpimbwe', *American Journal of Human Biology*, 21.4: pp. 478–87. <http://doi.org/10.1002/ajhb.20885>
- Borgerhoff Mulder, Monique. 2016. 'Review of *Demography and Evolutionary Ecology of Hadza Hunter-Gatherers* by Nicholas Blurton Jones (Cambridge University Press 2016)', *Human Nature*, 28.1: pp. 117–27. <http://doi.org/10.1007/s12110-016-9280-9>
- Bray, Joel, Emery Thompson, Melissa, Muller, Martin M., Wrangham, Richard W. and Machanda, Zarin P. 2018. 'The development of feeding behavior in wild chimpanzees (*Pan troglodytes schweinfurthii*)', *American Journal of Physical Anthropology*, 165.1: pp. 34–46. <https://doi.org/10.1002/ajpa.23325>
- Brent, Lauren J. N., Daniel W. Franks, Emma A. Foster, Kenneth C. Balcomb, Michael A. Cant, and Darren P. Croft. 2015. 'Ecological knowledge, leadership, and the evolution of menopause in Killer Whales', *Current Biology*, 25.6: pp. 746–50. <http://doi.org/10.1016/j.cub.2015.01.037>
- Cant, Michael A., and Rufus A. Johnstone. 2008. 'Reproductive conflict and the separation of reproductive generations in humans', *Proceedings of the National Academy of Sciences*, 105.14: pp. 5332–36. <http://doi.org/10.1073/pnas.0711911105>
- Carr-Saunders, A. M. 1922. *The Population Problem. A Study in Human Evolution* (Oxford: The Clarendon Press).
- Chan, Matthew H., Kristen Hawkes, and Peter S. Kim. 2016. 'Evolution of longevity, age at last birth and sexual conflict with grandmothering', *Journal of Theoretical Biology*, 393.145: pp. 145–57. <http://doi.org/10.1016/j.jtbi.2015.12.014>
- Chapais, Bernard. 2013. 'Monogamy, strongly bonded groups, and the evolution of human social structure', *Evolutionary Anthropology*, 22.2: pp. 52–65. <http://doi.org/10.1002/evan.21345>
- Charnov, E. L. 1993. *Life History Invariants* (Oxford, New York, Toronto: Oxford University Press).
- Clutton-Brock, T.H. 1991. *The Evolution of Parental Care* (Princeton, NJ: Princeton University Press).
- Coale, A. J., and P. Demeny. 1983. *Regional Model Life Tables and Stable Populations* (New York: Academic Press).
- Coe, M. J., D. H. Cumming, and J. Phillipson. 1976. 'Biomass and production of large African herbivores in relation to rainfall and primary production', *Oecologia (Berlin)*, 22.4: pp. 341–54. <https://doi.org/10.1007/bf00345312>
- Coxworth, James E., Peter Kim, John McQueen, and Kristen Hawkes. 2015. 'Grandmothering life histories and human pair bonding', *Proceedings of the National Academy of Sciences USA*, 112.38: pp. 11806–11811. <http://doi.org/10.1073/pnas.1599993112>
- Crittenden, Alyssa N., Nancy L. Conklin-Brittain, David A. Zes, Margaret J. Schoeninger, and Frank W. Marlowe. 2013. 'Juvenile foraging among the Hadza: implications for human life history', *Evolution and Human Behavior*, 34.4: pp. 299–304. <http://doi.org/10.1016/j.evolhumbehav.2013.04.004>
- Croft, Darren P., Rufus A. Johnstone, Samuel Ellis, Stuart Natrass, Daniel W. Franks, Lauren J.N. Brent, Sonia Mazzi, Kenneth C. Balcomb, John K.B. Ford, and Michael A. Cant. 2016. 'Reproductive Conflict and the Evolution of Menopause in Killer Whales', *Current Biology*, 27.2: pp. 1–7. <http://doi.org/10.1016/j.cub.2016.12.015>
- Croft, Darren P., Lauren J. N. Brent, Daniel W. Franks, Michael A. Cant. 2015. 'The evolution of prolonged life after reproduction', *Trends in Ecology & Evolution*, 30.7: pp. 407–16. <http://doi.org/10.1016/j.tree.2015.04.011>

- Davies, Nicholas B., John R. Krebs, and Stuart A. West. 2012. *An Introduction to Behavioural Ecology* (Chichester UK and Hoboken NJ: Wiley-Blackwell).
- Draper, P. 1989. 'African marriage systems: an evolutionary perspective', *Ethology & Sociobiology*, 10.1-3: pp. 145-69. [https://doi.org/10.1016/0162-3095\(89\)90017-4](https://doi.org/10.1016/0162-3095(89)90017-4)
- Diekmann, Yoan, Daniel Smith, Pascal Gerbault, Mark Dyble, Abigail E. Page, Nikhil Chaudhary, Andrea Bamberg Migliano, and Mark G. Thomas. 2017. 'Accurate age estimation in small-scale societies', *Proceedings of the National Academy of Sciences*, 114.31: pp. 8205-10. <http://doi.org/10.1073/pnas.1619583114>
- Dyson, T. 1977. 'The demography of the Hadza in historical perspective', in *African Historical Demography*, ed. by C. Fyfe and D. McMaster (Centre for African Studies, University of Edinburgh).
- Early, John D, and Thomas N. Headland. 1998. *Population Dynamics of a Philippine Rain Forest People: The San Ildefonso Agta* (Gainesville: University Press of Florida).
- Ellis, Samuel, Daniel W. Franks, Stuart Nattress, Michael A. Cant, Destiny L. Bradley, Deborah Giles, Kenneth C. Balcomb, Darren P. Croft. 2017. 'Postreproductive lifespans are rare in mammals', *Ecology and Evolution*, 8.5: pp. 1-13. <http://doi.org/10.1002/ece3.3856>
- Ellis, Samuel, Daniel W. Franks, Stuart Nattress, Thomas E. Currie, Michael A. Cant, Deborah Giles, Kenneth C. Balcomb, and Darren P. Croft. 2018. 'Analyses of ovarian activity reveal repeated evolution of post-reproductive lifespans in toothed whales', *Nature Scientific Reports*, 8.1: pp. 12833. <https://doi.org/10.1038/s41598-018-31047-8>
- Foster, Emma A., Daniel W. Franks, Sonia Mazzi, Safi K. Darden, Ken C. Balcomb, John K. B. Ford, Darren P. Croft. 2012. 'Adaptive prolonged postreproductive life span in Killer Whales', *Science*, 337.6100: pp. 1313. <http://doi.org/10.1126/science.1224198>
- Gage, Timothy B. 1988. 'Mathematical Hazard Models of Mortality: an Alternative to Model Life Tables', *American Journal of Physical Anthropology*, 76.4: pp. 429-41. <https://doi.org/10.1002/ajpa.1330760403>
- Gage, Timothy B. 1998. 'The comparative Demography of Primates', *Annual Reviews of Anthropology*, 27.1: pp. 197-221. <https://doi.org/10.1146/annurev.anthro.27.1.197>
- Grafen, Alan. 1990. 'Biological Signals as Handicaps', *Journal of Theoretical Biology*, 144.4: pp. 517-46. [https://doi.org/10.1016/s0022-5193\(05\)80088-8](https://doi.org/10.1016/s0022-5193(05)80088-8)
- Gurven, Michael, and Hillard Kaplan. 2007. 'Longevity among hunter-gatherers: a cross-cultural examination', *Population and Development Review*, 33.2: pp. 321-65. <http://doi.org/10.1111/j.1728-4457.2007.00171.x>
- Gurven, M., and R. S. Walker. 2006. 'Energetic demand of multiple dependents and the evolution of slow human growth', *Proceedings of the Royal Society of London B*, 273.1588: pp. 835-41. <http://doi.org/10.1098/rspb.2005.3380>
- Harris, Marvin. 1968. *The Rise of Anthropological Theory* (New York: Thomas Y. Crowell).
- Hassan, Fekri A. 1978. 'Demographic archaeology', *Advances in Archaeological Method and Theory*, 1: pp. 49-103. <https://doi.org/10.1016/b978-0-12-003101-6.50009-3>
- Hawkes, Kristen 1990. 'Why do men hunt? Benefits forrisky choices', in *Risk and Uncertainty in Tribal and Peasant Economics*, ed. by Elizabeth Cashdan (Boulder, San Francisco & London: Westview Press), pp. 145-66.
- Hawkes, Kristen, J. F. O'Connell and N. G. Blurton Jones 2001b. 'Hunting and nuclear families', *Current Anthropology*, 42.5: pp. 681-709. <https://doi.org/10.1086/322559>
- Hawkes, Kristen, James O'Connell and Nicholas Blurton Jones. 2018. 'Hunter-gatherer studies and human evolution: a very selective review', *American Journal of Physical Anthropology*, 165.4: pp. 777-800. <http://doi.org/10.1002/ajpa.23403>
- Hawkes, Kristen. 2006. 'Life history theory and human evolution: a chronicle of ideas and findings', in *The Evolution of Human Life History*, ed. by K. Hawkes and R. R. Paine (Santa Fe: School of American Research Press).

- Hawkes, K., and R. Bliege Bird. 2002. 'Showing off, handicap signaling, and the evolution of men's work', *Evolutionary Anthropology*, 11.2: pp. 58–67. <http://doi.org/10.1002/evan.20005>
- Hawkes, Kristen, James F. O'Connell, and Nicholas G. Blurton Jones. 1989. 'Hardworking Hadza grandmothers', in *Comparative Socioecology*, ed. by V. Standen and R. A. Foley (Oxford: Blackwell).
- Hawkes, Kristen, James F. O'Connell, and Nicholas G. Blurton Jones. 1991. 'Hunting income patterns among the Hadza: big game, common goods, foraging goals and the evolution of the human diet', *Philosophical Transactions of the Royal Society of London B*, 334.1270: pp. 243–51. <https://doi.org/10.1098/rstb.1991.0113>
- Hawkes, Kristen, James F. O'Connell, and Nicholas G. Blurton Jones. 1997. 'Hadza women's time allocation, offspring provisioning, and the evolution of long post-menopausal lifespans', *Current Anthropology*, 38.4: pp. 551–77. <https://doi.org/10.1086/204646>
- Hawkes, K., J. F. O'Connell, and N. G. Blurton Jones. 2001a. 'Hadza meat sharing', *Evolution and Human Behavior*, 22.2: pp. 113–42. [http://doi.org/10.1016/s1090-5138\(00\)00066-0](http://doi.org/10.1016/s1090-5138(00)00066-0)
- Hawkes, Kristen, James F. O'Connell, Nicholas G. Blurton Jones, Helen Alvarez, and Eric L. Charnov. 1998. 'Grandmothering, menopause, and the evolution of human life histories', *Proceedings of the National Academy of Sciences, USA*, 95.3: pp. 1336–39. <https://doi.org/10.1073/pnas.95.3.1336>
- Hawkes, K., A. R. Rogers, and E. L. Charnov. 1995. 'The male's dilemma: increased offspring production is more paternity to steal', *Evolutionary Ecology*, 9.6: pp. 662–77. <https://doi.org/10.1007/bf01237661>
- Hill, K., and A. M. Hurtado. 1991. 'The evolution of premature reproductive senescence and menopause in human females', *Human Nature* 2.4: pp. 313–50. <https://doi.org/10.1007/bf02692196>
- Hill, K., and A. M. Hurtado. 1996. *Ache Life History: the Ecology and Demography of a Foraging People* (New York: Aldine de Gruyter).
- Hill, Kim, Robert S. Walker, Miran Bozicevic, James Eder, Thomas Headland, Barry Hewlett, A. Magdalena Hurtado, Frank Marlowe, Polly Wiessner, and Brian Wood. 2011. 'Co-residence patterns in hunter-gatherer societies show unique human social structure', *Science*, 331.6022: pp. 1286–89. <http://doi.org/10.1126/science.1199071>
- Howell, N. 1979. *Demography of the Dobe Area !Kung* (New York: Academic Press).
- Howell, Nancy. 2010. *Life Histories of the Dobe !Kung* (Berkeley: University of California Press). <http://doi.org/10.1525/9780520946170>
- Hurtado, A. M., and K. Hill. 1992. 'Paternal effect on offspring survivorship among Ache and Hiwi hunter-gatherers: implications for modelling pair-bond stability', in *Father-Child Relations: Cultural and Biosocial Contexts*, ed. by B. Hewlett (New York: Aldine De Gruyter).
- Johnstone, Rufus, and Michael A. Cant. 2010. 'The evolution of menopause in cetaceans and humans: the role of demography', *Proceedings of the Royal Society B Biological Sciences*, 277.1701: pp. 3765–71. <http://doi.org/10.1098/rspb.2010.0988>
- Kaplan, H. 1997. 'The evolution of the human life course', in *Between Zeus and the Salmon: The Biodemography of Longevity*, ed. by K. Wachter and C. E. Finch (Washington DC: National Academy of Sciences Press).
- Kaplan, H., K. Hill, J. Lancaster, and A. M. Hurtado. 2000. 'A theory of human life history evolution: diet, intelligence, and longevity', *Evolutionary Anthropology*, 9.4: pp. 149–86. [https://doi.org/10.1002/1520-6505\(2000\)9:4%3C156::aid-evan5%3E3.0.co;2-7](https://doi.org/10.1002/1520-6505(2000)9:4%3C156::aid-evan5%3E3.0.co;2-7)
- Keckler, C. N. W. 1997. 'Catastrophic mortality in simulations of forager age-at-death: where did all the humans go?', in *Integrating Archaeological Demography: Multidisciplinary Approaches to Prehistoric Populations*, ed. by R. Paine (Carbondale IL: Southern Illinois University Press).
- Kim, Peter S., James E. Coxworth, and Kristen Hawkes. 2012. 'Increased longevity evolves from grandmothering', *Proceedings of the Royal Society B: Biological Sciences*, 279.1749: pp. 4880–84. <http://doi.org/10.1098/rspb.2012.1751>
- Kim, Peter S., John S. McQueen, and Kristen Hawkes. 2017. 'Why does women's fertility end in mid-life? Grandmothering and age at last birth', *Journal of Theoretical Biology*, 461: pp. 84–91. <https://doi.org/10.1016/j.jtbi.2018.10.035>

- Koenig, Andreas and Carola Borries. 2012. 'Hominoid dispersal patterns and human evolution', *Evolutionary Anthropology*, 21.3: pp. 108–12. <http://doi.org/10.1002/evan.21300>
- Lee, Richard B. 1968. 'What hunters do for a living, or, how to makeout on scarce resources', in *Man the Hunter*, ed. by R. B. Lee and I. DeVore (Chicago: Aldine), pp. 30–48.
- Lee, R. B. 1969. 'Eating Christmas in the Kalahari', *Natural History* (December): pp. 14–22, 60–63.
- Lee, R.B. 1979. *The !Kung San* (Cambridge: Cambridge University Press).
- Levitis, Daniel A., Oskar Burger and Laurie Bingaman Lackey. 2013. 'The human post-fertile lifespan in comparative evolutionary context', *Evolutionary Anthropology*, 22: pp. 66–79. <http://doi.org/10.1002/evan.21332>
- Loo, Sarah L., Kristen Hawkes, and Peter S. Kim. 2017. 'Evolution of male strategies with sex ratio dependent payoffs: connecting pair bonds with grandmothering', *Phil Trans Roy Soc B*, 372.1729: p. 20170041 <http://doi.org/10.1098/rstb.2017.0041>
- Lukas, D. and T. J. Clutton-Brock 2013. 'The evolution of social monogamy in mammals', *Science*, 341.6145: pp. 526–30. <http://doi.org/10.1126/science.1238677>
- Marlowe, Frank W. 2004a. 'Marital residence among foragers', *Current Anthropology* 45.2: pp. 277–84. <http://doi.org/10.1086/382256>
- Marlowe, Frank W. 2004b. 'Mate preferences among Hadza hunter-gatherers', *Human Nature*, 15.4: pp. 365–76. <http://doi.org/10.1007/s12110-004-1014-8>
- Marlowe, F. W. 2010. *The Hadza Hunter-Gatherers of Tanzania* (Berkeley, CA: University of California Press). <http://doi.org/10.1525/9780520945449>
- Marlowe, Frank W., and J. Colette Berbesque. 2012. 'The human operational sex ratio: effects of marriage, concealed ovulation, and menopause on mate competition', *Journal of Human Evolution*, 63.6: pp. 834–42. <http://doi.org/10.1016/j.jhevol.2012.09.004>
- Molleson, T., M. Cox, H. H. Waldron, and D.A. Whitaker. 1993. *The Spitalfields Project. Volume 2. The Anthropology* (York: Council for British Archaeology).
- Monden, Christiaan W. S., and Jeroen Smits. 2009. 'Maternal height and child mortality in 42 developing countries', *American Journal of Human Biology*, 21.3: pp. 305–11. <http://doi.org/10.1002/ajhb.20860>
- Moya, Cristina, and Rebecca Sear. 2014. 'Intergenerational conflicts may help explain parental absence effects on reproductive timing: a model of age at first birth in humans', *PeerJ*, 2: pp. e512. <https://www.doi.org/10.7717/peerj.512>
- Nesse, R. M. 2007. 'Runaway social selection for displays of partner value and altruism', *Biological Theory*, 2: pp. 143–55. <http://doi.org/10.1162/biot.2007.2.2.143>
- Obst, E. 1912. 'Von Mkalama ins Land der Wakindiga', *Mitteilungen der Geographischen Gesellschaft in Hamburg*, 26: pp. 3–45.
- Obst, E. 1915. 'Das abflusslose rumpfschollenland im nordöstlichen Deutsch-Ostafrika', *Mitteilungen der Geographischen Gesellschaft in Hamburg*, 24: pp. 7–268.
- O'Connell, J. F., K. Hawkes, and N.G. Blurton Jones. 1988a. 'Hadza scavenging: implications for Plio-pleistocene hominid subsistence', *Current Anthropology*, 29.2: pp. 356–63. <https://doi.org/10.1086/203648>
- O'Connell, J. F., K. Hawkes, and N. G. Blurton Jones. 1990. 'Re-analysis of large animal body part transport among the Hadza', *Journal of Archaeological Science*, 17.3: pp. 301–16. [https://doi.org/10.1016/0305-4403\(90\)90025-z](https://doi.org/10.1016/0305-4403(90)90025-z)
- O'Connell, J. F., K. Hawkes and N. G. Blurton Jones. 1999. 'Grandmothering and the evolution of Homo erectus', *Journal of Human Evolution*, 36.5: pp. 461–85. <https://doi.org/10.1006/jhev.1998.0285>
- Olesiuk, Peter F., Graeme M. Ellis, and John K. B. Ford. 2005. *Life history and Population Dynamics of northern Resident Killer Whales (Orcinus orca) in British Columbia* (Nainamo, BC: Fisheries and Oceans Canada Pacific Biological Station).

- Opie, C., Q. D. Atkinson, R. I. M. Dunbar et al. 2013. 'Male infanticide leads to social monogamy in primates', *Proceedings of the National Academy of Sciences USA*, 110.33: pp. 13328–32. <http://doi.org/10.1073/pnas.1307903110>
- Page, Abigail E., Nikhil Chaudhary, Sylvain Viguier, Mark Dyble, James Thompson, Daniel Smith, Gul. D. Salali, Ruth Mace, and Andrea Bamberg Migliano. 2017. 'Hunter-gatherer social networks and reproductive success', *Scientific Reports*, 7.1153: p. 1153. <http://doi.org/10.1038/s41598-017-01310-5>
- Peters, Charles R. 1987. 'Nut-like oil seeds: food for monkeys, chimpanzees, humans, and probably ape-men', *American Journal of Physical Anthropology*, 73.3: pp. 333–63. <https://doi.org/10.1002/ajpa.1330730306>
- Pretelli, Illaria, Ringen, R. and Lew-Levy, S. 2022. 'Foraging complexity and the evolution of childhood'. *Science Advances*, 8.41: pp. eabn9889. <https://doi.org/10.1126/sciadv.abn9889>
- Rodseth, Lars. 2012. 'From bachelor threat to fraternal security: male associations and modular organization in human societies', *International Journal of Primatology*, 33.5: pp. 1194–1214. <http://doi.org/10.1007/s10764-012-9593-4>
- Sahlins, M. 1974. *Stone Age Economics* (London: Tavistock Publications).
- Scelza, Brooke A. 2010. 'Fathers' presence speeds the social and reproductive careers of sons', *Current Anthropology*, 51.2: pp. 295–303. <http://doi.org/10.1086/651051>
- Schacht, Ryan, and Adrian V. Bell. 2016. 'The evolution of monogamy in response to partner scarcity', *Scientific Reports*, 6.1: p. 32472. <http://doi.org/10.1038/srep32472>
- Schacht, Ryan, Kristin Liv Rauch, and Monique Borgerhoff Mulder. 2014. 'Too many men: the violence problem?', *Trends in Ecology and Evolution*, 29.4: pp. 214–22. <http://doi.org/10.1016/j.tree.2014.02.001>
- Sear, Rebecca, and Ruth Mace. 2008. 'Who keeps children alive? A review of the effects of kin on child survival', *Evolution and Human Behavior*, 29.1: pp. 1–18. <http://doi.org/10.1016/j.evolhumbehav.2007.10.001>
- Smith, Eric A. and Rebecca Bliege Bird. 2000. 'Turtle hunting and tombstone opening: public generosity as costly signaling', *Evolution and Human Behavior*, 21.4: pp. 245–61. [http://doi.org/10.1016/s1090-5138\(00\)00031-3](http://doi.org/10.1016/s1090-5138(00)00031-3)
- Stott, Ian. 2016. 'Perturbation analysis of transient population dynamics using matrix projection models', *Methods in Ecology and Evolution*, 7.6: pp. 666–78. <https://doi.org/10.1111/2041-210x.12543>
- Strassman, Beverly I., and Wendy M. Garrard. 2011. 'Alternatives to the grandmother hypothesis', *Human Nature*, 22.1–2: pp. 201–22. <http://doi.org/10.1007/s12110-011-9114-8>
- Tuljapurkar, Shripad D., Cedric O. Puleston, and Michael D. Gurven. 2007. 'Why men matter: mating patterns drive evolution of human lifespan', *PLoS ONE*, 2.8: pp. e785. <http://doi.org/10.1371/journal.pone.0000785>
- Vigilant, Linda and Kevin E. Langergraber 2011. 'Inconclusive evidence for patrilocality in Neanderthals', *Proceedings of the National Academy of Sciences USA*, 108.18: pp. 87. <http://doi.org/10.1073/pnas.1100100108>
- Vincent, A.S. 1985. 'Plant foods in savanna environments: a preliminary report of tubers eaten by the Hadza of northern Tanzania', *World Archaeology*, 17.2: pp. 131–48. <https://doi.org/10.1080/00438243.1985.9979958>
- Vinicius, Lucio, Ruth Mace, and Andrea Migliano. 2014. 'Variation in male reproductive longevity across traditional societies', *PLoS ONE*, 9.11: pp. e112236. <http://doi.org/10.1371/journal.pone.0112236>
- von Rueden, C. R., and A. V. Jaeggi. 2016. 'Men's status and reproductive success in 33 nonindustrial societies: Effects of subsistence, marriage system, and reproductive strategy', *Proceedings of the National Academy of Sciences USA*, 113.39: pp. 10824–10829. <http://doi.org/10.1073/pnas.1606800113>
- Walker, P. L., J. R. Johnson, and P. M. Lambert. 1988. 'Age and sex biases in the preservation of human skeletal remains', *American Journal of Physical Anthropology*, 76.2: pp. 183–88. <https://doi.org/10.1002/ajpa.1330760206>
- Walker, Robert S., Michael Gurven, Oskar Burger, and Marcus J. Hamilton. 2008. 'The trade-off between number and size of offspring in humans and other primates', *Proceedings of the Royal Society of London B*, 275.1636: pp. 827–33. <http://doi.org/10.1098/rspb.2007.1511>

- West-Eberhard, Mary Jane, 1983. 'Sexual selection, social competition, and speciation', *The Quarterly Review of Biology*, 58.2: pp. 153–83. <https://doi.org/10.1086/413215>
- Wiessner, Polly W. 2014. 'Embers of society: firelight talk among the Ju/'hoansi Bushmen', *Proceedings of the National Academy of Sciences*, 111.39: pp. 14027–14035. <http://doi.org/10.1073/pnas.1404212111>
- Winking, Jeffrey and Michael Gurven. 2011. 'The total cost of father desertion', *American Journal of Human Biology*, 23.6: pp. 755–63. <http://doi.org/10.1002/ajhb.21207>
- Wood, Brian M. 2006. 'Prestige or provisioning? A test of foraging goals among the Hadza', *Current Anthropology*, 47.2: pp. 383–87. <http://doi.org/10.1086/503068>
- Wood, Brian M., and Frank W. Marlowe. 2013. 'Household and kin provisioning by Hadza men', *Human Nature*, 24.3: pp. 280–317. <http://doi.org/10.1007/s12110-013-9173-0>
- Wood, B. M., and F. W. Marlowe. 2014. 'Toward a reality-based understanding of Hadza men's work', *Human Nature*, 25.4: pp. 620–30. <https://doi.org/10.1007/s12110-014-9218-z>
- Woodburn, J. C. 1968a. 'An introduction to Hadza ecology', in *Man the Hunter*, ed. by R. B. Lee and I. DeVore (Chicago: Aldine).
- Woodburn, J. C. 1968b. 'Stability and flexibility in Hadza residential groupings', in *Man the Hunter*, ed. by R. B. Lee and I. DeVore (Chicago: Aldine).
- Woodburn, J. C. 1979. 'Minimal politics: the political organization of the Hadza of north Tanzania', in *Politics and Leadership: a Comparative Perspective*, ed. by W. Snack and P. Cohen (Oxford: Clarendon Press).
- Wright, Brianna M., Eva H. Stredulinsky, Graeme M. Ellis, and John K. B. Ford. 2016. 'Kin-directed food sharing promotes lifetime natal philopatry of both sexes in a population of fish-eating killer whales, *Orcinus orca*', *Animal Behaviour*, 115: pp. 81–95. <http://doi.org/10.1016/j.anbehav.2016.02.025>
- Zahavi, Amotz, and Avishag Zahavi. 1997. *The Handicap Principle* (Oxford: Oxford University Press).