



Contents lists available at ScienceDirect

Evolution and Human Behavior

journal homepage: www.elsevier.com/locate/ens

Grandpaternal care and child survival in a pastoralist society in western China

Juan Du^a, Abigail E. Page^{b,*}, Ruth Mace^c^a State Key Laboratory of Grassland Agro-ecosystem, College of Ecology, Lanzhou University, China^b Department of Population Health, London School of Hygiene and Tropical Medicine, United Kingdom^c Department of Anthropology, University College London, United Kingdom

ARTICLE INFO

Keywords:

Grandfathers
Grandmothering
Child survivorship
Allomothering
Sexual division of labour

ABSTRACT

Human parents require significant support to raise multiple, highly dependent offspring. Grandmothers are often highlighted as key allomothers (non-maternal caregivers) and their presence is frequently associated with increased child survivorship, leading some to describe humans as cooperative breeders. Equally well documented is the diversity of human childcare systems, where a wide range of individuals support parents including male kin. However, the role of grandfathers has been less well documented, and they seem to have an inconsistent relationship with child survivorship, dependent on socio-ecological factors. Here, we explore the relationship between grandparental allomothering and child survivorship using demographic and time budget data from a pastoralists community in western China. We find that under-five mortality is negatively associated with grandpaternal, but not grandmaternal, living status. Pastoralists in Maqu have recently transitioned from mobile to half-settled livelihoods in which women are more economically active than males. As a result, women's childcare workloads have decreased, while older men (who are excluded from the household economy) supervise children. Our results suggest that patterns of childcare are flexible and highlight the need to consider social and ecological factors to understand allomothering and child survival.

1. Introduction

Unlike other great apes, humans combine both fast and slow life history traits (Charnov & Berrigan, 1993; (Thompson & Sabbi, 2020) which results in humans rearing several dependent children simultaneously, requiring the assistance of others (Kramer, 2010; Sear & Coall, 2011). Previous research has highlighted the role of grandmothers as key allomothers (non-maternal caregivers) (Charnov & Berrigan, 1993; Hawkes et al., 1998; Hrdy, 2000). Grandmothers have close genetic relationships with their grandchildren ($r = 0.25$), and due to their likely (but not necessarily) post-reproductive status, avoid reproductive conflict with the mother (their daughter or daughter-in-law) (Hrdy, 2000; Mace, 2013). Further, given grandmothers postreproductive status, it is a key point of comparison to other cooperative breeding species (e.g., within the mammalian order - dogs, rodents and primates) where adults forgo their own reproduction to provide and care for others, often related, offspring (Lukas & Clutton-Brock, 2012). In Sear and Mace (2008) systematic review on kin effects on offspring survival in natural fertility populations, maternal grandmothers were most likely to

positively predict child survivorship, which has been consistently found elsewhere (Beise, 2005; Beise & Volland, 2002; Chapman, Lahdenperä, Pettay, Lynch, & Lummaa, 2021; Michalski & Shackelford, 2005; Sear, Steele, McGregor, Mace and McGregor, 2002; Strassmann & Garrard, 2011). Possible mechanisms include assistance with food production (Hawkes, O'Connell, & Blurton Jones, 1997), household tasks (Gibson & Mace, 2005), high cost direct childcare (Page et al., 2021; Scelza, 2009), and providing informational and emotional support (Scelza, 2011; Scelza & Hinde, 2019). Consequently, grandmothers have been argued to be key allomothers (Hrdy, 2009), and have predominated the literature.

The cooperative childrearing literature, however, is not limited to grandmothers and a wide range of allomothers have been demonstrated to be important in studies focusing on child outcomes and allomaternal investments (Chapman et al., 2021; Coall & Hertwig, 2010; Meehan, Helfrecht, & Quinlan, 2014; Sear & Mace, 2008a; Sheppard & Sear, 2016). Allomothering in humans cannot be captured by a singular kin category, but is a function of the socioecological context (Emmott & Page, 2019; Hassan, Lawson, Schaffnit, Urassa, & Sear, 2021; Leonetti,

* Corresponding author at: LSHTM, Kepple Street, London WC1E 7HT, United Kingdom.

E-mail address: abigail.page@lshtm.ac.uk (A.E. Page).

<https://doi.org/10.1016/j.evolhumbehav.2022.06.001>

Received 15 November 2021; Received in revised form 10 March 2022; Accepted 6 June 2022

Available online 14 June 2022

1090-5138/© 2022 The Authors. Published by Elsevier Inc. This is an open access article under the CC BY license (<http://creativecommons.org/licenses/by/4.0/>).

Nath, Hemam, & Neill, 2005; Page et al., 2021; Sear & Mace, 2008). In particular, grandmaternal care and its consequences are influenced by interpersonal and structural contexts, causal pathways and the outcomes explored (Sadruddin et al., 2019). For instance, in a matrilineal farming society in Malawi, the presence of maternal grandmothers was associated with *higher* child mortality as kin co-residence can result in household resource competition (Sear, 2008). This suggests why in patrilineal societies often (non-resident) maternal grandmothers are associated with positive outcomes (Strassmann & Garrard, 2011), and why paternal grandparents have been associated with poorer outcomes (Beise & Volland, 2002; Jamison, Cornell, Jamison, & Nakazato, 2002; Sheppard & Sear, 2016). Finally, in some hunter-gatherer groups, grandmothers appear to play a small role in childcare and provisioning (Crittenden & Marlowe, 2008; Kramer, 2010), perhaps as a product of mortality and co-residence trends (Hill & Hurtado, 2009), among other factors (Page et al., 2021).

While fewer studies have been conducted on grandpaternal effects, cross-cultural reviews tend to find that grandfathers have little, or for patrilineal grandfathers, negative associations with child outcomes (Sear & Coall, 2011; Strassmann & Garrard, 2011). In Lahdenperä, Russell, and Lummaa's (2007) review of the literature on grandfathering in 2007, the majority of ten studies included revealed null effects. Their own study in preindustrial Finland (1719–1898), in addition to historical studies in rural Germany (1700–1899, (Kemkes-grothenthal, 2005) and Japan (1671–1871, (Jamison et al., 2002)) found that grandfathers were negatively associated with child survivorship, particular paternal grandfathers. Only one study, by Beise (2005) has found a positive relationship between grandfather's presence and child survivorship in 17th century Québec, Canada, but the effect was limited to maternal grandfathers when children were aged 3–5 years. Lahdenperä et al. (2007) conclude that the evidence for a 'grandfathering effect' is lacking. Since little research has been conducted on grandfathers and survivorship since, this consensus remains largely unchanged. A few studies have explored the associations between grandfather presence and child height, finding little evidence of consistent trends in Oromo agropastoralists from Ethiopia (Gibson & Mace, 2005), Guatemala (Sheppard & Sear, 2016), South Africa (Cunningham, Elo, Herbst, & Hosegood, 2010) and Thailand (Snopkowski & Sear, 2013). Overall, the evidence suggests that grandfathers invest less in their grandchildren than grandmothers, particular in terms of direct childcare (Kramer, 2010; Page, Emmott, et al., 2021; Thomese & Liefbroer, 2013), financial help (Karimli, Ssewamala, & Ismayilova, 2012; Snopkowski & Sear, 2015) and emotional support (Danielsbacka, Tanskanen, Jokela, & Rotkirch, 2011; Pashos & McBurney, 2008; Tanskanen & Danielsbacka, 2018). Nonetheless, grandfathers do appear more important in high income populations. For instance, across ten European countries 49% of grandfathers reported providing grandchild care in the preceding 12 month period (Hank & Buber, 2009) and grandfathers are more often emotionally and actively engaged with their grandchildren (Coall & Hertwig, 2010; Coall, Hilbrand, Sear, & Hertwig, 2016).

To understand the differences between grandmaternal and grandpaternal caregiving many have explored sex differences in parental investment and reproduction (Coall & Hertwig, 2010). As there is nothing unique about paternal care in mammals – and fathers are often lumped in with other allomothers in cooperative breeding models (Woodroffe & Vincent, 1994) – then the reproductive strategies which apply to fathers can be extended to grandfathers. The dynamics of male care are complex and sex differences in caregiving are influenced by a number of factors (Sear, 2011) - all of which are subject to change over time and space - such as paternity certainty, the adult/operational sex ratio, degree of reproductive variance and intensity of sexual selection (Kokko & Jennions, 2008; Queller, 1997) and the kinship system (Wu et al., 2013). As a consequence, while mammalian males do often prioritize mating effort (Rosenbaum, Vigilant, Kuzawa, & Stoinski, 2018), this is not consistently the case and male care has evolved in a diverse number of mammalian species when payoffs are reduced for abandonment and

increasing for caregiving (Maynard Smith, 1977; Reynolds, Goodwin, & Freckleton, 2002). Such is the case in humans, in whom the high energetics costs of reproduction go beyond maternal capacity, requiring the help of others, be that from fathers, other related males (Woodroffe & Vincent, 1994) or the wide social networks which define human child-rearing (Emmott & Page, 2019; Helfrecht, Roulette, Lane, Sintayehu, & Meehan, 2020).

Fathering in humans is facultative (Rosenbaum et al., 2021). The importance of males in indirect (e.g. resource provisioning (Gettler et al., 2021; Gurven & Hill, 2010; Hill & Hurtado, 2009; Kaplan et al., 2000; Wood & Marlowe, 2013) and defence (Hill & Hurtado, 1996)) and direct investments (e.g. childcare, (Griffin & Griffin, 1992; Hewlett, 1993; Winking, Gurven, Kaplan, & Stieglitz, 2009)) is evident. It is also the case, however, that male investments are highly variable (Sear, 2011), paternal death and/or absence frequently does not impact child survival (Sear & Mace, 2008a), as other allomothers step in (Meehan et al., 2014; Winking & Koster, 2015). Male care then can be understood as a product of the socioecological context, dependent on mode of subsistence, kinship and residence structures, available mating opportunities, the mating/marriage system, and the roles of mothers and allomothers (Blurton Jones, Marlowe, Hawkes and O'Connell, 2000; Marlowe, 1999; Rosenbaum et al., 2021; Schacht, Davis, & Kramer, 2018; Sear, 2011; Sear & Mace, 2008a). For instance, in the Yucatec Maya subsistence changes altered paternal investment pay-offs and, as a result, paternal care increased (Schacht et al., 2018). Such flexibility is also recognised in the cooperative childrearing literature (Hassan et al., 2021; Page, Migliano, et al., 2021; Vallengia, 2009), highlighting who cares is sensitive to local changes in the costs and benefits of helping (Fawcett, van den Berg, Weissing, Park, & Buunk, 2010; Gurven & Schniter, 2010; Schacht et al., 2018). Over recent decades, Maqu Tibetans, the focus of this paper, have been experiencing a series of ecological and livelihood changes from their previous highly mobile pastoralist to part time settled lifestyle (Peng-Peng, Mancini, Du, & Mace, 2021) a part time settled lifestyle, altering the economic roles of men and women.

The Tibetan grazing land has supported pastoralism for thousands of years with nomads moving at different frequencies between seasons depends, depending on the availability of water and grass for livestock (Næss, 2013). In the past, a clear sexual division of labour was present, with males conducting most of the herding and herd protection work away from the homestead, and women doing most of the work at the home base, including processing animal by-products. Since the early 1990s, however, privatisation was implemented to confront the problems of grassland degradation and communal access, promoting settlement. These have influenced how resources are owned and inherited across generations, which has, in turn, influenced the sex-specific roles of Maqu herders. From 2003 onwards, Maqu herders started to move into settled houses (Levine, 2015), and increasingly expanded into the market economy (Gruschke, 2008; Gyal, 2015; Ptackova, 2012; Ptackova, 2015; Yeh, 2005). Following government policy, pastures were fenced off and leased to families as rangeland for 50 years (Wu & Richard, 1999; Yamaguchi, 2011). As a result, previous conflicts at the pastures' boarders ceased, removing males from their traditional roles of safeguarding distant livestock and homeland, reducing their contributions to the household economy (Yan, Wu, Yeshi, & Ru, 2005). In contrast, women's household tasks remained unchanged while their 'home base' herding work – planting oats to feed livestock due to limited grass access, fetching water over long distances for livestock and the household - increased as the herds were now closer to home, contained within enclosed pastures (Du & Mace, 2018; Yeh, 2003).

Maqu women appear to have become household providers in addition to their domestic tasks (Manderscheid, 2001; Tashi & Foggini, 2012). This emphasis on women's work was promoted by traditional Tibetan gender roles, as 'good housewives' are defined as "staying at home and working hard". In contrast, men are considered as "Mei Chu Xi" or "losers" if they conduct any work around the home. As a result,

men were released from traditional herding work far from home and were not expected to take on any increase in workload closer to home which fell within the 'female domain' (Gelek, 2006). Men, particularly younger men, had more free time to socialise, play basketball, gamble and consume alcohol. Older men, however, were less likely to be involved in these social activities, as gambling was more fashionable among younger men while among the more devout Buddhist older generation it had negative social and moral associations. Older men therefore, often stayed within the home, acting as allomothers when the women (both old and young) were busy. While this childcare included more active roles (such as feeding children), it frequently consisted of 'low' investment care, and could be combined with watching TV or otherwise resting. Nonetheless, this was more intensive than the alternative; when mothers and other allomothers were unavailable children were left unsupervised for long periods of time, placed into a plastic basket when they were infants or fastened by a rope to a pole when they started to walk, reducing their access to dangerous objects. While simply being proximate, or watching a child from a distance, may not take significant effort, it does ensure that the caregiver can intervene when required which can be potentially life saving (Emmott & Page, 2019; Meehan, 2005; Page, Myers, Dyble, & Migliano, 2019; Page et al., 2019)

Here, we explore the implications of these labour shifts on allomothering. Given the observed role of older males as allomothers when women had little time for childcare and few alternatives for childcare, we predicted that 1) grandfathers existence (i.e., being alive) would positively predict grandchild survivorship (ages 0–5 years) while 2) grandmothers existence would have no such effect as we hypothesised that older males had more time available for caregiving when women's economic roles were increased. In addition, we conducted an exploratory analysis in a sub-sample of the demographic dataset to discover how different individuals invested their time. While a cross-sectional study cannot speak to causality, our findings highlight the importance of grandfathers and male kin in specific socioecological contexts where stereotypical gender roles for childcaring are loosened.

2. Material and methods

2.1. Study population

This research was conducted in Maqu County, an administrative district in the southwest region of Gannan Tibetan autonomous prefecture in Gansu province, northwest part of PRC. Maqu is a part of Amdo Tibet and lies at the intersection of Qinghai, Gansu and Sichuan provinces. The average altitude of Maqu reaches '3,500-3,800 meters above sea level with an average temperature of 1.2 °C across the year and annual average rainfall of 611.9mm' (information from Maqu records). Most of the native people are herders of yaks and sheep; 89% of their income is from selling livestock directly. Due to limited availability of formal education until the late 1980s, it is extremely difficult for herders in this area to find jobs in nearby towns and most of the family income comes from selling livestock and dairy products. Prior to the late 1980's implementation of restrictive family planning policies, limiting women to three births, fertility rates were relatively high in this area, alongside child mortality. Most women gave birth at home, with relatives nearby who attended the and assisted with births. Leading causes of death included ill health, particularly gastro-intestinal disease and malnutrition (Du & Mace, 2018).

The traditional Tibetan residential system is patrilocal, with women residing with or close to her husband's family after marriage, which means paternal grandparents have closer proximity to the grandchildren than do maternal grandparents. Although many women are now marrying within the same township. The marital system used to include polygamy (both polygyny and polyandry) but now is predominately monogamous. As a consequence, while rates of paternity uncertainty were likely higher in the past, in keeping with the cross-cultural literature (Anderson 2006), levels of uncertainty are unlikely to be high.

Cohabitation and trial marriages are widely practiced, with unmarried women staying at their boyfriend's house for a period of time prior to marriage, together with the man's parents and siblings. The ability to work hard is considered a very important quality for wives; her working ability is often assessed during the trial marriage, and the relationship ends if the woman is found lacking.

The detailed demographic data we use in this study were collected in June–October 2014 and March–December 2015 in Maqu by JD with two field assistants. This research was approved by The Yhe College of Ecology Lanzhou University and University College London. Informed consent was given by all participants.

2.2. Demographic data

Data were collected in three townships across 5 villages from 768 households. In the demographic survey, we asked one adult member (usually the head of the household or the adult present at the time of the survey, $n_{\text{males}} = 573$ and $n_{\text{females}} = 195$) in each household to report information of their family structure, the residence pattern, education and whether their parents were alive. The questionnaire consisted of three parts, the first was a family census including everyone living in the same household. If a person is absent from the household, we asked where he/she was to obtain dispersal and residential information. We also asked each individual information about their parents, their birth year, age and Zodiac year (Zodiac year helps to determine the birth year of the previous generation when respondent recall was limited). The second part of the survey was about the herding system, the number of livestock, the subsistence system in the past and at present, how they evaluate the quality of the grassland change and concerns they had. The third part of the survey covered marriage, birth histories and sibling information. For this question, we asked each adult woman ($n = 1354$) and man ($n = 1535$) in separated spaces about their birth history, including date of birth for each child, and of death if they died. Descriptive data for this sample can be found in the SI (Table S2).

2.3. Time-budget data

As a post hoc analysis we collected time-budget data in 2017 in one of the villages previously involved in demographic data collection. In a small convenience sample, we asked currently available adult men ($n = 33$) and women ($n = 27$) to complete a 24-h activity recall. Older individuals were more likely to completed the recall activity because they were less busy due to reduced workloads. We informed them in advance about the time allocation data collection to improve recall. They reported all their activities, from the first thing they do when they woke-up until they went to bed. This included: farm work, housework, sleeping, leisure time, childcare and more. Owing to the compulsory education system, any children above age 5 were sent to primary school, so here we are focused on childcare of children aged 0–5 years. Descriptive data for this sample and data can be found in the SI (Table S3–11).

2.4. Statistical analysis

We used discrete-time event history analysis to test whether there was an association between grandparental status (living/dead) and under five mortality. Event history analysis models the time until an event occurs and is able to accommodate censored and time varying variables. We created time-varying categorical variables of whether grandparents were living in the same household with children. Using a model selection approach, with the R Package MuMin (Barton, 2015), we examined different candidate models each with a different combination of the grandparents from the maternal and paternal line. The best-fitting models were selected based on the Akaike's Information Criterion (see SI Table1). The dependent variable was under-five survivorship. Control variables included: child's gender; the child's birth

cohort (as during the 1990's the three-child policy was implemented, restricting births and thus limiting the number of grandchildren. Prior to this period, grandparental effects may have been diluted among more grandchildren); mother's age at birth; and household wealth (captured in count of livestock). We were unable to control for grandparental age as this accurate aging for older individuals was not available. We right censored children at age five five, when child survival is most dependent on caregiving, and prior to formal education.

We conducted post hoc permutation tests to explore systematic differences in time allocation between men, women, parents and grandparents. In the permutation tests 100,000 simulations shuffled the existing data randomly to produce 100,000 simulated mean differences. The *p*-value is then produced based on the number of times out of 100,000 that the simulated mean difference was either higher, lower or equal to the mean difference of the actual sample.

All code and data for this manuscript can be found on the OSF project page: https://osf.io/bh9ya/?view_only=6d201b5a998c4de4820db99e014b8967.

3. Results

3.1. Descriptives

In the demographic sample, 2886 children were born, of which 46% (*n* = 1353) were girls. Mothers had a mean age of first birth of 24.96 years (*SD* = 5.95) and had on average 3.5 children. Of these children, 46% had a living maternal grandmother (MGM), compared to 59% for maternal grandfather (MGF) and 55% and 70% for paternal grandmother (PGM) and paternal grandfather (PGF), respectively.

3.2. Survival models by grandparental status

In model selection, paternal grandparents were consistently selected in the best model of child survival. The best fit cox regression model (SI Table 1, Figs. 1 & 2) showed that child mortality was predicted by mother's age of giving birth (HR: 0.96, *p* < 0.001, 95% CI [0.94, 0.98]), and birth order; third born children had a 32% higher hazard of dying prior to age 5 (*p* = 0.05, 95% CI [1.00, 1.75]). In line with our previous work (Du & Mace, 2018) boys were also at an increased hazard of death (HR = 1.33, 95% CI [1.09–1.62], *p* ≤ 0.001). Paternal grandfathers, followed by maternal grandfathers had the strongest association with grandchild survivorship. Paternal grandfathers, when alive, were associated with a 34% decrease in hazard of under-five mortality (*p* < 0.001, 95% CI [0.52, 0.83]) compared to when paternal grandfathers had died. Similarly, maternal grandfathers were associated with a 24% decreased in hazard of death (*p* = 0.02, 95% CI [0.60, 0.96]).

In comparison, the results for grandmothers were less consistent. Paternal grandmothers' presence had no relationship with grandchild survivorship (*p* = 0.901). Furthermore, maternal grandmothers were, insignificantly, negatively associated with child survivorship (HR = 1.25, *p* = 0.061, 95% CI [0.99, 1.58]), as highlighted by the overlapping lines in the Fig. 2 for MGM.

3.3. Time-budget data

3.3.1. Time budgets by age and sex

There were 33 males (mean age = 39.22, *SD* = 14.27) and 27 females (mean age = 37.79, *SD* = 12.85) in the time budget sample. Daily activities were divided into four main categories: herding related labour, housework, childcare and leisure activities (Fig. 3).

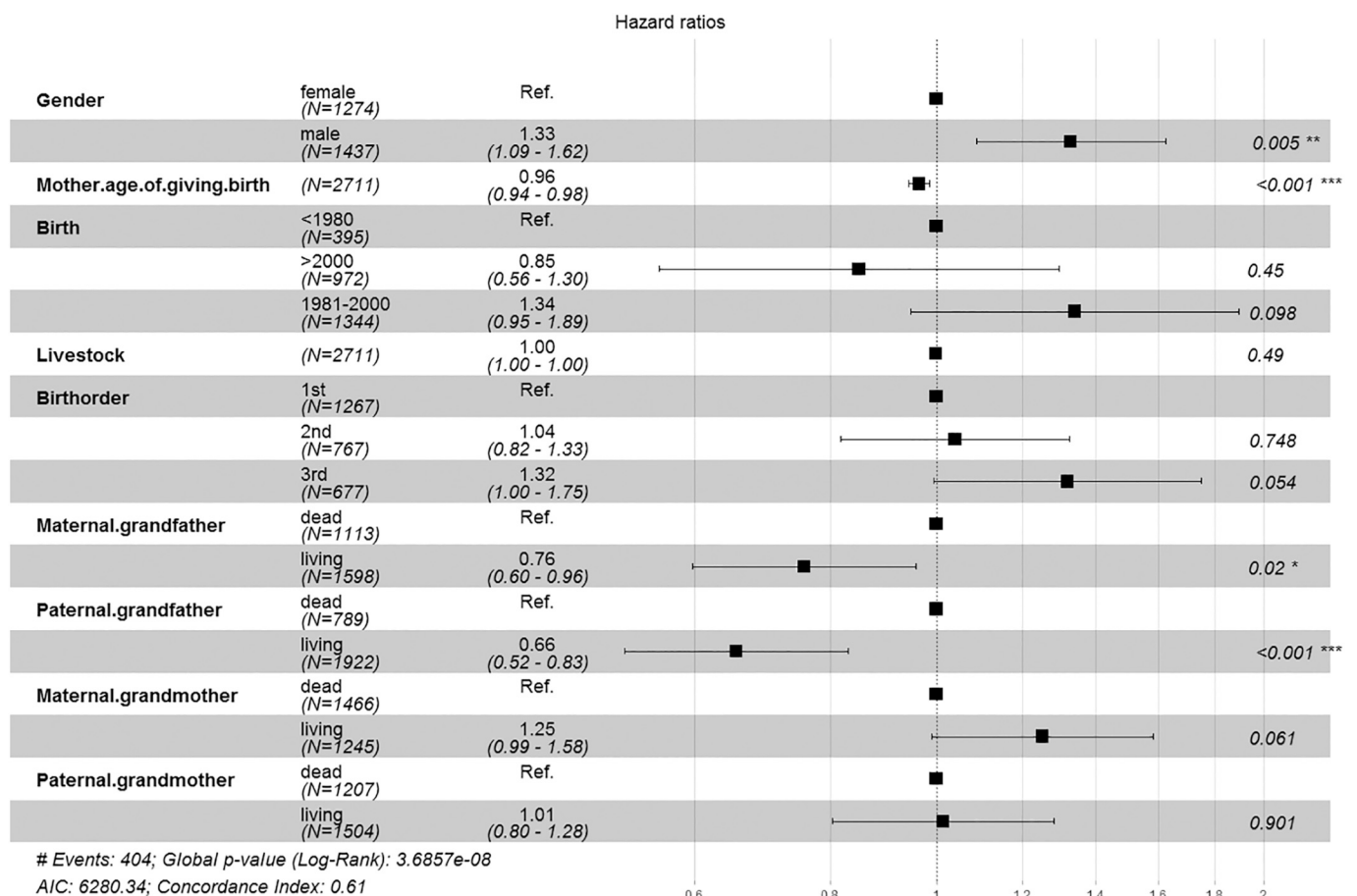


Fig. 1. Forest plot showing the hazard ratio and 95% confidence intervals from the full model. A lower hazard ratio indicates a decreased risk of child mortality.

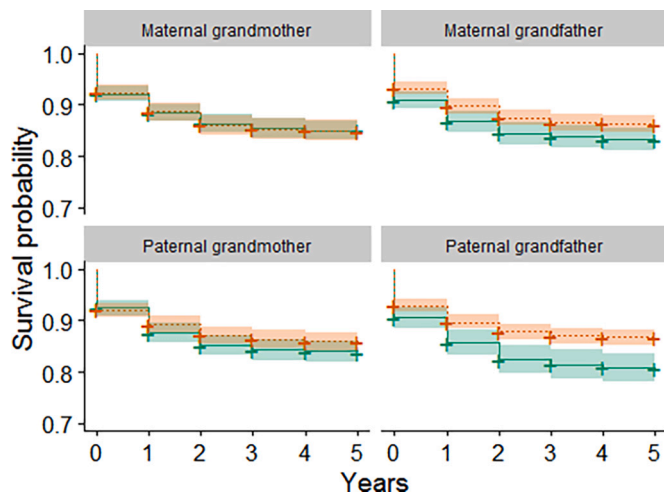


Fig. 2. Survivalship curves for children aged 0–5 years by grandparental status. Living (orange dashed line) and dead (green solid line). The shaded areas represent 95% CI. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

In the permutation tests (SI Tables 4–11), women did more herding work (women = 0.34 h (SD = 0.24) versus men = 0.24 h (SD = 0.21), $p = 0.050$) and housework (women = 0.14 h (SD = 0.12) versus men = 0.04 h (SD = 0.070), $p < 0.001$) than men. However, women spent less time in childcare activities (women = 0.28 h (SD = 0.16) versus men = 0.36 h (SD = 0.22), $p = 0.044$) and leisure activities (women = 0.11 h (SD = 0.20) versus men = 0.19 h (SD = 0.21), $p = 0.079$). Individuals aged 25 and under conducted less childcare than older individuals ($<25 = 0.23$ h (SD = 0.16) versus $>25 = 0.36$ h (SD = 0.20), $p = 0.011$), (we set a threshold of 25 because the average age for giving birth is 24.96 (SD = 5.95) while young people did more herding work than the older generation ($\leq 25 = 0.37$ h (SD = 0.2121) versus $>25 = 0.26$ h (SD = 0.23), $p = 0.045$), indicating the importance of age and sex in structuring activities.

3.3.2. Time budgets by parents and grandparents

Breaking the sample into parents ($n = 28$) and grandparents ($n = 32$, Fig. 3), it appeared that mothers and fathers reported conducting similar amounts of childcare tasks (mother = 0.31 h (SD = 0.16) vs. father = 0.26 h (SD = 0.18), $p = 0.268$), as well as similar levels of engagement in herding (mothers = 0.37 h (SD = 0.20) vs. fathers = 0.33 h (SD = 0.22), $p = 0.357$). Fathers tended to spend more time in leisure than mothers (mothers = 0.10 h (SD = 0.17) vs. fathers = 0.19 h (SD = 0.19), $p = 0.145$) perhaps related to mothers increased time allocation to housework (mothers = 0.12 h (SD = 0.10) vs. fathers = 0.03 h (SD = 0.05) $p = 0.017$).

The comparisons between grandparents revealed much more stark differences in the division of labour. Grandmothers spent more time in herding-related housework (GM = 0.32 h (SD = 0.28) vs. GF = 0.17 h (SD = 0.19), $p = 0.033$) and conducted more household tasks (GM = 0.16 h (SD = 0.14) vs. GF = 0.05 h (SD = 0.08), $p = 0.001$) than grandfathers. In contrast, grandfathers spent more time in leisure activities (GM = 0.11 h (SD = 0.24) vs. GF = 0.18 h (SD = 0.22), $p = 0.177$), although the evidence is not strong due to large standard deviations. However, compared to grandmothers, grandfathers reported spending 44.9% more time looking after their grandchildren (GM = 0.25 h (SD = 0.16) vs. GF = 0.45 h (SD = 0.22), $p = 0.001$). It is notable from Fig. 3 that grandfathers, on average, conducted more childcare tasks than mothers and fathers. While the grandparental sample becomes extremely small when broken by lineage ($n_{MGF} = 3$ and $n_{PGF} = 15$), limiting our inferences, there was no significant difference between maternal and paternal grandfathers in terms of childcare (MGF = 0.38 h

(SD = 0.69) vs. PGF = 0.46 h (SD = 0.24), $p = 0.279$) and other activities (see SI Tables 4–11). Nonetheless, paternal grandfathers spent a significant proportion of activities in childcare, more than any other individual.

4. Discussion

Our findings presented here on grandparental effects on child survivorship demonstrate a pattern in opposition to the differential grandparental investment literature (Coall & Hertwig, 2010). As predicted based on gendered divisions of labour among the herders in Maqu, we found that grandfather's existence was associated with a 34–24% reduction in child mortality from ages 0–5 years. This was predicted due to observations of lack of older male involvement in food production and increased involvement in childcare. Increasing childcare due to decreased economic engagement has been found in a number of other studies, underlining the need to consider the opportunity costs of male care (Danielsbacka et al., 2011; Danielsbacka & Tanskanen, 2012; Hank & Buber, 2009; Rosenbaum et al., 2021). Nevertheless, grandfather effects are generally rare and inconsistent; Sear and Mace (2008) review found that in 83% of studies maternal grandfathers had no effect on child survivorship, while in 25% of cases paternal grandfathers were associated with decreased grandchild survivorship, and 50% reported no relationships. Nonetheless reviews in high-income contexts do find grandpaternal care to be positively related to a child's mental and physical development, demonstrating that grandfathers have important roles to play in specific contexts (Coall et al., 2016; Coall & Hertwig, 2010).

Many studies rely on correlations between child mortality and grandparental status (Coall & Hertwig, 2010; Gurven & Schniter, 2010) and, as a result, it is easy to question unusual results as spurious. To this end we conducted a time allocation survey to uncover potential mechanisms. This indicated that, unlike other studies (Gibson & Mace, 2005; Kramer, 2010; Page, Emmott, et al., 2021; Sheppard & Sear, 2016), grandfathers were conducting significantly more childcare than grandmothers, as well as mothers and fathers, while the reverse was true for herding. This unusual trend suggests a mechanism; mothers with access to grandfathers were able to reduce childcare investment, and devote more time to herding increasing the household resources to the benefit of children. Somewhat similar results have been found in the Agta foragers of the Philippines where grandpaternal childcare was associated with a reduction in high-investment maternal childcare (Page, Emmott, et al., 2021). It is interesting to note that in both these populations, whether due to increased female workloads or higher reproductive costs, have fewer grandmothers alive than grandfathers, contra commonly documented trends (Coall & Hertwig, 2010; Page, Emmott, et al., 2021; Page, Myers, et al., 2019). Therefore, wider demographics may also influence who is available to help. Overall, this suggests that grandfathers' investments may reduce maternal childcare workloads, allowing her to re-invest this time and energy into alternative activities. Or equally possible is that mothers care remains unchanged, but grandfathers provide higher quality childcare resulting in improved survivorship. Further study is required to understand these dynamics in greater depth in a larger sample, however these early results are both consistent and strong.

While our findings are out of step with the wider literature, they are in keeping with our predictions given recent socioecological changes experienced by herders in Maqu. Pirie (2005) described the unequal working allocation in Maqu, highlighting the high female workload in the family (regardless of age), due to minimised male herding (Pirie, 2005). Our results similarly demonstrate that women were more heavily involved in herding and household labour than men. This finding is surprising as cross-culturally mothers tend to conduct the highest proportion of childcare tasks, easily overtaking fathers, grandmothers and grandfathers (Helfrecht et al., 2020; Konner, 2018; Kramer, 2010; Meehan & Hawks, 2013). The sexual division of labour literature posits

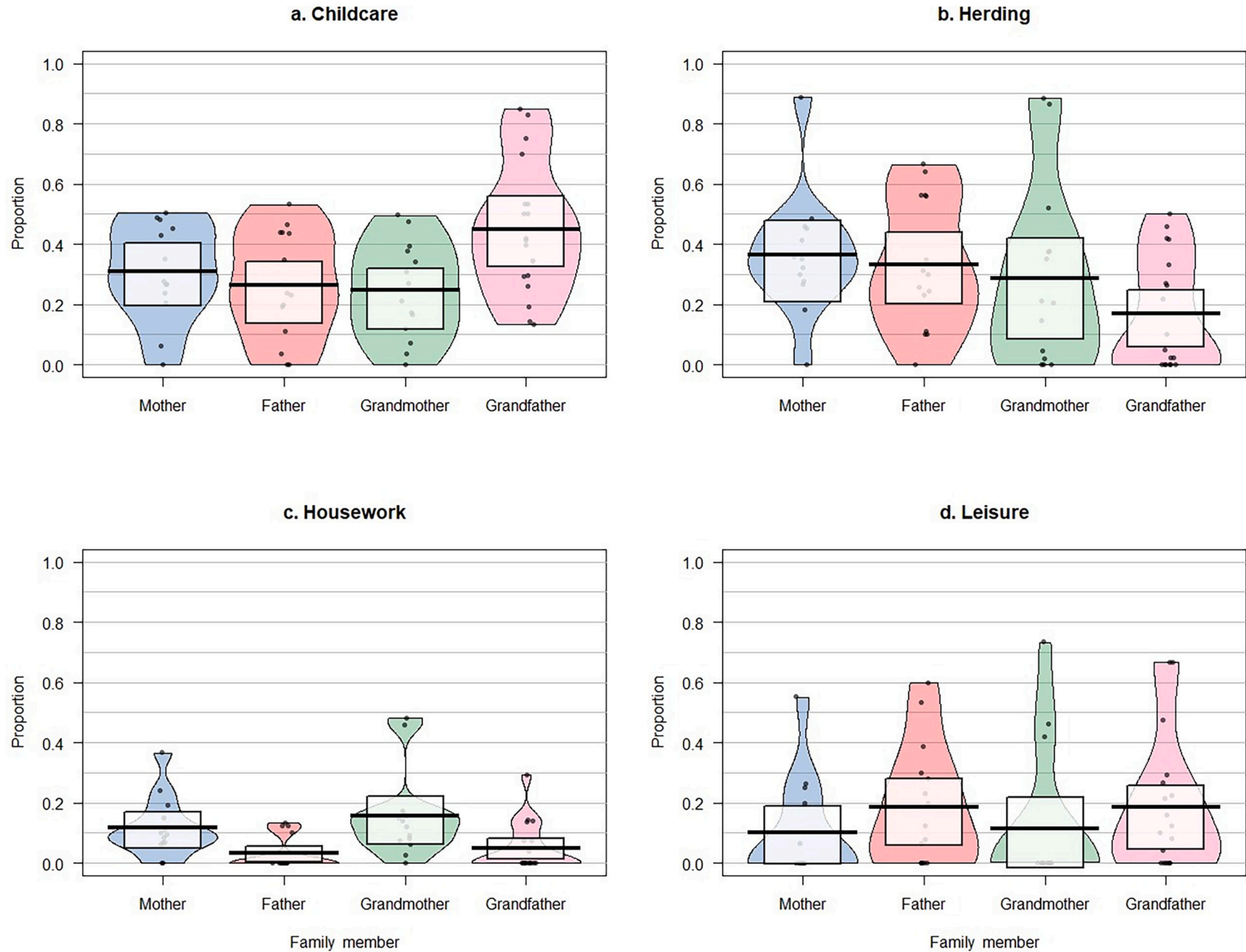


Fig. 3. Plots showing the proportion of time spent in Childcare(a), Herding(b), Housework(c) and Leisure activities(d), divided by four different family members: Mother, Father, Grandmother, Grandfather.

that women specialise in childrearing while men specialise in provisioning (Gurven & Hill, 2009; Lovejoy, 1981; Marlowe, 2003; Sear, 2021), as much economic activity is 'incompatible' with motherhood (Hames, 1988; Hurtado, Hawkes, Hill, & Kaplan, 1985; Scelza & Bliege Bird, 2008). As mothers gestate and lactate they are 'primed' to engage in childcare tasks, while other roles have increased opportunity costs (Becker, 1985; Gurven & Hill, 2009; Gurven, Winking, Kaplan, von Rueden, & McAllister, 2009; Starkweather, Shenk, & McElreath, 2020 for a review). As specialisation can be more efficient, fathers engage in other complementarily tasks, such as food production, which are less compatible with direct childcare (Gurven et al., 2009). Yet, as noted by a large number of behavioural ecologists, there is significant variability in gendered roles and gender role reversals occur, like we see here, due to socioecological changes which alter the costs and benefits of reproductive strategies (Henshaw, Fromhage, & Jones, 2019; Mattison et al., 2021; Starkweather et al., 2020). For instance, among the Shodagor fisher-traders from Bangladesh mothers were able to engage in more risky and less childcare compatible trading when they had access to allomothers and a husband able to provide childcare (Starkweather et al., 2020). This reveals that universal concepts of the sexual division of labour overlooks the variability in gender roles and context-specific solutions for household labour allocation (Henshaw et al., 2019; Mattison et al., 2021; Starkweather et al., 2020).

Surprisingly, given the size of the literature on the matrilineal bias (Perry & Daly, 2017) in child investments, in Maqu we found the strongest evidence for paternal effects. While we made no predictions based on lineage, it is of interest to reflect on this finding and the role of proximity to aiding direct caregiving like childcare. The local resource competition hypothesis states that close proximity with kin increases resource competition. Thus, in patrilocal settings patrilineal grandparents are more likely a drain on household resources, resulting in negative outcomes for grandchildren (Strassmann & Garrard, 2011). In Maqu, however, patrilocal residence may facilitate grandpaternal childcare, which we suspect is promoting child survivorship. Similarly, in rural Greece Pashos (2000) found that paternal grandparents were frequently reported to be more caring than maternal grandparents, while in urban and western settings it is consistently the maternal grandparents (Bishop, Meyer, Schmidt, & Gray, 2009; Danielsbacka et al., 2011; Huber & Breedlove, 2007; Pollet, Nelissen, & Nettle, 2009; Waynforth, 2012). Close proximity reduces the costs of helping, as well as increasing trust between kin (Pashos, 2000). As argued by Chapman et al. (2021), it is important to look beyond superficial similarities between societies (such as resident systems) and consider how the interactions between mating and residence patterns, subsistence modes, sexual divisions of labour and religion influence the relationship between lineage and grandchild survivorship. While the relationship between paternal grandfathers and child survivorship was the strongest, it is important to underline that maternal grandfathers were also positively associated with child survival, suggesting that, in Maqu, sex-effects related to household economics may be more important than lineage effects. In line with a sex-specific effect, while the results for grandmothers were less consistent and the 95% confidence intervals spanned 1, it does appear that grandmothers were negatively associated with child survivorship, in opposition to much of the grandparental investment literature (Sear & Mace, 2008; Strassmann & Garrard, 2011).

Key limitations to this study are similar to other demographic investigations into grandparental investment and child survivorship. Firstly, this is a cross-sectional study and we cannot speak to causality. Phenotypic correlations between grandparents, parents and children are expected, as long-lived grandparents are more likely to be wealthier, which is passed on to their children and grandchildren (Coall & Hertwig, 2010). However, as pointed out by Sear and Mace (2008), if phenotypic correlations were driving the relationship, we would not expect such differences between specific grandparents. Nonetheless, we agree that it is essential to understand mechanism (Gurven & Schniter, 2010; Page, Emmott, et al., 2021) and to this end conducted the exploratory time

allocation study. This was unfortunately small in size (in terms of number of individuals and time span), and left us unable to speak with confidence about differential investment by lineage. Further work should now be conducted to explore if grandfathers are more likely to conduct childcare tasks, as compared to other allomothers.

5. Conclusion

Maqu pastoralists from western China we have demonstrated that child survivorship to age five is positively predicted by paternal grandfather's existence, an uncommon finding. We propose that this is the result of recent socioeconomic changes as the Amdo Tibetans transitioned from mobile to half-settled livelihoods where women are more economically active than men. Contra to the common portrayals of the sexual division of labour, we find that in Maqu, mothers do not spend more time in childcare than fathers, and instead are heavily involved in the household and herding economy. It seems that grandfathers pick up this additional childcare labour, suggesting a pathway between grandpaternal existence and child survivorship. Multiple studies have now highlighted that there are no universals in human childrearing - beyond the fact that mothers are not alone in this task - and as a result we should not over focus on one specific allomother to the exclusion of others. Who cares, and the consequences of this care, is a function of the socioecological context which impacts the opportunity costs and benefits associated with one investment type over another. To fully understand human childcare, we should further investigate how these factors impact allomothering, underscoring the importance of human flexibility and diversity.

Funding

R.M is funded by the European Research Council and A.E.P received funding from the MRC & DFID (MR/P014216/1).

Data sharing statement

The data associated with this research are available at OSF project page: https://osf.io/bh9ya/?view_only=6d201b5a998c4de4820db99e014b8967

Declaration of Competing Interest

Declaration of Competing Interest

Acknowledgements

We would like to thank Bai Pengpeng, Jiu Cili, Gong Baocao, and Zhaxi for help in collecting data and the Human Evolutionary Ecology Group in UCL and Evolutionary Demography Group at LSHTM for their, as always, invaluable feedback.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.evolhumbehav.2022.06.001>.

References

- Anderson, K. G. (2006). How well does paternity confidence match actual paternity? Evidence from worldwide nonpaternity rates. *Current Anthropology*, 47, 513–520.
- Barton, K. (2015). *Multi-model inference*.
- Becker, G. S. (1985). Human capital, effort, and the sexual division of labor. *Journal of Labor Economics*, 3, S33–S58. <https://doi.org/10.1086/298075>
- Beise, J. (2005). The helping grandmother and the helpful grandmother: The role of maternal and paternal grandmothers in child mortality in the 17th and 18th century population of French settlers in Quebec, Canada. In E. Voland, A. Chasiotis, & W. Schiefelhovel (Eds.), *Grandmotherhood: The evolutionary significance of the second half of the female life* (pp. 215–238). New Brunswick: Rutgers University Press.

- Beise, J., & Voland, E. (2002). A multilevel event history analysis of the effects of grandmothers on child mortality in a historical German population. *Demographic Research*. <https://doi.org/10.4054/DemRes.2002.7.13>
- Bishop, D. I., Meyer, B. C., Schmidt, T. M., & Gray, B. R. (2009). Differential investment behavior between grandparents and grandchildren: The role of paternity uncertainty. *Evolutionary Psychology*, 7, 66–77. <https://doi.org/10.1177/147470490900700109>
- Blurton Jones, N. G., Marlowe, F. W., Hawkes, K., & O'Connell, J. F. (2000). Paternal investment and hunter-gatherer divorce rate. In L. Cronk, N. A. Chagnon, & W. Irons (Eds.), *Adaptation and human behavior*. New York: Aldine de Gruyter.
- Chapman, S. N., Lahdenperä, M., Pettay, J. E., Lynch, R. F., & Lummaa, V. (2021). Offspring fertility and grandchild survival enhanced by maternal grandmothers in a pre-industrial human society. *Scientific Reports*, 11, 1–11. <https://doi.org/10.1038/s41598-021-83353-3>
- Charnov, E. L., & Berrigan, D. (1993). Why do female primates have such long lifespans and so few babies? Or life in the slow lane. *Evolutionary Anthropology*, 1, 191–194. <https://doi.org/10.1002/evan.1360010604>
- Coall, D. A., Hilbrand, S., Sear, R., & Hertzwig, R. (2016). A new niche? The theory of grandfather involvement. In A. Buchanan, & A. Rotkirch (Eds.), *Grandfathers* (pp. 21–44). London: Palgrave macmillan.
- Coall, D. A., & Hertzwig, R. (2010). Grandparental investment: Past, present, and future. *The Behavioral and Brain Sciences*, 33, 1–19. <https://doi.org/10.1017/S0140525X09991105>
- Crittenden, A. N., & Marlowe, F. W. (2008). Allomaternal care among the Hadza of Tanzania. *Human Nature*, 19, 249–262. <https://doi.org/10.1007/s12110-008-9043-3>
- Cunningham, S. A., Elo, I. T., Herbst, K., & Hosegood, V. (2010). Prenatal development in rural South Africa: Relationship between birth weight and access to fathers and grandparents. *Population Studies (NY)*, 64, 229–246. <https://doi.org/10.1080/00324728.2010.510201>
- Danielsbacka, M., & Tanskanen, A. O. (2012). Adolescent grandchildren's perceptions of grandparents' involvement in UK: An interpretation from life course and evolutionary theory perspective. *European Journal of Ageing*, 9, 329–341. <https://doi.org/10.1007/s10433-012-0240-x>
- Danielsbacka, M., Tanskanen, A. O., Jokela, M., & Rotkirch, A. (2011). Grandparental child care in Europe: Evidence for preferential investment in more certain kin. *Evolutionary Psychology*, 9, 3–24.
- Du, J., & Mace, R. (2018). Parental investment in Tibetan populations does not reflect stated cultural norms. *Behavioral Ecology*, 29, 106–116. <https://doi.org/10.1093/beheco/axr134>
- Emmott, E. H., & Page, A. E. (2019). Alloparenting. In T. K. Shackelford, & V. A. Weekes-Shackelford (Eds.), *Encyclopedia of evolutionary psychological science* (pp. 1–14). Cham: Springer International Publishing. https://doi.org/10.1007/978-3-319-16999-6_2253-1
- Fawcett, T. W., van den Berg, P., Weissing, F. J., Park, J. H., & Buunk, A. P. (2010). Intergenerational conflict over grandparental investment. *The Behavioral and Brain Sciences*, 33, 1–59.
- Gettler, L. T., Lew-levy, S., Sarma, M. S., Miegakanda, V., Doherty, M., Meyer, J. S., & Boyette, A. H. (2021). Children's fingernail cortisol among BaYaka foragers of the Congo Basin: Associations with fathers' roles (p. 376). *Sci: Philos. Trans. R. Soc. B Biol.*
- Gibson, M. A., & Mace, R. (2005). Helpful grandmothers in rural Ethiopia: A study of the effect of kin on child survival and growth. *Evolution and Human Behavior*, 26, 469–482. <https://doi.org/10.1016/j.evolhumbehav.2005.03.004>
- Gelek, L. (2006). Anthropological Field Survey on Basic Education Development in the Tibetan Nomadic Community of Maqu, Gansu. *China. Asian Ethnicity*, 7, 37–41.
- Griffin, P. B., & Griffin, M. B. (1992). Fathers and childcare among the Cagayan Agta. In B. S. Hewlett (Ed.), *Father-child relations: Cultural and biosocial contexts* (pp. 297–320). New Brunswick: Transaction Publishers.
- Gruschke, A. (2008). Nomads without pastures? Globalization, regionalization, and livelihood security of nomads and former nomads in northern Khams. *Journal of the International Association of Tibetan Studies*, 1–40.
- Gurven, M., & Hill, K. (2009). Why do men hunt? *Current Anthropology*, 50, 51–74. <https://doi.org/10.1086/595620>
- Gurven, M., & Hill, K. (2010). Moving beyond stereotypes of men's foraging goals. *Current Anthropology*, 51, 265–267. <https://doi.org/10.1086/651291>
- Gurven, M., Winking, J., Kaplan, H., von Rueden, C., & McAllister, L. (2009). A bioeconomic approach to marriage and the sexual division of labor. *Human Nature*. <https://doi.org/10.1007/s12110-009-9062-8>
- Gurven, M. D., & Schniter, E. (2010). An evolutionary perspective can help unify disparate accounts of grandparental investment. *The Behavioral and Brain Sciences*, 33, 1–59.
- Gyal, H. (2015). The politics of standardising and subordinating subjects: The nomadic settlement project in Tibetan areas of Amdo. *Nomadic Peoples*, 19, 241–260. <https://doi.org/10.3197/np.2015.190206>
- Hames, R. (1988). The allocation of parental care among the Ye'kawana. In L. Betzig, M. Borgerhoff Mulder, & P. Turke (Eds.), *Human reproductive behavior: A Darwinian perspective* (pp. 237–251). Cambridge: Cambridge University Press.
- Hank, K., & Buber, I. (2009). Grandparents caring for their grandchildren: Findings from the 2004 survey of health, ageing, and retirement in Europe. *Journal of Family Issues*, 30, 53–73.
- Hassan, A., Lawson, D. W., Schaffnit, S. B., Urassa, M., & Sear, R. (2021). Childcare in transition: Evidence that patterns of childcare differ by degree of market integration in North-Western Tanzania. *OSF Prepr.*, 1–41. <https://doi.org/10.31219/osf.io/gtc6k>
- Hawkes, K., O'Connell, J. F., & Blurton Jones, N. G. (1997). Hadza women's time allocation, offspring provisioning and the evolution of long postmenopausal life spans. *Current Anthropology*, 38, 551–577.
- Hawkes, K., O'Connell, J. F., Jones, N. G. B., Alvarez, H., Charnov, E. L., Blurton Jones, N. G., ... Charnov, E. L. (1998). Grandmothering, menopause, and the evolution of human life histories. *Proceedings of the National Academy of Sciences*, 95, 1336–1339.
- Helfrecht, C., Roulette, J. W., Lane, A., Sintayehu, B., & Meehan, C. L. (2020). Life history and socioecology of infancy. *American Journal of Physical Anthropology*, 1–11. <https://doi.org/10.1002/ajpa.24145>
- Henshaw, J. M., Fromhage, L., & Jones, A. G. (2019). Sex roles and the evolution of parental care specialization. *Proceedings of the Royal Society B: Biological Sciences*, 286. <https://doi.org/10.1098/rspb.2019.1312>
- Hewlett, B. S. (1993). *Intimate fathers: The nature and context of Aka Pygmy paternal infant care*. Michigan: University of Michigan Press.
- Hill, K., & Hurtado, A. M. (1996). *Aché life history: The ecology and demography of a foraging people*. New Haven: Aldine de Gruyter. [https://doi.org/10.1016/S1090-5138\(97\)00035-4](https://doi.org/10.1016/S1090-5138(97)00035-4)
- Hill, K., & Hurtado, A. M. (2009). Cooperative breeding in South American hunter-gatherers. *Proceedings of the Biological Sciences*, 276, 3863–3870. <https://doi.org/10.1098/rspb.2009.1061>
- Hrdy, S. (2009). *Mothers and others*. Cambridge: Harvard UP.
- Hrdy, S. B. (2000). *Mother nature: Maternal instincts and the shaping of the species*. London: Vintage.
- Huber, B. R., & Breedlove, W. L. (2007). Evolutionary theory, kinship, and childbirth in cross-cultural perspective. *Cross-Cultural Research*, 41, 196–219. <https://doi.org/10.1177/1069397106298261>
- Hurtado, A. M., Hawkes, K., Hill, K., & Kaplan, H. (1985). Female subsistence strategies among Ache hunter-gatherers of Eastern Paraguay. *Human Ecology*, 13, 1–28. <https://doi.org/10.1007/BF01531086>
- Jamison, C. S., Cornell, L. L., Jamison, P. L., & Nakazato, H. (2002). Are all grandmothers equal? A review and a preliminary test of the 'grandmother hypothesis' in Tokugawa Japan. *American Journal of Physical Anthropology*, 119, 67–76. <https://doi.org/10.1002/ajpa.10070>
- Kaplan, H., Hill, K. I. M., Lancaster, J., Hurtado, M., Hill, J., Lancaster, J., ... Hurtado, A. M. (2000). A theory of human life history evolution: Diet, intelligence, and longevity. *Evolutionary Anthropology*, 9, 156–185. [https://doi.org/10.1002/1520-6505\(2000\)9:4<156::AID-EVAN5>3.3.CO;2-Z](https://doi.org/10.1002/1520-6505(2000)9:4<156::AID-EVAN5>3.3.CO;2-Z)
- Karimli, L., Ssewamala, F. M., & Ismayilova, L. (2012). Extended families and perceived caregiver support to AIDS orphans in Rakai district of Uganda. *Children and Youth Services Review*, 34, 1351–1358. <https://doi.org/10.1016/j.childyouth.2012.03.015>
- Kemkes-grothenthaef, A. (2005). Of grandmothers, grandfathers and wicked step-grandparents. Differential impact of paternal grandparents on grandoffspring survival. *Historical Social Research*, 30, 219–239.
- Kokko, H., & Jennions, M. D. (2008). Parental investment, sexual selection and sex ratios. *Journal of Evolutionary Biology*, 21, 919–948.
- Konner, M. (2018). Nonmaternal care: A half-century of research. *Physiology & Behavior*, 193, 179–186. <https://doi.org/10.1016/j.physbeh.2018.03.025>
- Kramer, K. L. (2010). Cooperative breeding and its significance to the demographic success of humans. *Annual Review of Anthropology*, 39, 417–436. <https://doi.org/10.1146/annurev.anthro.012809.105054>
- Lahdenperä, M., Russell, A. F., & Lummaa, V. (2007). Selection for long lifespan in men: Benefits of grandfathering? *Proceedings of the Royal Society B: Biological Sciences*, 274, 2437–2444. <https://doi.org/10.1098/rspb.2007.0688>
- Leonetti, D. L., Nath, D. C., Hemam, N. S., & Neill, D. B. (2005). *Kinship organization and the impact of grandmothers on reproductive success among the matrilineal khasi and patrilineal Bengali of Northeast India, grandmotherhood the evolutionary significance of the second half of female life*. Rutgers University Press, New Brunswick.
- Levine, N. E. (2015). Transforming inequality: Eastern Tibetan pastoralists from 1955 to the present. *Nomadic Peoples*, 19, 164–188. <https://doi.org/10.3197/np.2015.190202>
- Lovejoy, C. O. (1981). The origin of man. *Science*, 211, 341–350.
- Lukas, D., & Clutton-Brock, T. (2012). Life histories and the evolution of cooperative breeding in mammals. *Proceedings of the Royal Society B: Biological Sciences*, 279, 4065–4070. <https://doi.org/10.1098/rspb.2012.1433>
- Mace, R. (2013). Cooperation and conflict between women in the family. *Evolutionary Anthropology*, 22, 251–258. <https://doi.org/10.1002/evan.21374>
- Manderscheid, A. (2001). Decline and re-emergence of nomadism: Tibetan pastoralists revive a nomadic way of life and production. *GeoJournal*, 53, 173–182. <https://doi.org/10.1023/A:1015728719305>
- Marlowe, F. (1999). Male care and mating effort among Hadza foragers. *Behavioral Ecology and Sociobiology*, 46, 57–64. <https://doi.org/10.1007/s002650050592>
- Marlowe, F. W. (2003). A critical period for provisioning by Hadza men. Implications for pair bonding. *Evolution and Human Behavior*, 24, 217–229. [https://doi.org/10.1016/S1090-5138\(03\)00014-X](https://doi.org/10.1016/S1090-5138(03)00014-X)
- Mattison, S. M., MacLaren, N. G., Liu, R., Reynolds, A. Z., Baca, G. D., Mattison, P. M., ... Wander, K. (2021). Gender differences in social networks based on prevailing kinship norms in the Mosuo of China. *Social Science*, 10, 253. <https://doi.org/10.3390/socsci10070253>
- Maynard Smith, J. (1977). Parental investment: A prospective analysis. *Animal Behaviour*, 25, 1–9.
- Meehan, C. L. (2005). The effects of residential locality on parental and alloparental investment among the Aka foragers of the central African Republic. *Human Nature*, 16, 58–80. <https://doi.org/10.1007/s12110-005-1007-2>
- Meehan, C. L., & Hawks, S. (2013). Cooperative breeding and attachment among the Aka foragers. In N. Quinn, & J. M. Mageo (Eds.), *Attachment reconsidered: Cultural perspectives on a Western theory* (pp. 85–113). New York: Palgrave macmillan.

- Meehan, C. L., Helfrecht, C., & Quinlan, R. J. (2014). Cooperative breeding and Aka children's nutritional status: Is flexibility key? *American Journal of Physical Anthropology*, 153, 513–525. <https://doi.org/10.1002/ajpa.22415>
- Michalski, R. L., & Shackelford, T. K. (2005). Grandparental investment as a function of relational uncertainty and emotional closeness with parents. *Human Nature*, 16, 293–305. <https://doi.org/10.1007/s12110-005-1012-5>
- Næss, M. W. (2013). Climate change, risk management and the end of nomadic pastoralism. *International Journal of Sustainable Development & World Ecology*, 20, 123–133. <https://doi.org/10.1080/13504509.2013.779615>
- Page, A. E., Emmott, E. H., Dyble, M., Smith, D., Chaudhary, N., Viguier, S., & Migliano, A. B. (2021). Children are important too: Juvenile playgroups and maternal childcare in a foraging population, the Agta. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 376, 20200026. <https://doi.org/10.1098/rstb.2020.0026>
- Page, A. E., Myers, S., Dyble, M., & Migliano, A. B. (2019). Why so many Agta boys? Explaining 'extreme' sex ratios in Philippine foragers. *Evolutionary Human Sciences*, 1, Article e5. <https://doi.org/10.1017/ehs.2019.4>
- Page, A. E., Thomas, M. G., Smith, D., Dyble, M., Viguier, S., Chaudhary, N., Salali, G. D., Thompson, J., Mace, R., & Migliano, A. B. (2019). Testing adaptive hypotheses of alloparenting in Agta foragers. *Nature Human Behaviour*. <https://doi.org/10.1038/s41562-019-0679-2>
- Page, A. E., Migliano, A., Smith, D., Viguier, S., Dyble, M., & Hassan, A. (2021). Sedentarisation and maternal childcare networks: Role of risk, gender and demography. *Philosophical Transactions of the Royal Society B: Biological Sciences*. In press.
- Pashos, A. (2000). Does paternal uncertainty explain discriminative grandparental solicitude? A cross-cultural study in Greece and Germany. *Evolution and Human Behavior*, 21, 97–109. [https://doi.org/10.1016/S1090-5138\(99\)00030-6](https://doi.org/10.1016/S1090-5138(99)00030-6)
- Pashos, A., & McBurney, D. H. (2008). Kin relationships and the caregiving biases of grandparents, aunts, and uncles: A two-generational questionnaire study. *Human Nature*, 19, 311–330. <https://doi.org/10.1007/s12110-008-9046-0>
- Peng-Peng, B., Mancini, M., Du, J., & Mace, R. (2021). Matching local knowledge and environmental change with policy changes in rangeland tenure. *Human Ecology*, 49, 341–352. <https://doi.org/10.1007/s10745-021-00235-y>
- Perry, G., & Daly, M. (2017). A model explaining the matrilineal bias in alloparental investment. *Proceedings of the National Academy of Sciences of the United States of America*, 114, 9290–9295. <https://doi.org/10.1073/pnas.1705910114>
- Pirire, F. (2005). Segmentation within the state: The reconfiguration of Tibetan tribes in China's reform period. *Nomadic Peoples*, 9, 83–102. <https://doi.org/10.3167/082279405781826074>
- Pollet, T. V., Nelissen, M., & Nettle, D. (2009). Lineage based differences in grandparental investment: Evidence from a large British cohort study. *Journal of Biosocial Science*, 41, 355–379. <https://doi.org/10.1017/S0021932009003307>
- Ptackova, J. (2012). Implementation of resettlement programmes amongst pastoralist communities in eastern Tibet. In H. Kreutzmann (Ed.), *Pastoral practices in high Asia. Advances in Asian human-environmental research* (pp. 217–234). London: Springer. https://doi.org/10.1007/978-94-007-3846-1_12
- Ptackova, J. (2015). Hor - a sedentarisation success for Tibetan pastoralists in Qinghai? *Nomadic Peoples*, 19, 221–240. <https://doi.org/10.3197/np.2015.190205>
- Queller, D. C. (1997). Why do females care more than males? *Proceedings of the Royal Society B: Biological Sciences*, 264, 1555–1557. <https://doi.org/10.1098/rspb.1997.0216>
- Reynolds, J. D., Goodwin, N. B., & Frecleton, R. P. (2002). Evolutionary transitions in parental care and live bearing in vertebrates. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 357, 269–281. <https://doi.org/10.1098/rstb.2001.0930>
- Rosenbaum, S., Kuzawa, C. W., McDade, T. W., Avila, J., Bechayda, S. A., & Gettler, L. T. (2021). Fathers' care in context: 'facultative,' flexible fathers respond to work demands and child age, but not to alloparental help, in Cebu, Philippines. *Evolution and Human Behavior*. <https://doi.org/10.1016/j.evolhumbehav.2021.05.003>
- Rosenbaum, S., Vigilant, L., Kuzawa, C. W., & Stoinski, T. S. (2018). Caring for infants is associated with increased reproductive success for male mountain gorillas. *Scientific Reports*, 8, 15223. <https://doi.org/10.1038/s41598-018-33380-4>
- Sadrudin, A. F. A., Ponguta, L. A., Zonderman, A. L., Wiley, K. S., Grimshaw, A., & Panter-Brick, C. (2019). How do grandparents influence child health and development? A systematic review. *Social Science & Medicine*. <https://doi.org/10.1016/j.socscimed.2019.112476>
- Scelza, B. A. (2009). The grandmaternal niche: Critical caretaking among Martu Aborigines. *American Journal of Human Biology*, 21, 448–454. <https://doi.org/10.1002/ajhb.20934>
- Scelza, B. A. (2011). The place of proximity. *Human Nature*, 22, 108–127. <https://doi.org/10.1007/s12110-011-9112-x>
- Scelza, B. A., & Blythe Bird, R. (2008). Group structure and female cooperative networks in Australia's western desert. *Human Nature*, 19, 231–248. <https://doi.org/10.1007/s12110-008-9041-5>
- Scelza, B. A., & Hinde, K. (2019). Crucial contributions: A biocultural study of grandmothering during the perinatal period. *Human Nature*, 30, 371–397.
- Schacht, R., Davis, H. E., & Kramer, K. L. (2018). Patterning of paternal investment in response to socioecological change. *Frontiers in Ecology and Evolution*, 6, 1–12. <https://doi.org/10.3389/fevo.2018.00142>
- Sear, R. (2008). Kin and child survival in rural Malawi: Are matrilineal kin always beneficial in a matrilineal society? *Human Nature*, 19, 277–293. <https://doi.org/10.1007/s12110-008-9042-4>
- Sear, R. (2011). Parenting and families. In V. Swami (Ed.), *Evolutionary psychology: A critical introduction* (pp. 215–250). Wiley-Blackwell.
- Sear, R. (2021). The male breadwinner nuclear family is not the 'traditional' human family, and promotion of this myth may have adverse health consequences. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 376.
- Sear, R., & Coall, D. (2011). How much does family matter? Cooperative breeding and the demographic transition. *Population and Development Review*, 37, 81–112. <https://doi.org/10.1111/j.1728-4457.2011.00379.x>
- Sear, R., & Mace, R. (2008). Who keeps children alive? A review of the effects of kin on child survival. *Evolution and Human Behavior*, 29, 1–18. <https://doi.org/10.1016/j.evolhumbehav.2007.10.001>
- Sear, R., Steele, F., McGregor, I. A., Mace, R., & McGregor, I. A. (2002). The effects of kin on child mortality in rural Gambia. *Evolution and Human Behavior*, 24, 25–42. <https://doi.org/10.1353/dem.2002.0010>
- Sheppard, P., & Sear, R. (2016). Do grandparents compete with or support their grandchildren? *Royal Society Open Science*, 3, Article 160069. <https://doi.org/10.1098/rsos.160069>
- Snopkowski, K., & Sear, R. (2013). Kin influences on fertility in Thailand: Effects and mechanisms. *Evolution and Human Behavior*, 34, 130–138. <https://doi.org/10.1016/j.evolhumbehav.2012.11.004>
- Snopkowski, K., & Sear, R. (2015). Grandparental help in Indonesia is directed preferentially towards needier descendants: A potential confounder when exploring grandparental influences on child health. *Social Science & Medicine*, 128, 105–114. <https://doi.org/10.1016/j.socscimed.2015.01.012>
- Starkweather, K. E., Shenk, M. K., & McElreath, R. (2020). Biological constraints and socioecological influences on women's pursuit of risk and the sexual division of labour. *Evolutionary Human Sciences*, 2. <https://doi.org/10.1017/ehs.2020.60>
- Strassmann, B. I., & Garrard, W. M. (2011). Alternatives to the grandmother hypothesis. *Human Nature*, 22, 201–222. <https://doi.org/10.1007/s12110-011-9114-8>
- Tanskanen, A. O., & Danielsbacka, M. (2018). Grandparents and child wellbeing. *Intergenerational Fam. Relations*, 100–119. <https://doi.org/10.4324/9781315107806-6>
- Tashi, G., & Foggia, J. M. (2012). Resettlement as development and progress? Eight years on: Review of emerging social and development impacts of an "ecological resettlement" project in Tibet autonomous region, China. *Nomadic Peoples*, 16, 134–151. <https://doi.org/10.3167/np.2012.160110>
- Thomese, F., & Liefbroer, A. C. (2013). Child care and child births: The role of grandparents in the Netherlands. *Journal of Marriage and the Family*, 75, 403–421. <https://doi.org/10.1111/jomf.12005>
- Thompson, M. E., & Sabbi, Kristin (2020). Evolutionary Demography of the Great Apes. In O. Burger, R. Lee, & R. Sear (Eds.), *Human Evolutionary Demography*. OSF preprint <https://osf.io/d2thj/>.
- Valeggia, C. R. (2009). Flexible caretakers: Responses of Toba families in transition. In G. R. Bentley, & R. Mace (Eds.), *Substitute parents: Biological and social perspective on alloparenting across human societies* (pp. 100–114). New York: Berghahn Books.
- Waynforth, D. (2012). Grandparental investment and reproductive decisions in the longitudinal 1970 British cohort study. *Proceedings of the Royal Society B: Biological Sciences*, 279, 1155–1160. <https://doi.org/10.1098/rspb.2011.1424>
- Winking, J., Gurven, M., Kaplan, H., & Stieglitz, J. (2009). The goals of direct paternal care among a south Amerindian population. *American Journal of Physical Anthropology*, 139, 295–304. <https://doi.org/10.1002/ajpa.20981>
- Winking, J., & Koster, J. (2015). The fitness effects of men's family investments: A test of three pathways in a single population. *Human Nature*, 26, 292–312. <https://doi.org/10.1007/s12110-015-9237-4>
- Wood, B. M., & Marlowe, F. W. (2013). Household and kin provisioning by Hadza men. *Human Nature*, 24, 280–317. <https://doi.org/10.1007/s12110-013-9173-0>
- Woodroffe, R., & Vincent, A. (1994). Mother's little helpers: Patterns of male care in mammals. *Trends in Ecology & Evolution*, 9, 294–297. [https://doi.org/10.1016/0169-5347\(94\)90033-7](https://doi.org/10.1016/0169-5347(94)90033-7)
- Wu, J. J., He, Q. Q., Deng, L. L., Wang, S. C., Mace, R., Ji, T., & Tao, Y. (2013). Communal breeding promotes a matrilineal social system where husband and wife live apart. *Proceedings of the Royal Society B: Biological Sciences*, 280. <https://doi.org/10.1098/rspb.2013.0010>
- Wu, N., & Richard, C. (1999). The privatization process of rangeland and its impacts on pastoral dynamics in the Hindu-Kush Himalaya: The case of Western Sichuan, China. In *Proceedings of the VI international rangeland congress, Townsville, Australia*.
- Yamaguchi, T. (2011). Transition of mountain pastoralism: An agrodiversity analysis of the livestock population and herding strategies in Southeast Tibet, China. *Human Ecology*, 39, 141–154. <https://doi.org/10.1007/s10745-010-9370-y>
- Yan, Z., Wu, N., Yeshi, D., & Ru, J. (2005). A review of rangeland privatisation and its implications in the Tibetan Plateau, China. *Nomadic Peoples*, 9, 31–52.
- Yeh, E. T. (2003). Tibetan range wars: Spatial politics and authority on the grasslands of Amdo. *Development and Change*, 34, 499–523. <https://doi.org/10.1111/1467-7660.00316>
- Yeh, E. T. (2005). Green governmentality and pastoralism in Western China: "Converting pastures to grasslands." *Nomadic Peoples*, 9, 9–29. <https://doi.org/10.3167/082279405781826164>