Kin selection and sexual conflict drive the duration of breastfeeding

Juan Du* [1 2], Ilaria Pretelli[3] , Min Niu[1] ,Yaming Huang[1], Liqiong Zhou [1], Yuan Chen [2], Ruth Mace *[2 3]

1. State Key Laboratory of Grassland and Agro-Ecosystems, College of Ecology, Lanzhou University, 222 Tianshui South Road, Lanzhou, Gansu 730000, PRC
2. Department of Anthropology, University College London, 14 Taviton Street, London WC1H 0BW, UK
3. Institute for Advanced Study in Toulouse, Toulouse School of Economics, and University of Toulouse Capitole, 31080 Toulouse Cedex 06, France

*Corresponding authors: juan.du.13@ucl.ac.uk and r.mace@ucl.ac.uk

Abstract

Whilst breastfeeding is highly beneficial to infants, mothers frequently do not breastfeed for as long as health guidelines recommend. Here, we show this discrepancy is arising from multiple individuals being involved in offspring care. The support of other family members is modifying the opportunity costs of breastfeeding. We test whether predictions from inclusive fitness theory can help explain the duration of breastfeeding by using demographic data and causally validated, Bayesian Cox linear regression models. We exploit the fact that different residence patterns generate variation in the relatedness within households, and hence different patterns of cooperation and conflict. We analyze the feeding histories of 580 Tibetan children born post-2010 from 5 regions in southwest China with 4 distinct post-marital residence patterns: Patrilocal, Matrilocal, Duolocal, and Neolocal. Our findings reveal that relatedness to the co-resident family of the child, the mother and the father are associated with breastfeeding duration, but in different ways, where child's and mother's average relatedness to the household is positively associated with prolonged breastfeeding duration but father's average relatedness to the rest of the household is associated with shorter breastfeeding duration. Both parent-offspring conflict and sexual conflict between parents are shaping patterns of breastfeeding in ways predicted by inclusive fitness theories of parental investment. Our research highlights the importance of the relatedness of co-resident family members in understanding breastfeeding behaviour. Patriarchal norms of high fertility may be directly mediated by patrilineal relatives curtailing the duration of breastfeeding.

Keywords: cooperative breeding; average relatedness; bargaining power; breastfeeding cessation; patriarchy; residence patterns

Introduction

In the crucial early stages of life, children are inherently reliant on caregivers for nutrition (Andreas et al., 2015), of which breast milk is the most important component (Binns et al., 2016). The broad endorsement of breastfeeding by the global healthcare community underscores its significance (WHO, 2003; 2014). For infants, breastfeeding acts as a protective shield, reducing mortality from infectious diseases and ensuring better development (Duijts et al., 2010). For mothers, breastfeeding potentially mitigates the risks of postpartum depression and many other physical problems (Chowdhury et al., 2015; Rivi et al., 2020; Page et al., 2021). However, whilst the World Health Organization (WHO) recommends at least six months of exclusive breastfeeding and two years before the cessation of breastfeeding, most mothers do not follow these recommendations (Hoddinott, 2014; Theurich et al., 2019).

Human females can only reproduce with the help of others, which may come from husbands, grandmothers or other family members (Hrdy, 2009; Mace and Sear, 2005). Breastfeeding mothers need the support of these allocarers to maintain themselves, their other children, and general household subsistence during this energetically expensive time. Most studies, as well as public health recommendations on breastfeeding, have primarily centred on mothers (Emmott & Mace, 2015; Emmott, 2023; Trickey & Ashmore, 2017). However, the influence of other kin and the broader familial structure—including the relationships between the mother, child, and other household members—on breastfeeding practices remains under-studied. Humans are considered 'cooperative breeders', which means that, as in species that breed communally, reproductive decisions are not made exclusively by mothers, but from fathers and extended kin (Sear and Coall, 2011). Kin selection theory (Hamilton, 1964) provides a useful framework for understanding how conflicts of interests among family members shape reproductive decision-making, including parent-offspring conflict and sexual conflict (Croft et al., 2021; Trivers, 1974; Haig, 1993). Informed by kin selection theory, we investigate whether the relatedness of mothers, fathers, or children to the co-resident family influences breastfeeding practices in a manner that maximizes their inclusive fitness.

From an evolutionary standpoint, it is optimal for parents to balance investment in current and potential future offspring, which can lead to divergence in optimal strategies between parents and children and hence parent-offspring conflicts over breastfeeding duration and intensity (Volk, 2009; Trivers, 1974; Tully & Ball, 2013; Tracer, 2024). The presence of other caregivers within a community or family, can substantially offset the costs of breastfeeding, enabling mothers to engage in fewer domestic and subsistence-related tasks when breastfeeding (Batan et al., 2013; Hawkes et al., 1997; Hurtado et al., 1992; Quinlan & Quinlan, 2008). Cross-cultural research suggests that the presence of female kin, especially grandmothers, play a crucial role in enhancing infant survival and well-being (Bove et al., 2002; Hadley, 2004; Hawkes et al., 1998; Sear & Coall, 2011; Scelza & Hinde, 2019). In societies where intergenerational transfers of resources are less emphasized, siblings often play a pivotal role in child caring. Their cooperative efforts in tasks such as food acquisition or childcare become especially salient (Gurven, 2004; Hill & Hurtado, 2009). However, kin influence is not always beneficial for the mother. In some cultures, mothers-in-law or husbands may prioritize high fertility at the expense of exposing mothers to higher costs of reproduction (Leonetti et al., 2007; Leonetti et al., 2005; Emmott & Mace, 2015). This generates the potential for intersexual conflict, as fathers and their relatives might be more invested than mothers in increasing the number of offspring, rather than the quality (Sear et al 2013; Moya et al., 2016). This trade-off can influence breastfeeding duration and overall parental investment strategies, shaping broader reproductive outcomes.

The choice of where to live after marriage, i.e. residence patterns, significantly influences an individual's relationship with their household, affecting both kinship support and competition (Du et al, 2023). Women often face resource disadvantages in patrilineal societies and men in matrilineal contexts (Hill et al., 2011; Marlowe, 2004). These post-marital residence patterns impact the sexual division of labour, bargaining power, social networks, and child-rearing practices (Chen et al., 2023; Ember & Ember, 1971; Korotayev, 2003; Prall et al., 2018; Ji et al., 2014). We leverage the variation in genetic relatedness generated by different residence patterns as a proxy for bargaining power within the household. Under patrilocal residence (when women dispersed at marriage and men are philopatric) mothers are less related to the group than are fathers or children; whereas in matrilocal residence households (where males dispersed at marriage and females are philopatric) the opposite is true and men are less related to the group than are mothers and children. In duolocal residence, neither men nor women disperse and remain with their natal kin throughout life (fathers and mothers live apart and children stay with their mother) and in this case father's relatedness to the household where the child resides is very low, mother's relatedness to other family member is very high, and child's average relatedness to the household is somewhere between father's and mother's, because they are more likely to be surrounded by individuals from their mother's side. In neolocal residence, where couples establish a new household independent of both natal families, children have high relatedness to the household, as their mother, father and full siblings are all likely to be co-resident—resulting in an average relatedness close to 0.5. Therefore, depending on the composition of the household, the interest of different family members can have a large impact on the duration of breastfeeding, we propose two main hypotheses and another composite hypothesis:

- *Parent-offspring conflict (H1)*: It is in the child's best interest to prolong the breastfeeding period. Parents, on the contrary, should prefer shorter breastfeeding to move on to produce new offspring. Given this trade-off, we expect that in households where children are more related to the rest of the co-resident family members, breastfeeding duration will be longer, whereas when both parents have higher relatedness, breastfeeding will be shorter (H1 - note that the correlation between child-parents relatedness and with co-resident family members may introduce complexity when testing this hypothesis, see our inferential approach in SI section 2 and 3).

- *Sexual conflict (H2)*: Parents themselves have different parental investment strategies, in this case concerning breastfeeding, which generates intersexual conflict. In particular, mothers are expected to prefer longer breastfeeding, as females' investment is typically biased towards ensuring the survival and well-being of their current offspring, while fathers prefer to have a shorter breastfeeding duration, as men favour higher fertility rather than the quality of each offspring. The costs of high fertility fall more heavily on mothers than on fathers. According to this hypothesis, mother and father will have opposing effects on the length of breastfeeding (H2).
- Both mechanisms(*H3*): It is possible that both these mechanisms play a role in shaping breastfeeding duration, which would create a situation where children's relatedness has a very positive effect on breastfeeding duration, mothers' relatedness has an overall positive effect, and fathers' relatedness has a negative effect (henceforth H3). This is especially true if most of the breastfeeding falls somewhere between the optimum for the mother and the optimum for the father.

By examining these hypotheses, we aim to explore how variations in family structure and differences in the average relatedness among family members shape patterns of cooperation and conflict within households. We investigate how these family dynamics ultimately influence breastfeeding decisions, either by providing support that facilitates prolonged breastfeeding or by introducing conflicts that may lead to earlier weaning. Understanding these interactions can shed light on the mechanisms that govern parental investment and childcare strategies in cooperative breeding systems.

Results

Cox regression model:

We employ three different models to address i) how different covariates influence breastfeeding duration (model 1, which includes mothers' birth cohort, household size, the sex and birth order of the child, see methods); ii) the relation between residence patterns and duration of breastfeeding (model 2, which includes all the control variables but household size, as this is a confounder here, see supplementary information, section 3.2, and post-marital residence patterns of the household as a predictor of interest); iii) how relatedness of children, mothers and fathers to the other household members is associated with breastfeeding termination (model 3, which includes the control variables and relatedness of children and their parents as predictors). We choose to base our inference primarily on the estimates provided by this last model on the base of a causally principled approach that relies on the use of Direct Acyclic Graphs (DAGs) and synthetic data simulations (see methods and supplementary information, section 3.3). We further examine whether the observed qualitative direction of effects is consistent with simulations generated from parameter sets reflecting the different hypotheses (H1-H3), thus assessing the degree to which our empirical findings could plausibly arise under each scenario.

In our control model (1), we find no effect of gender of the children on the duration of breastfeeding; both sons (LHC=0.021, 89% PI:-1.098-1.146) and daughters (LHC=-0.027, 89% PI:-1.161-1.104) have an equal likelihood of being weaned. Similarly, the birth order—whether firstborn or subsequently born—shows no difference in the odds of weaning ($\text{LHC}_{\text{first born}}$=0.069, 89 % PI:-1.099-1.215; $\text{LHC}_{\text{second born}}$ =-0.071, 89% PI:-1.248-1.083). Additionally, the cohort to which the mother belongs does not influence the decision to breastfeed; children of mothers born in the earliest examined cohort (<1980, LHC=0.043, 89% PI: -0.902-0.980), the middle period (1980-1990, LHC=-0.002, 89% PI: -0.958-0.938) and the most recent cohort (>=1990,LHC=-0.036,89% PI: -1.009-0.923) are equally likely to cease breastfeeding. Offspring birth order is often recognized as a primary reason for biased parental investment (Wander and Mattison, 2013). However, we did not find this to be the case in our data. This discrepancy may be becuase here mothers gave birth in a more recent generation (post-2010). During this period, compulsory education and family planning policies were fully implemented, limiting women to a specific number of offspring (2-3, depending on the region). In contrast, household size is significantly associated with breastfeeding duration, with duration of breastfeeding decreasing in larger households (LHC=1.197, 89% PI:0.437-1.959).

Results from model 2 show that duolocal, matrilocal and neolocal residence are associated with a slightly longer duration of breastfeeding and, while the effect of each residence pattern overlaps with zero, there are reliable differences between the strategies, with patrilocality being consistently associated with shorter breastfeeding compared to duolocal residence (LHC=-0.831, 89% PI:-1.251- -0.391), matrilocal (LHC=-0.449, 89% PI:-0.801- -0.098) and neolocal (LHC=-0.550, 89% PI:-0.912- -0.191) (see Figure 1, SI Table 2.5, where the lower the Log hazard coefficients, the longer breastfeeding is expected to be; and Figure 2, which shows the distributions of breastfeeding duration data by residence patterns).

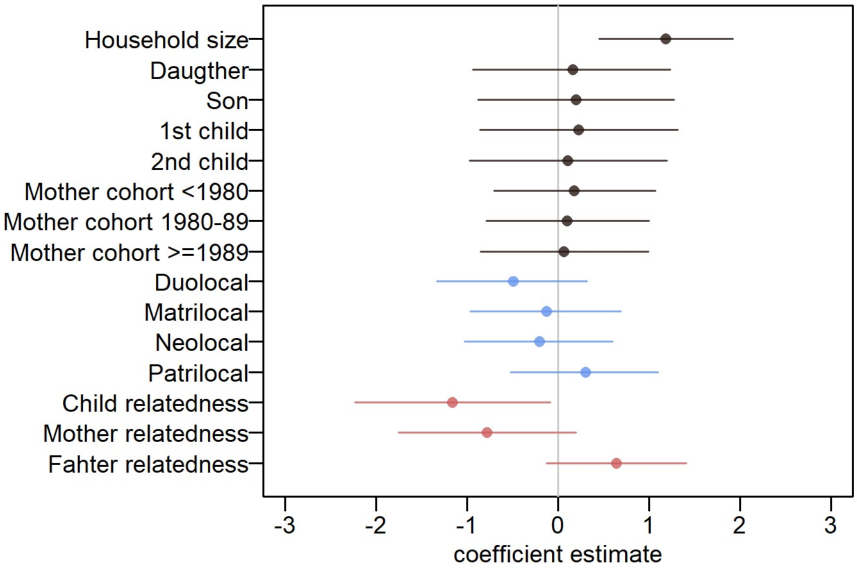

Figure 1: Posterior Log Hazard Coefficients estimates for the relevant predictors.

Negative coefficient estimate means positive effects on breastfeeding; positive coefficient estimate means negative effects on breastfeeding. In black results from model 1, in blue from model 2 and in red from model 3. Note that coefficients for the effect of patrilocality differ significantly from the other residence strategy, even though the effect of each specific residence strategy on breastfeeding duration overlaps with zero (Duolocal vs. Patrilocal:-0.831 (-1.251 , -0.391), Matrilocal vs. Patrilocal : -0.449 (-0.801 , -0.098), Neolocal vs. Patrilocal: -0.550 (-0.912 , -0.191), all values refer to mean and 89% posterior density).

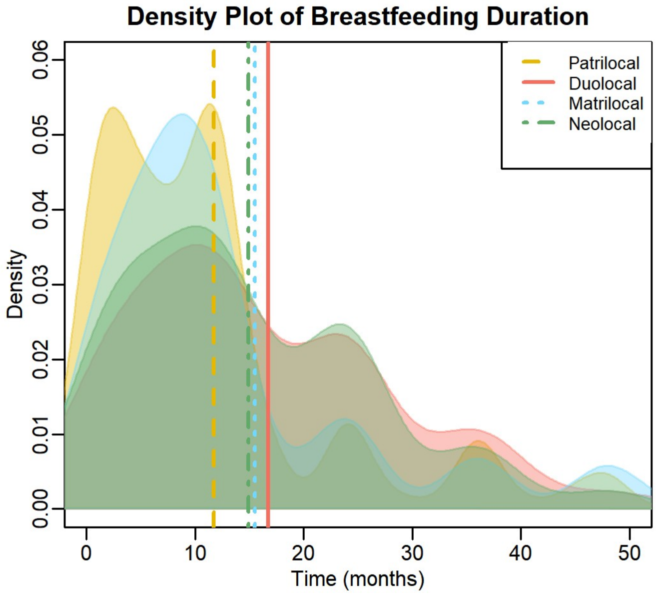

Figure 2: Density plots of individual children's duration of breastfeeding under different residence patterns (Yellow: Patrilocal; Red: Duolocal; Blue: Matrilocal; Green: Neolocal), line stands for the mean value of breastfeeding length (Solid: Duolocal; Dashed: Patrilocal; Dotted: Matrilocal; Dotdash: Neolocal).

Under different residence patterns, infants and parents have different average relatedness to the co-resident family members (Figure 3). Model 3 finds that although the posterior densities overlap with zero, the majority of the posterior mass lies on one side of zero. Specifically, the proportion of the posterior density that crosses zero is 0.043 for child's relatedness (≥ 0), 0.101 for mother's relatedness (≥ 0), and 0.090 for father's relatedness (≤ 0). These results indicate that the model is reasonably confident about the direction of the effect, where both between-sex conflict and parent-offspring conflict are important for breastfeeding decisions (see Figure 1 and SI Table 4).

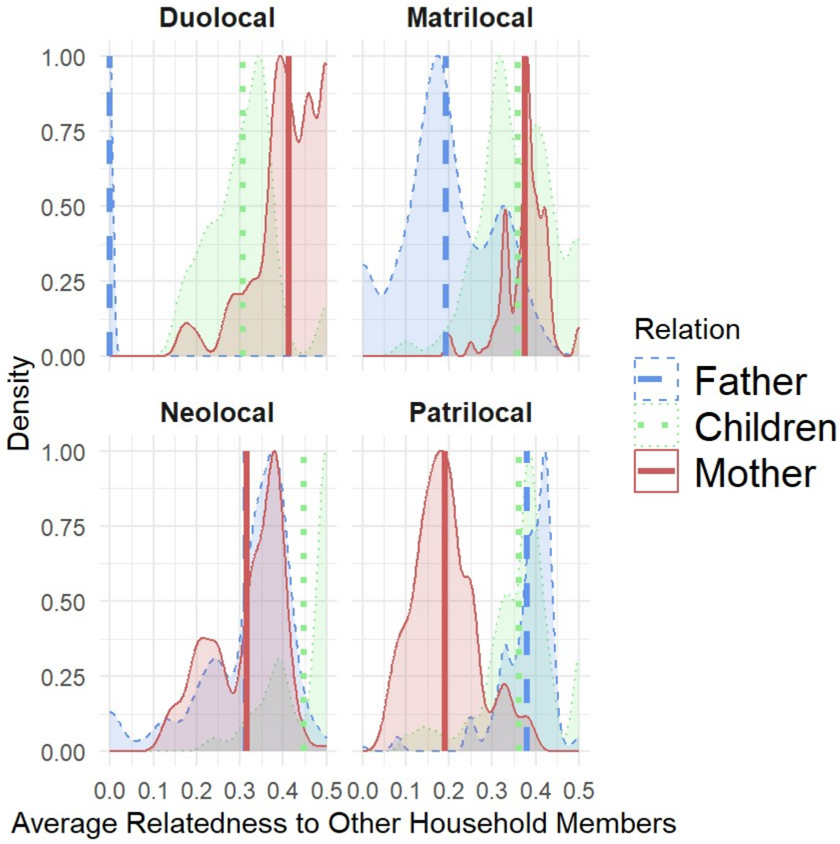

Figure 3: Density plots of individuals' average relatedness to the other household members under different post-marital residence patterns from demographic data. (Blue:Father; Green: Child; Red:Mother. Lines show the mean value of the average relatedness of each family member: Solid:Mother; Dashed:Father; Dotted:Child).

A similar result is given by our comparison between real and simulated data, where the synthetic data that yield results most similar to the real ones are generated by a combination of positive effects for the child's and mother's relatedness and negative effect of the father's relatedness. Figure 4 shows that the hypothesis-generating data most similar to the real ones is H3, i.e. a combination of both parent-offspring and intersexual conflict.

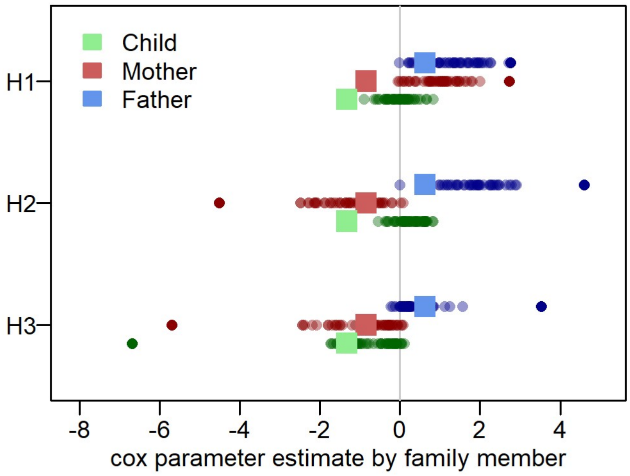

Figure 4: Plot showing log Hazard coefficients from Cox regression model 3 fit on the real data (light colour squares, repeated in comparison to each hypothesis, N=580) and fit on 50 simulations of 100 breastfeeding duration generated according to the different hypotheses (darker colour circles). Green stands for child's effects on breastfeeding; Red stands for mother's effects on breastfeeding and blue stands for father's effects on breastfeeding.

Additionally, we aimed to find a set of generative parameters for our simulation that could generate data most similar to the real data, once evaluated by Model 3, and then compare this 'most-likely parameters set' to our causal models. We find that generative parameters for Child, Mother and Father's relatedness most consistent with the real ones are positive for the first two and negative for the latter(Table 1), which is consistent with H3.

Table 1: Descriptive statistics for a distribution of 250 parameter values that generate simulated data best matching the real data (cox model results from the real data are compared to those from 300 simulated datasets, and the generative parameters for the most similar dataset are retained. This process is repeated 300 times to obtain a parameter distribution that can be interpreted in the framework of the hypotheses described above. See supplementary information for more details).

	Intercept	Child	Mother	Father
Mean	-0.21	0.97	0.67	-0.59
5%	-2.41	0.00	-0.26	-2.60
94%	1.01	4.19	3.39	0.00

Table 2: Reasons given for weaning by 44 women under 3 different residence patterns.

Category	Neolocal	Patrilocal	Matrilocal
physical costs	3 (19%)	2(14%)	2(14%)
opportunity costs	5(31%)	8(57%)	3(21%)
social norms	4(25%)	2(14%)	6(43%)
Others	4(25%)	2(14%)	3(21%)

Self-reported reasons of weaning (Table 2) suggests that behaviours likely to reduce time and energy spent by women on food production, such as breastfeeding, will not be welcomed. Breastfeeding is a demanding maternal caregiving behaviour, not merely a health practice. Among these reasons, opportunity costs—referring to women who cease breastfeeding due to conflicts with their work obligations—account for the largest proportion (36%). Social norms (27%) and physical reasons (16%) follow as the second and third most common factors influencing weaning decisions. The sample size is not large enough for powerful statistical analysis, but it is notable that under patrilocal residence, opportunity costs stand out as the most common reason given (57%) compared to the other three reasons. Social norms are also often cited as reasons for weaning, especially under matrilocal residence (43%), showing that women may be following guidance or copying acquaintances rather than consciously evaluating costs and benefits. They may also prefer to assert they are following a norm to avoid criticism. In all five regions, the most reliable sources of income come from labour on farmland or grassland. Our accelerometer data indicate that males in both duolocal and patrilocal systems engage in significantly less agricultural and animal husbandry work than females (Chen et al., 2023), suggesting that women's labour requirements are even more intense in these residence patterns. A key limitation of this result is the relatively small sample size, which limits the generalizability of our findings regarding how residence patterns affect self-reported weaning reasons.

Discussion

Our findings demonstrates that variation in residence patterns is associated with breastfeeding duration, providing evidence for both parent-offspring conflict and intersexual conflict. The interplay between mother-infant conflict over weaning and bargaining power derived from maternal relatedness is difficult to disentangle, as both mechanisms predict a longer breastfeeding period in matrilocal and duolocal residence, where mothers reside with their natal family. However, whilst there is strong evidence of parent-offspring conflict between father and infant, the relatedness data suggests that the mother's interests and the child's interests are in fact closely aligned here - high relatedness to the group for mother and infant both enable longer breastfeeding. This outcome is what we would predict when the breastfeeding duration achieved is usually somewhere between the optimum for the mother and the father (West and Gardner 2013).

An additional explanation for the observed longer breastfeeding duration in matrilocal and duolocal households, as well as the relatively small effect of maternal relatedness, is the reduced parent-offspring conflict between the mother and the child. Matrilineal societies are associated with weaker marriage ties and higher divorce rates as also observed here (Mattison, 2011; Parkin, 2021, Du and Mace, 2019). That means mother's future offspring are, on average, less closely related to the focal child than in patrilineal societies where marriages are more stable. This prediction on weaning conflict goes back to Trivers original formulation of parent-offspring conflict (Trivers 1974). Females in patrilineal and matrilineal families have different bargaining power, so we assume that will directly influence breastfeeding duration. The significant opportunity costs associated with breastfeeding are further exemplified by findings that breastfeeding mothers often engage in fewer domestic and professional tasks than their non-breastfeeding counterparts (Batan et al., 2013; Hawkes et al., 1997; Quinlan and Quinlan 2008, Chen et al., 2023). The involvement of other caregivers within a community or family, can substantially offset the demands and opportunity costs of breastfeeding (Page et al., 2021; Emmott and Mace 2015; Emmott 2023; Emmott et al., 2020a; Myers et al., 2021). This support network enhances the flexibility inherent in human reproductive strategies. However, the impact of allomaternal care on breastfeeding duration depends on the type of support provided. In contexts where allomothers assist mothers through resource provisioning and domestic tasks, this reduces the opportunity costs of breastfeeding, facilitating longer nursing durations (Emmott et al., 2020a; Emmott & Mace, 2015; Quinlan & Quinlan, 2008). Conversely, when allomothers provide direct care to children, the opportunity costs of breastfeeding may be higher, as nursing mothers cannot easily benefit from this support without separating from their children (Emmott et al., 2020a; Emmott & Mace, 2015; Myers et al., 2021).

Some mathematical models suggest that male reproductive strategies may not always align with shorter birth intervals, particularly when sequential partnering is not feasible or when high child mortality reduces the fitness benefits of rapid reproduction (Moya et al., 2016; Morita et al., 2016), as child survival and quality become more important. However, our findings suggest that Patriarchal norms tend to promote higher fertility than would be optimal for maternal and child health. Our previous research from same study sites has demonstrated that women play a central role in subsistence and economic activities (Du and Mace 2018; Chen et al., 2023). Early weaning may be a trade-off between reproductive pressure and economic necessity.

Inclusive fitness theory is a powerful predictive framework to understand parental investment and here we show how it applies also to breastfeeding practices. Breastfeeding mothers need support to maintain themselves, their other children, and general household subsistence during this energetically expensive time. Different residence patterns generate specific constellations of household members, who can choose to support or not support breastfeeding mothers and the interests of the focal children. However, we found that large households can be detrimental to breastfeeding duration, perhaps due to reduced average relatedness. Households make decisions regarding the division of labour and resource allocation, which can proximally impact breastfeeding duration. While we cannot empirically test these mechanisms with the current data, our results are consistent with the idea that these proximate causes are influenced by the bargaining power individuals exert by virtue of their relatedness. It is misleading to interpret reproductive decision-making in the context of mothers alone (UNICEF, 2017). Here we show how the family structure, and the relatedness of children and parents to their co-resident household members are shaping breastfeeding duration.

Methods

Descriptive Statistics

This study collected data from five distinct regions within western China (353 female respondents, for a total of 580 children with complete information for analysis), each presenting varied ecological, economic, and cultural landscapes while sharing the same religion and government (Figure 5, SI Table 2.1 and 3.1 for descriptive statistics). The regions studied include two locations in the Gannan Tibetan Autonomous Prefecture of Gansu province (Zhuoni and Maqu), two in Garzê Tibetan Autonomous Prefecture of Sichuan province (Zhaba and Lugu), and one (Shangrila) in the Diqing Tibetan Autonomous Prefecture of Yunnan province. In each region, we collected data from different villages that are clustered by culture, language and ecology (Figure 5). The study area is atypical for the coexistence of four residence patterns (matrilocal, patrilocal, duolocal and neolocal) in five nearby regions inhabited by ethnically Tibetan farmers and herders, which yields the variation in average relatedness between children and parents to the rest of the household (Figure 3, SI Table 1).

The primary source of family income from these regions are varied: In Maqu, yak and sheep herding serves as the principal source of living income generation, whereas farming products are predominantly used for family or livestock consumption (Du & Mace, 2018; Gelek, 2006). *Yarsa gambu* (a fungus) is collected in summer and contributes to the family economy, but its significance has declined in recent decades (Xing and Wang, 2023). Zhuoni features a mix of barley farming and livestock rearing, and family income comes either from livestock, farming or by doing temporary labour in town (Zhou et al., 2022). In Zhaba, Lugu, and Shangrila, family income is primarily from farming, supplemented by limited herding and gathering mushrooms or medicinal fungi. Additionally, there is income from temporary labour and tourism, though these sources are inconsistent and fluctuate annually. Very few individuals in any of these rural communities work in salaried or office-based jobs (Chen et al., 2023; Huang et al., 2025).

Despite a common religion and many other cultural similarities across these Tibetan populations, they operate under varying kinship and post-marital residence patterns: Maqu and Zhuoni are grouped as Amdo Tibetans, who practice a patrilineal system and predominantly feature patrilocal residences (Zou, 2006). Zhaba and Lugu are located in Sichuan province and follow a matrilineal system and duolocal residence pattern (Chen et al., 2023; Jiao & Zhong, 2017). Shangrila located in the Diqing Tibetan prefecture, and was grouped as Kang Tibetans, it operates under a matrilineal system with matrilocal residences (Du et al., 2023. See SI section 1 for more information).

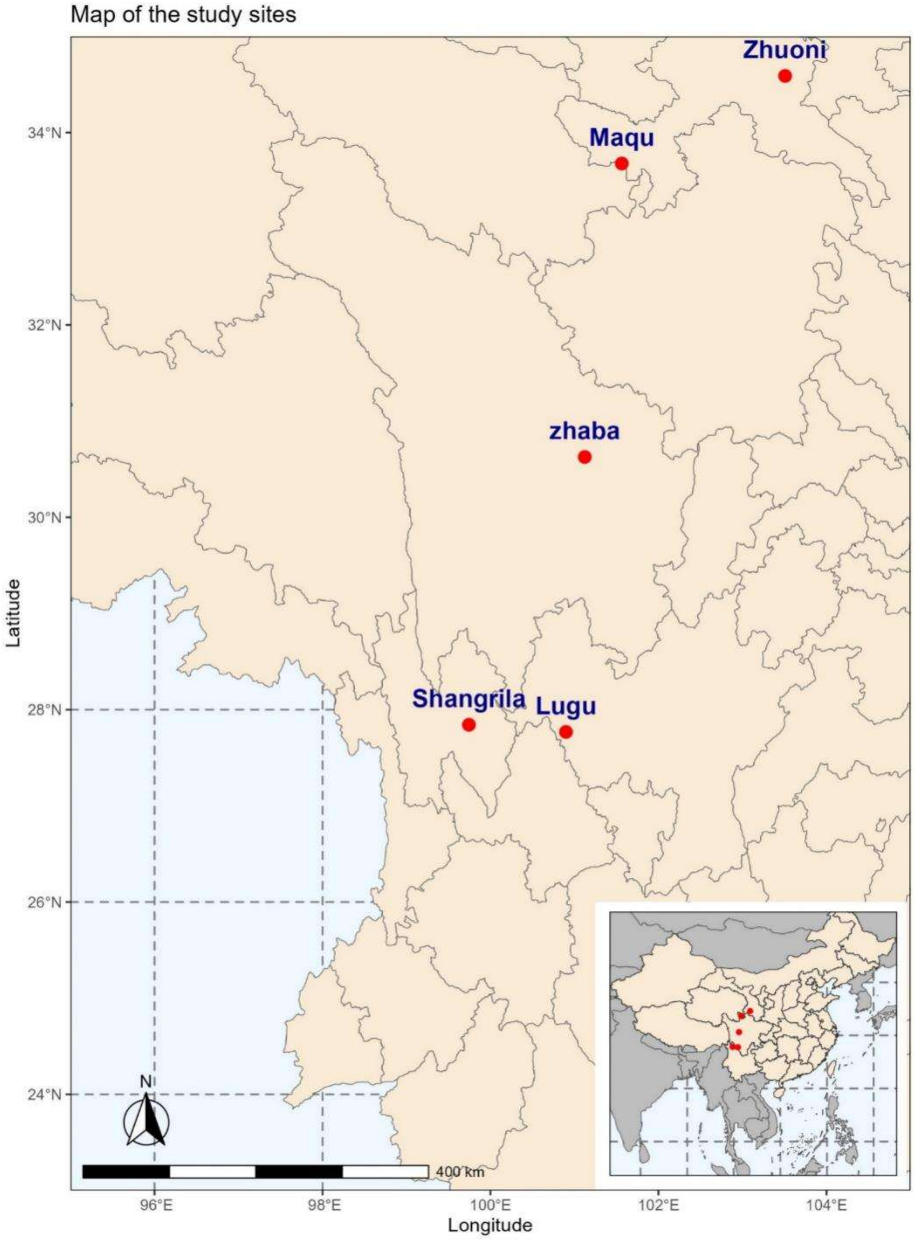

Figure 5: Map of the five study sites. 5 different regions were indicated on the map with red dots, note that in each region, there are different villages where we collected data. The border was shown based on the provincial level in China.

We walked from one household to another to collect demographic data, accompanied by local assistants in all five regions. The survey was systematically structured into two main sections: household structure and individual details. For the household structure data, we gathered sociodemographic information from the head of the household or any other adult well-acquainted with the household, if the head was absent during our visit. This data covered all co-resident household members, including year of birth and marriage, their parents, dispersal history, frequency of living in the household, financial status, and the predominant subsistence system. For individual questionnaires, we interviewed adult men and women in separate settings about their marital histories, siblingship, and reproductive histories. For female participants, the survey included detailed data on each child's birth date, delivery methods, breastfeeding duration, specifics of any alternative feeding practices, and reasons of weaning. We collected data for all adult men and women in the households, but this study includes only families with children born after 2010, to ensure the relevancy of post-marital residence details and the accuracy of mothers' recollection of breastfeeding practices. This approach yielded comprehensive breastfeeding information for a sample of 284 daughters and 296 sons (SI Table 2). The cessation of breastfeeding was defined as the termination of all breastfeeding and was censored at 2 years (24 months), in line with the health recommendation from WHO (2023). Households were classified according to post-marital residence patterns into patrilocal (females disperse at marriage), matrilocal (males disperse at marriage), duolocal (neither sex disperse at marriage), and neolocal (both sexes disperse at marriage) categories, representing various familial structures and living arrangements. Note that even though most people living in each of the five regions follow the main descendance pattern (matrilineal vs patrilineal), not all couple reside accordingly, e.g. some families can follow a matrilocal residence pattern in a patrilineal community and so on. In different regions, residence patterns and relatedness between family members show notable variations. In the Zhaba Region, the most common form of residence is duolocal at 53.4%. At Lugu, duolocal residence is prominent at 16.5%, duolocal residence is unique to Zhaba and Lugu and doesn't manifest in other regions, but other forms of post-marital residence are observed in at least some households in the other three regions. For the Zhuoni and Maqu Regions, patrilocal residence is predominant. In Zhuoni, it's at 63.1%, and in Maqu, the percentage is 48.8. In Shangrila, matrilocal is the major residence form at 47%. (SI Table 1).

Genetic relatedness in this paper is defined as the average degree of relatedness for individual i (i.e. either the focal child, the mother or the father) to the household of residence of the child, or $\overline{r_i}$. It is generated from pedigree data as reported in household level interviews and the method is standard calculation of relatedness from Hamilton (1964). Per each person i, we sum the genealogical relatedness of i (Wright, 1922) to each other members of household j and divide by the number of other household members (excluding i), n (Figure 6)

$$\bar{r}_i = \frac{\sum_{j=1}^{n} r_{i,j}}{n}$$

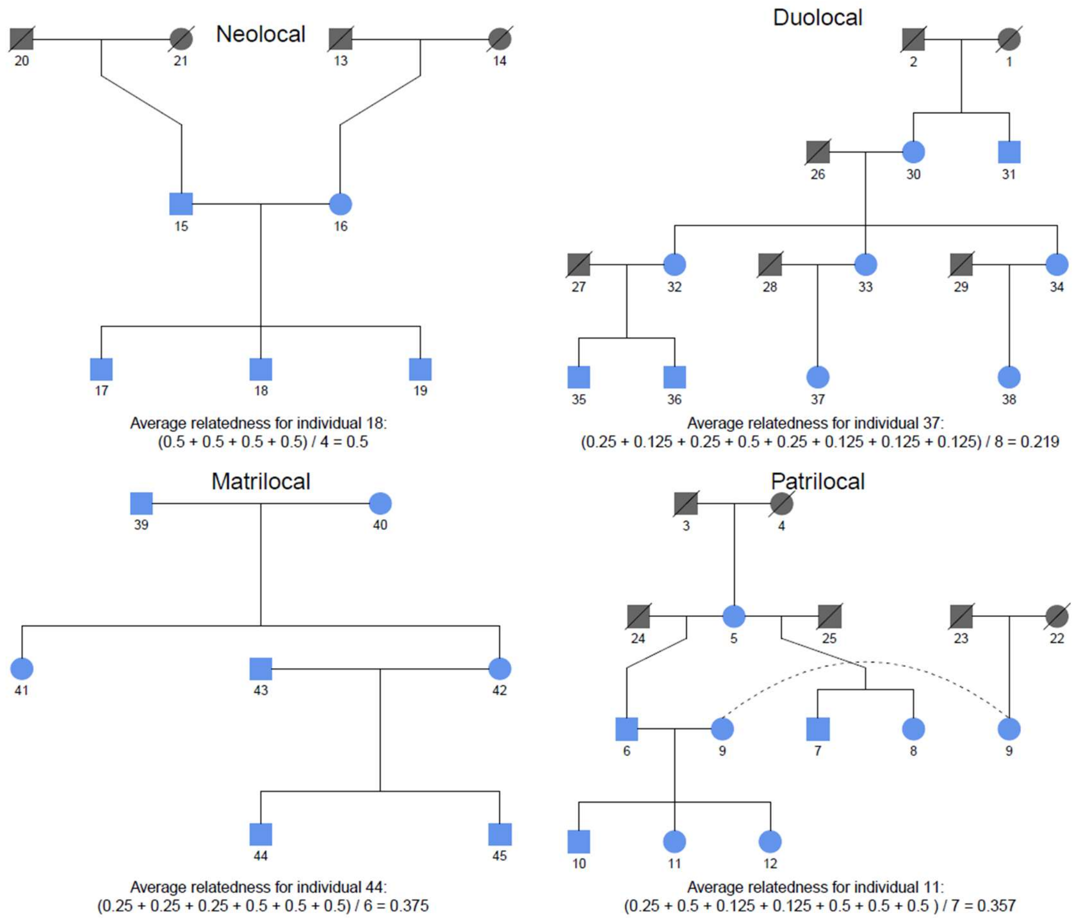

Figure 6: Examples of pedigrees for each residence type. Circles are female, squares are male. Barred individuals are individuals present in the dataset who are not part of the household (dead, not co-resident fathers, etc.). For each person, average relatedness is calculated by summing the genealogical relatedness to all other

members of household and dividing by the number of other co-resident household members (excluding themselves).

To integrate our understanding of decision-making regarding breastfeeding, we interviewed 44 women in Shangrila about their reasons for weaning, and we categorized their reasons into four parts (Table 2): physical costs, social norms, opportunity costs and others (see SI Table 3 for details of self-reported reasons).

Statistical analysis

We used Cox proportional-hazards regressions to test which variables were associated with termination of breastfeeding. We hence approach the problem as a survival analysis, where relatedness of individuals and other predictors affect the risk of breastfeeding termination. This approach also allows us to deal with censoring issues, i.e. when children are still breastfed at the time of the interview; we also censored all breastfeeding durations that exceeded 24 months because of both lower reliability of the reported duration, and lower physiological relevance of breastfeeding after this time, for both the child and the mother (SI Figure 2). We controlled for mother’s birth cohort, children's birth order, children's sex and household size (except for model 2, where household size is on the path of residence type). Mothers’ birth cohorts were separated into 10-year intervals (from <=1980, 1980-1989 to >=1990). Some women had more than one child in the sample, so we controlled for women ID, and we added village as random effects in the model to control the influence of ecology and culture. Household size was included as an ordinal, monotonically increasing predictor. Household size varies under different residence patterns (in Duolocal households is 7.769 ± 2.921, in Neolocal is 5.504 ± 1.400, in Patrilocal is 6.831 ± 1.898 and in Matrilocal is 6.780 ± 1.916). The average relatedness of each individual to the household was calculated using the ‘Kinship’ package (Kinship2 version 1.9.6) based on the genealogical data. Bayesian Cox models were written in Stan language and included weakly regularizing priors (more details in the supplementary information, section 4). The models were run using

CmdrStan package (version 0.5.3) for 3000 iterations after 1000 warmup iterations. Model convergence was confirmed by low rhat values (≈1) and high number of effective samples. Plots were draw with packages ggplot2, contsurvplot, rnaturalearth and ggspatial. All the analysis were conducted in R (version 4.2.2). Data and reproducible code can be found at: [fully reproducible GitHub repository to be shared upon acceptance]. Ethical clearance was obtained from UCL Research Ethics and Lanzhou University.

Causal model

The comparison of the hypotheses considered in the present paper is complicated by the potential equifinality (i.e. different causal models can produce similar data, making them practically difficult to distinguish in real-world datasets). This challenge arises from the mechanism of genetic inheritance, which inherently correlates the relatedness of child and parent's relatedness to the rest of the family. As a result, it becomes difficult to isolate whether observed effects are driven by the parent's relatedness, the child's relatedness, or both (see supplementary information section 2 for a more in-depth description of the problems this causes for causal inference). To navigate these complexities and address these non-mutually exclusive hypotheses, we employ a multi-method approach that includes causally validated Cox regression models, and comparisons between synthetic datasets (see SI section 5) and empirical data on demographic and breastfeeding durations collected in 2016 and 2017.

We address both the selection of covariates for our Cox model and the issues generated by considering the genetic relatedness of parents and offspring with a principled causal approach. First, we employ Direct Acyclic Graphs to define the scope of our inferential approach. Figure 7 illustrates all the variables we consider in our analysis. As we are mainly interested in estimating the effect of Mother, Father and Child's average relatedness on breastfeeding duration (addressed in model 3), the correct set of predictors includes these three variables, as well as Village. Moreover, we include Household size, Mother birth cohort, Child Sex and Birth order as covariates to improve our estimate. We describe these variables in detail in the supplementary information, section 3.1.

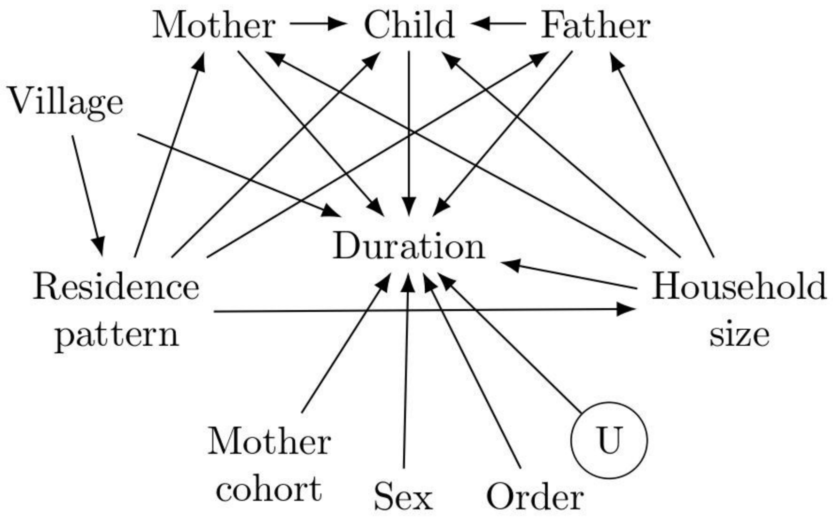

Figure 7: Direct acyclic graph describing relationships between analysed variables that are influencing breastfeeding duration. Note that some variables are believed to be important parameters affecting breastfeeding. i.e. physical constraints or household wealth were not available. The effect of these, as well as other unmeasured variables, marked by the circled U in the graph, is likely captured by individual mothers' random effects. Moreover, we do not think that residence patterns will directly affect breastfeeding duration but rather the geographical location, in this case village, which stands for cultural and ecological differences, influences the residence patterns and breastfeeding duration.

Additionally, we performed further analyses to address the fact that children and their parents always share half of their genome. This creates a correlation between the average relatedness of children and that of their parents to the rest of their household, one that could generate equifinality, or the risk that the different hypotheses we consider could generate indistinguishable data.

We hence generated multiple simulations of breastfeeding duration according to the different hypotheses and compared the results that our Model 3 (which includes predictors for all Child, Mother and Fathers' relatedness) generates when using real data and simulated ones (Figure 4). We also run the same comparison of real and simulated data with different Cox models (e.g. including only one relatedness at a time, or a combination of them) to evaluate how these models can distinguish between the generating hypotheses (see SI Figure 6). The set of predictors used in model 3 appeared to be better able to address the problem of equifinality and distinguish between the hypotheses (see supplementary information, section 3.3), which includes control variables and average relatedness of child and parents to the rest of the family. Additionally, this approach is particularly helpful because, unlike fully parametric models, the Cox model does not specify a full likelihood for the event times. This prevents the use of conventional posterior predictive checks to validate model fit. In response, we adopt a simulation-based strategy that plays an analogous role: by generating datasets under competing hypotheses and fitting the same model to these synthetic datasets, we assess which mechanisms could plausibly give rise to the observed posterior distributions.

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Contributions

J.D.and R.M. designed the study; J.D., Y.C., Y.-M.H., P.-P.B.,L.-Q.Z. and M.N.,collected the data; J.D., Y.C., performed the data management; J.-D., and I.P. analysed the data; J.D.,I.P and R.M. co-wrote the manuscript.

Corresponding authors

Correspondence to Juan Du (dujuan@lzu.edu.cn), Yuan Chen (yuan.chen.20@ucl.ac.uk)and Ruth Mace (r.mace@ucl.ac.uk)

References

Andreas, N. J., Kampmann, B., & Mehring Le-Doare, K. (2015). Human breast milk: A review on its composition and bioactivity. *Early Human Development*, *91*(11), 629–635. https://doi.org/10.1016/j.earlhumdev.2015.08.013

Batan, M., Li, R., & Scanlon, K. (2013). Association of child care providers breastfeeding support with breastfeeding duration at 6 months. *Maternal and Child Health Journal*, *17*(4), 708–713. https://doi.org/10.1007/s10995-012-1050-7

Binns, C., Lee, M., & Low, W. Y. (2016). The Long-Term Public Health Benefits of Breastfeeding. *Asia-Pacific Journal of Public Health*, *28*(1), 7–14. https://doi.org/10.1177/1010539515624964

Bove, R. B., Valeggia, C. R., & Ellison, P. T. (2002). Girl helpers and time allocation of nursing women among the Toba of Argentina. *Human Nature*, *13*(4), 457–472. https://doi.org/10.1007/s12110-002-1003-8

Chen, Y., Ge, E., Zhou, L., Du, J., & Mace, R. (2023). Sex inequality driven by dispersal. *Current Biology*, *33*(3), 464-473.e4. https://doi.org/10.1016/j.cub.2022.12.027

Chowdhury, R., Sinha, B., Sankar, M. J., Taneja, S., Bhandari, N., Rollins, N., Bahl, R., & Martines, J. (2015). Breastfeeding and maternal health outcomes: A systematic review and meta-analysis. In *Acta Paediatrica, International Journal of Paediatrics* (Vol. 104, pp. 96–113). https://doi.org/10.1111/apa.13102

Croft, D. P., Weiss, M. N., Nielsen, M. L. K., Grimes, C., Cant, M. A., Ellis, S., Franks, D. W., & Johnstone, R. A. (2021). Kinship dynamics: Patterns and consequences of changes in local relatedness. In *Proceedings of the Royal Society B: Biological Sciences* (Vol. 288, Issue 1957). Royal Society Publishing. https://doi.org/10.1098/rspb.2021.1129

Duijts, L., Vincent, W. V. Jaddoe;, & Albert Hofman;Henriëtte A. Moll. (2010). Prolonged and exclusive breastfeeding reduces the risk of infectious diseases in infancy. *Pediatrics*, *126*(1), e18–e25.

Du, J., Huang, Y., Bai, P., Zhou, L., Myers, S., Page, A. E., Mace, R., & Du, J. (2023). Post-marital residence patterns and the timing of reproduction : evidence from a Tibetan matrilineal society. *Proceedings of The Royal Society B:Biological Science*, *290*(20230159).

Du, J., & Mace, R. (2018). Parental investment in Tibetan populations does not reflect stated cultural norms. *Behavioral Ecology*, *29*(1), 106–116. https://doi.org/10.1093/beheco/arx134

Ember, M., & Ember, C. R. (1971). The Conditions Favoring Matrilocal versus Patrilocal Residence. *American Journal of Semiotics*, *73*(3), 571–594. https://doi.org/10.5840/ajs2012281-29

Emmott, E. H. (2023). Improving Breastfeeding Rates. In *Improving Breastfeeding Rates*. Cambridge University Press. https://doi.org/10.1017/9781009217491

Emmott, E. H., & Mace, R. (2015). Practical Support from Fathers and Grandmothers Is Associated with Lower Levels of Breastfeeding in the UK Millennium Cohort Study. *Plos One*, *10*, e0133547. https://doi.org/10.1371/journal.pone.0133547

Gelek, L. (2006). Anthropological field survey on basic education development in the Tibetan nomadic community of Maqu , Gansu. *Asian Ethnicity*, *7*(April 2014), 37–41. https://doi.org/10.1080/14631360500505777

Gurven, M. (2004). To give and to give not: The behavioral ecology of human food transfers. *Behavioral and Brain Sciences*, *27*(4), 543–560. https://doi.org/10.1017/s0140525x04000123

Hadley, C. (2004). The costs and benefits of kin: Kin networks and children's health among the Pimbwe of Tanzania. *Human Nature*, *15*(4), 377–395. https://doi.org/10.1007/s12110-004-1015-7

Hamilton, W. D. D. (1964). The genetical evolution of social behaviour. *Journal of Theoretical Biology*, *7*(1), 1–16. https://doi.org/10.1016/0022-5193(64)90038-4

Haig, D. (1993). Genetic conflicts in human pregnancy. Quarterly Review of Biology 68(4): 495-532.

Hawkes, K., O'Connell, J. F., & Blurton Jones, N. G. (1997). Hadza Women'sTime Allocation, Offspring Provisioning, and the Evolution of Long Postmenopausal Life Spans. *American Journal of Physical Anthropology*, *38*(4), 159–181.

Hawkes, K., O'Connell, J. F., Blurton-Jones, N. G., Alvarez, H., & Charnov, E. (1998). Grandmothering, menopause, and the evolution of human life histories. *Proceedings of the National Academy of Sciences*, *95*(3), 1336–1339. https://doi.org/10.1073/pnas.95.3.1336

Hill, K., & Hurtado, A. M. (2009). Cooperative breeding in South American hunter-gatherers. *Proceedings of the Royal Society B*, *276*(1674), 3863–3870. https://doi.org/10.1098/rspb.2009.1061

Hill, K. R., Walker, R. S., Božičević, M., Eder, J., Headland, T., Hewlett, B., Magdalena Hurtado, A., Marlowe, F., Wiessner, P., & Wood, B. (2011). Co-Residence Patterns in Hunter-Gatherer Societies Show Unique Human Social Structure. *Science*, *331*, 1286–1289. https://www.science.org

Hoddinott, J. (2014). *Household Expenditures , Child Anthropometric Status and the Intrahousehold Division of Income : Evidence from the Cote d ' Ivoire*. *May*.

Huang Y, Bai P, Zhou L, Mace R, Du J. (2025). A rapid decline in gender bias relates to changes in subsistence practices over demographic changes in a formerly matrilineal community. iScience. 28(2):111926. https://10.1016/j.isci.2025.111926.

Hurtado, A. M., Hill, K., Kaplan, H., Hurtado, I., & Hurtado, M. (1992). Trade-offs Between Female Food Acquisition and Child Care among Hiwi and Ache Foragers. *Human Nature*, *3*(3), 185–216.

Hrdy, Sarah B. (2009). Mothers and Others: The Evolutionary Origins of Mutual Understanding. Cambridge,ma: Belknap Press.

Liao, H., & Zhong, Z. (2017). *Survey and research summary of Tibetan literature and history in Zhaba*. Southwest Jiaotong University Press.

Ji, T., Xu, JJ. & Mace, R. (2014). Intergenerational and Sibling Conflict Under Patrilocality. Human Nature. 25, 66–79. https://doi.org/10.1007/s12110-013-9188-6

Korotayev, A. (2003). Division of Labor by Gender and Postmarital Residence in Cross-Cultural Perspective: A Reconsideration. *Cross-Cultural Research*, *37*(4), 335–372. https://doi.org/10.1177/1069397103253685

Leonetti, D. L., Nath, D. C., & Hemam, N. S. (2007). In-law conflict: Women's reproductive lives and the roles of their mothers and husbands among the Matrilineal Khasi. *Current Anthropology*, *48*(6), 861–890. https://doi.org/10.1086/520976

Leonetti, D.L.;Nath, D.C.; Hemam N.S.;Neill, D. (2005). Kinship Organization and Grandmother ' s Impact on Reproductive Success among the Matrilineal Khasi and Patrilineal Bengali of N . E . India . In E. Voland, A. Chasiotis, & A. Schiefenhov (Eds.), *Grandmotherhood: the evolutionary significance of the second half of female life* (Issue January 2005, pp. 194–214). Rutgers University Press.

Mace, R & Sear R. (2005). “are humans cooperative breeders?,” in e. voland, a.Chasiotis, and w. Schiefenhoevel (eds.), Grandmotherhood: The Evolutionary Significance ofthe Second Half of Female Life. new Brunswick: rutgers university Press.

Mattison, S.M. (2011). Evolutionary contributions to solving the “Matrilineal Puzzle”: A test of Holden, Sear, and Mace’s Model. Human Nature, 22(1), 64–88. 10.1007/s12110-011-9107-7.

Wander, K., & Mattison, S. M. (2013). The evolutionary ecology of early weaning in Kilimanjaro, Tanzania. Proceedings of the Royal Society B: Biological Sciences, 280(1768), 20131359.

Mekebo, G. G., Argawu, A. S., Likassa, H. T., Ayele, W., Wake, S. K., Bedada, D., Hailu, B., Senbeto, T., Bedane, K., Lulu, K., Daraje, S., Lemesa, R., Aga, G., Alemayehu, E., Kefale, B., Bechera, T., Tadesse, G., Galdassa, A., Olani, J., … Diriba, G. (2022). Factors influencing exclusive breastfeeding practice among under-six months infants in Ethiopia. *BMC Pregnancy and Childbirth*, *22*(1). https://doi.org/10.1186/s12884-022-04955-x

Moya C, Snopkowski K, SearR. (2016). What do men want? Re-examiningwhether men benefit from higher fertility thanis optimal for women.Philosophical Transactions of the Royal Society. B371: 20150149.http://dx.doi.org/10.1098/rstb.2015.0149

Morita M, Ohtsuki H, Hiraiwa-Hasegawa M. (2016). Does Sexual Conflict between Mother and Father Lead to Fertility Decline? : A Questionnaire Survey in a Modern Developed Society. Human Nature. 27(2):201-19. doi: 10.1007/s12110-016-9254-y.

Page, A. E., Emmott, E. H., & Myers, S. (2021). Testing the buffering hypothesis: Breastfeeding problems, cessation, and social support in the UK . *American Journal of Human Biology*, *May*, 1–20. https://doi.org/10.1002/ajhb.23621

Parkin, R. 2021. The fragility of marriage in matrilineal societies.

Panigrahi, A., & Sharma, D. (2019). Exclusive breast feeding practice and its determinants among mothers of children aged 6–12 months living in slum areas of Bhubaneswar, eastern India. *Clinical Epidemiology and Global Health*, *7*(3), 424–428. https://doi.org/10.1016/j.cegh.2018.11.004

Prall, S. P., Yetish, G., Scelza, B. A., & Siegel, J. M. (2018). The influence of age- and sex-specific labor demands on sleep in Namibian agropastoralists. *Sleep Health*, *4*(6), 500–508. https://doi.org/10.1016/j.sleh.2018.09.012

Quinlan, R. J., & Quinlan, M. B. (2008). Human lactation, pair-bonds, and alloparents : AA cross-cultural analysis. *Human Nature*, *19*(1), 87–102. https://doi.org/10.1007/s12110-007-9026-9

Rivi, V., Petrilli, G., & Blom, J. M. C. (2020). Mind the Mother When Considering Breastfeeding. *Frontiers in Global Women’s Health*, *1*, 1–5. https://doi.org/10.3389/fgwh.2020.00003

Scelza, B. A., & Hinde, K. (2019). Crucial Contributions: A Biocultural Study of Grandmothering During the Perinatal Period. *Human Nature*, *30*(4), 371–397. https://doi.org/10.1007/s12110-019-09356-2

Sear, R., & Coall, D. (2011). How Much Does Family Matter? Cooperative Breeding and the Demographic Transition. *Population and Development Review*, *37*(SUPPL. 1), 81–112. https://doi.org/10.1111/j.1728-4457.2011.00379.x

Theurich, M. A., Davanzo, R., Busck-Rasmussen, M., Díaz-Gómez, N. M., Brennan, C., Kylberg, E., Bærug, A., McHugh, L., Weikert, C., Abraham, K., & Koletzko, B. (2019). Breastfeeding rates and programs in europe: A survey of 11 national breastfeeding committees and representatives. *Journal of Pediatric Gastroenterology and Nutrition*, *68*(3), 400–407. https://doi.org/10.1097/MPG.0000000000002234

Tracer, D.P, (2024) Evolutionary and empirical perspectives on ‘demand’ breastfeeding: The baby in the driver’s seat or the back seat?. Evolution, Medicine, and Public Health, 12(1), 24–32, https://doi.org/10.1093/emph/eoae003

Trivers, R. L. (1974). *Parent-Offspring Conflict*. *14*, 249–264. https://academic.oup.com/icb/article/14/1/249/2066733

Trickey, H., & Ashmore, S. (2017). Infant feeding: Changing the conversation. Infant, 13(1), 26–8. www.infantjournal.co.uk/pdf/inf_073_ngi.pdf.

Tully, K. P., & Ball, H. L. (2013). Trade-offs underlying maternal breastfeeding decisions: A conceptual model. *Maternal and Child Nutrition*, *9*(1), 90–98. https://doi.org/10.1111/j.1740-8709.2011.00378.x

UNICEF UK. (2017). Baby friendly initiative: Call to action. www youtube.com/watch?v=7yNvkk_LfpU.

Volk, A. A. (2009). Human Breastfeeding is Not Automatic: Why That’s So and What it Means for Human Evolution. *Journal of Social, Evolutionary, and Cultural Psychology* , *3*(4), 305–314. www.jsecjournal.org

West, S.A., Gardner. A. (2013). Adaptation and inclusive fitness. Current Biology. 23(13):577-584. https://10.1016/j.cub.2013.05.031.

WHO. (2003). Global Strategy for Infant and Young Child Feeding. *World Health Organizationorld*, 1–30. https://doi.org/ISBN 92 4 156221 8

WHO. (2014). *Comprehensive implementation plan on maternal, infant and young child nutrition*.

Wright, S. (1922). Coefficients of inbreeding and relationship. American Naturalist, 56(645), 330–338.

Xing, HY., Wang, X. (2023), Interembedding and integration: The construction of ethnic communities in economic interactions—An investigation based on the cordyceps trade in the northwestern tibetan region, Journal of Shanghai Institute of Socialism,2023(3),60-75. https://doi.org/10.3969/J.ISSN.1672-0911.2023.03.060

Zhou, L., Ge, E., Micheletti, A. J. C., Chen, Y., Du, J., & Mace, R. (2022). Monks relax sibling competition over parental resources in Tibetan populations. *Behavioral Ecology*, *33*(6), 1070–1079. https://doi.org/10.1093/beheco/arac059

Zou, Z. (2006). *Monk’s System in Tibetan Buddhist Temple and Ecological Environment in Tibetan Area-View of the South Gansu Tibetan Area during the Period of Republic of China*. Shanxi Normal University.

Supplementary information for Manuscript titled ‘Kin selection and sexual conflict drive the duration of breastfeeding’ - considerations for causal inference

The following document provides additional information for the manuscript titled ‘Kin selection and sexual conflict drive the duration of breastfeeding’. It is organized in 5 sections, as follows: Section 1 provides ethnographic details of the studied populations. Section 2 describes the data on genetic relatedness, how these were generated and the issues they represent for statistical inference. Section 3 describes in detail the variables used in the analysis and the inferential strategy, which uses a Direct Acyclic Graph to state assumed causal relationships between the variables and clearly describes how the hypotheses compared by this manuscript would affect the data. Section 4 includes additional information on the survival analysis method employed for this paper. Section 5 describes the steps taken to verify that the covariance between genetic relatedness data in our sample would not make it impossible to compare the different hypotheses presented here.

1 Study populations

This study collected data from five Tibetan populations in western China, comprising 350 female respondents and a total of 580 children. Each population exists in diverse ecological, economic, dialectal, and cultural landscapes, yet they share the same religion and governmental structure. The regions studied include two locations in the Gannan Tibetan Autonomous Prefecture of Gansu province (Zhuoni and Maqu), two in Sichuan province (Zhaba and Lugu), of which Zhaba belongs to Garzê Tibetan Autonomous Prefecture, and one (Shangrila) in the Diqing Tibetan Autonomous Prefecture of Yunnan province.

Individuals living in Zhaba and Lugu are part of matrilineal groups where female family members inherit most of the family resources, and grandmothers are the heads of the households (Wu et al., 2013). Families in these regions tend to live in large communal houses, with brothers and sisters of three generations residing together. Men visit their wives at night, but do not live with them or their offspring, a practice known as ‘walking marriage’ or ‘visiting marriage’. This post-marital residence system is referred to as ‘duolocal residence’ (Wu et al., 2013). Men invest more resources in their natal families rather than their wives’ families (He et al., 2022, Wu et al., 2013; Chen et al., 2023). There was some polygamy in the past (Shih, 2009; He et al., 2022). The people in Zhaba and Lugu primarily rely on farming as their main source of income. During the summer, they collect mushrooms, and those living near the river run guest houses during the tourist season as an additional income source (Mattison, 2010). Domestic labour, except for building work, is mostly performed by women. Men are rarely seen in the fields, except during planting and harvest times, and are more regularly involved in income-generating activities associated with the market economy (Chen, 2023).

Tibetans living in Amdo are called Amdobas. Amdobas who practice farming alongside herding are known as Rongbas, while nomadic herders who cannot rely on farming as their main subsistence are called Brogpa. In this study, Tibetans living in Maqu are referred to as Brogpa, whereas those living in Zhuoni are called Rongbas. The Rongbas from Zhuoni are agro-pastoralists and have been more influenced by Han Chinese culture compared to the Maqu Brogpas. The Brogpa in Maqu lead a more traditional pastoral lifestyle, with livestock and their dairy byproducts being the main sources of income. Some Brogpa also collect yartsa gumbu (Chinese: 冬虫夏草) in late spring and early summer, but this source of income is reducing from 2008, for the sake of grassland protection policy (Fan, 2005; Xiang and Wang, 2023). For Rongbas in Zhuoni, yaks, sheep, and pigs are important sources of family income. They also grow barley, wheat, soybeans, and potatoes to feed livestock and for family consumption (Zhou et al., 2022). The younger generations are now significantly influenced by market integration, often finding labour work in towns or cities. Polygyny, polyandry, and serial monogamy were more commonly practiced in Maqu's history than after 1980. At the time of the interview, there were only five cases of fraternal polyandry in Maqu (Du, 2017). It is rare for Brogpa in Maqu to marry individuals from other ethnic groups, whereas Rongbas in Zhuoni frequently marry Han and other ethnic minority groups. Both populations practice a patrilineal system, where men are the leaders of the family and hold absolute authority and power. However, our previous work in Maqu has shown that the absolute dominance of males is changing due to women's irreplaceable contribution to the family economy (Du and Mace, 2018).

Shangrila is in Diqing Tibetan autonomous prefecture, Yunnan province. This area is comprised of half-farming and half-pastoral land. The majority of the people living here are Tibetans, sharing a Tibetan dialect that differs from that of other regions (Wang, 2018; Leanwangdui, 2003).Traditionally, Shangri-La Tibetans had three forms of marriage: polyandry, polygyny and monogamy (Wang, 2021), but the population now is predominately monogamous (Leanwangdui, 2003). Both exogamous and endogamous marriage are common, though parents have power in deciding who their children marry, preferring marriages with natal or neighbouring village members (Wang 2021). First born children, irrespective of sex, commonly co-reside with their parents and stay at their natal family after marriage and inherit parental wealth, whereas later born will either marry into other villages or stay in the same village, albeit not in the same house as their parents. It is rare to get married outside of the township (Du et al., 2023; Zhou, 2010).

In all regions, the education level was relatively low, but the situation improved somewhat when compulsory education was implemented in China (Wu, 2013; Du, 2017). Additionally, the family structure shifted from traditional extended families to more nuclear households following the implementation of the one-child policy in the late 1980s. Under this policy, most Han Chinese were allowed to have one child, while Tibetans were permitted to have two to three children, depending on the specific ethnic minority area they lived in (Attané and Courbage, 2000). In this study, we use village as a proxy for geographical and ecological differences between these groups and for ethnicity, which is linked to cultural practices and prevalent subsistence strategies (Chen et al., 2023). In Maqu, where the population density is very low, we define a village as several families that stay in the same herding group which usually involves sharing pastureland and adhering to the same social norms regarding herding and production. In the other four areas, a village refers to natural villages (Chinese: 自然村) that are primarily based on geographical factors. Although individuals living in the same village or herding group are geographically close to each other, and they do help each other in the harvesting time (Bai et al., 2021;Thomas, 2018), household is still the central unit of daily activities, as resources do not flow between households. For Amdo Tibetans, pastureland were privatized, so the size of land each family got depends on the size of the family member (Du and Mace, 2018; Bai et al., 2021). In Lugu and Zhaba, farming and herding are mainly for family consumption, and other forms of labour income will not be shared between each households (Mattison, 2010).

Note that even though most people living in each of the five regions follow the main descendance pattern (matrilineal vs patrilineal), not all couple reside accordingly, e.g. some families can follow a matrilocal residence pattern in a patrilineal community and so on.

2 Genetic relatedness and why it can cause problems to causal inference

The present paper leverages genetic relatedness of individuals within a household as a measure of their bargaining power to define breastfeeding duration, i.e. their ability to define how long should a child be breastfed according to their (fitness) interests. We consider genetic relatedness of each focal child and that of their parents to the rest of the household.

Note that this is calculated *relative to the child's household*, so that, if the father is not co-resident with the child, their average relatedness is set to zero to represent the fact that absent fathers cannot influence decisions on breastfeeding duration. The values have been calculated from pedigree data with the R package `Kinship2`, version 1.9.6 (Sinnwell et al., 2014).

As described in the main text, we posit that the child's interest is to prolong breastfeeding as long as possible, as breastfeeding is associated with better health outcomes. Parents, on the contrary, should prefer a shorter breastfeeding duration in order to move on to produce new offspring, creating the conditions for a parent-offspring conflict. But the parents themselves have different investment in the length of the duration, which per se generates intersexual conflict. In particular, the mother is expected to prefer a longer breastfeeding duration, as females are expected to invest more in each offspring, while men should prefer shorter duration, as they have an interest in increasing the number of offspring rather than the quality. Additionally, social conditions and labour requirements at the household level influence breastfeeding duration, as breastfeeding women cannot engage in several productive activities or have limited labour outputs (reduced hours of work, reduced production per hour). We hence expect that in households where the mother has higher average relatedness to the rest of the members, these are more likely to cover for her missing labour and thus favour longer breastfeeding duration compared to households where the father has higher relatedness.

As mentioned, this approach hinges on using on the average relatedness level of children and parents to the household as a predictor of breastfeeding duration, which creates problems for causal inference, as the genetic relatedness of parents and offspring is tightly correlated by mechanisms of genetic inheritance. Because offspring inherit half of the chromosomes from each parent, children are always 0.5 related to each of their parents. The relation between the average relatedness to the whole household of children and that of the parents, however, depends on the structure of the household itself. In a case limit where the household is composed by only a child and their unrelated parents, the relatedness of the parents to the rest of the household is $\frac{0.5+0}{2} = 0.25$, as each parent shares half of their genome with their child and none with the partner. The child shares half of their genome with each parent, making the child's average relatedness $\frac{0.5+0.5}{2} = 0.5$ equivalent the sum of their parents' average relatedness $0.25 + 0.25 = 0.5$. But parents can also be related to each other, and as the number of the member of a household increases, the average genetic relatedness of a child to the rest of the household approximates the sum of the relatedness of the parents divided by two $\frac{relatednessMother+relatednessFather}{2} = relatednessChild$ (for example in the limit case where there is an infinite number of siblings of the focal child, each related 0.5 to both the parents and the focal child, i.e. where everyone is approximately 0.5 related to each other, given that the fact that the parents are not related to each other would be swamped by the infinite number of siblings all 0.5 related to both parents and focal child, or $\frac{0.5+0.5}{2} = 0.5$)[1]. This is important because it imposes a serious collinearity problem to the children's and parents' relatedness (and it guides our simulation exercise, see below).

Differences in household composition and in relatedness between the parents (who can be cousins, for example) generate variation in the ratio of parents' and children's relatedness. The area of western China where data was collected offers just such variation, as there coexist multiple ethnic groups who differ in preferred residence patterns. Moreover, not all households within an ethnic group follow the mainstream residence type. This creates a reasonable amount of variation between and within ethnic groups in choice of residence (i.e. duolocal, matrilocal, neolocal or patrilocal). The resulting variability in how related are individuals within a household (see figure 1, main text) can be leveraged for the statistical analysis. SI Table 1 reports average relatedness between Mothers, Fathers and Children and the rest of their households by residence type (at the household level).

Table 1: Average relatedness of mothers, fathers and children to other household members.

	Duolocal (N=128)	Matrilocal (N=131)	Neolocal (N=132)	Patrilocal (N=189)	Total (N=580)
Mother					
Mean (SD)	0.41 (0.08)	0.38 (0.05)	0.32 (0.08)	0.19 (0.07)	0.31 (0.11)
Range	0.17 - 0.50	0.20 - 0.50	0.14 - 0.50	0.05 - 0.38	0.05 - 0.50
Child					
Mean (SD)	0.31 (0.08)	0.36 (0.08)	0.45 (0.07)	0.36 (0.08)	0.37 (0.09)

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[1] Note that these represent limit cases used to illustrate the range of mathematical relations between parents' and child's relatedness values

	Duolocal (N=128)	Matrilocal (N=131)	Neolocal (N=132)	Patrilocal (N=189)	Total (N=580)
Range	0.16 - 0.50	0.10 - 0.50	0.23 - 0.50	0.10 - 0.50	0.10 - 0.50
Father					
Mean (SD)	0.00 (0.00)	0.19 (0.11)	0.31 (0.11)	0.38 (0.06)	0.24 (0.17)
Range	0.00 - 0.00	0.00 - 0.43	0.00 - 0.48	0.08 - 0.50	0.00 - 0.50

However, the significant correlation between parents' and children's relatedness can generate problems for causal inference and requires careful consideration. We thus develop a workflow that aims on the one hand to define a causal inference strategy for causal effects of relatedness on breastfeeding duration. On the other hand, we attempt to address in a principled way how predictions driven by competing hypotheses manifest themselves in the data, controlling for the risk of equifinality, as generated by covariation in the genetic relatedness data. We begin by using Direct Acyclic Graphs (DAGs) as a tool to illustrate causal connections between the relevant variables (see next section). This helps in one hand to construct statistical models that are able to produce the correct inference to understand the effect of the relevant variables (i.e. define causal queries and choose the appropriate control sets), but also as a lead to build simulations. The use of simulations is helpful in this case to guide our intuition on what the statistical models can tell us about the *real* effects of genetic relatedness. Because of the correlation in genetic relatedness, we could observe the phenomenon of equifinality: different causal models can produce the same distribution in the data and thus be practically non-distinguishable in the real data (e.g. the model could estimate the same values for parameter relative to the effect of mother's relatedness if the causal effect came from *her* relatedness or from that of her child). Simulating data according to realistic relatedness patterns and following different causal models allows us to observe in a controlled (simulated) setting *what* the statistical models can tell us (i.e. which hypotheses are virtually indistinguishable in the real data), but also guide us in the interpretation of the results of the analyses on the real data.

2.1 Estimating multicollinearity

While collinearity between relatedness of family members *must* arise from the combination of residence strategies and genetic inheritance, standard measures of multicollinearity do not reveal an excessively problematic pattern. Variance Inflation Factor values for a linear regression including child, mother and father as predictors are 2.32 , 2.64 and 3.32 respectively. While these values indicate that some collinearity is present (obviously) they are well within the threshold of 5 usually considered problematic. A calculation of correlations (correlation matrix) returns values below the warning level of 0.7 (mother-child: 0.14, father-child: 0.42, mother-father: -0.63). This means that, while we still believe that it is important to address the necessary correlation between the average relatedness of parents and children, the coefficients returned by the statistical models we used should be reliable, at least in the direction of the correlation, if not as precise.

Additional concern could be raised by the observation that mothers' and fathers' relatedness appears to be negatively correlated (-0.63 in the correlation matrix). This arises because of the clustering within matrilocal and patrilocal households, where mothers and fathers are respectively more related to the rest of the household. Once controlling for residence pattern, no correlation appears within patrilocal or duolocal households, a positive correlation emerges within matrilocal households and a negative correlation still appears within neolocal households (see figure SI1). This depends on relocation strategies, as most likely the relatives beyond the nuclear family do not join a household independently. Or, once someone from the matriline or patriline moves in, it is more likely the other people from that side of the family join the household (e.g. John's sister moves in with her three kids, but then Mary's sister cannot also move because of lack of space). Indeed, the majority of focal children in neolocal households lives in medium or large households (87%), and in 29 of these families, other individuals that are not part of the nuclear family (reproductive couple and their children) live under the same roof. These are most commonly grandparents (~70% of the non-nuclear family members of the household), following a widespread pattern in which widowed or otherwise lonely older individuals move in with their children. These are obviously related to either the mother or the father of the focal child, and it is very unlikely that grandparents from both sides join the same households, thus creating a negative relatedness pattern. Similarly, unpartnered siblings of the reproductive couple can join the household, sometimes bringing together their offspring (12% of non-nuclear family members of the household are aunts and uncles and 2% are cousins). Finally, half siblings of the focal child and great-grandparents can also join a neolocal household.

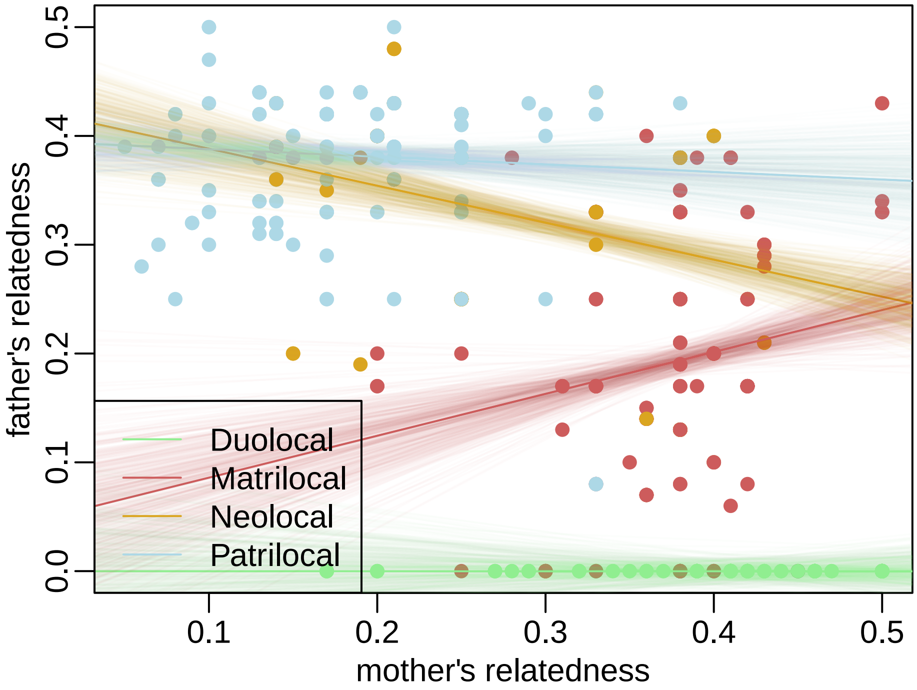

Figure 1: Correlation between mothers' and fathers' relatedness by residence strategy. Green represents Duolocal; Red represents Matrilocal; Yellow represents Neolocal; Blue represents Patrilocal.

Ultimately, while the correlation between the average relatedness of family members is is a feature of the data and unavoidable within this dataset, we believe that the data will yield the relevant information, given that the level of multicollinearity is estimated to be relatively low and should not distort the results.

3 Variables used and inference strategy

We first describe all the variables considered in the analysis and ways by which they influence the outcome, before describing the causal inference strategy we used.

3.1 Description of variables

- Age at stop breastfeeding: this is our outcome variable. It is the age at which the child was not breastfed anymore. SI figure 2 shows the duration of breastfeeding in our sample. The majority of mothers wean within the first 12 months (66%) and only 13% takes longer than two years (although we can see a large variation by residence type, as only 11% of mothers in neolocal households breastfeed after this time). Note that values corresponding to yearly marks are much more frequent than expected at random. This can reflect a real phenomenon, i.e. children are more likely weaned at round years, because of cultural reasons, for example. But it is more likely that people tend to answer to uncertain, time-related questions with round numbers (a phenomenon known as age-heaping when the question is ‘how old are you’). At least in part to deal with these issues, the data used for this analysis has been censored at 2 years (i.e. number of months up to 24 during which each child was breastfed, not exclusively). Moreover, some of the data is censored because of time of observation: a mother of a fifteen months old child reports she is still breastfeeding, but we have no information on how long that will last. Note that the variable used in the analysis is the similar column named ‘time’, which contains the same information unless the data is censored at 24 months, in which case it contains the number 24 (this passes the correct censored values to the model). Moreover, the variable ‘status’ indicates whether the data has been censored or not.

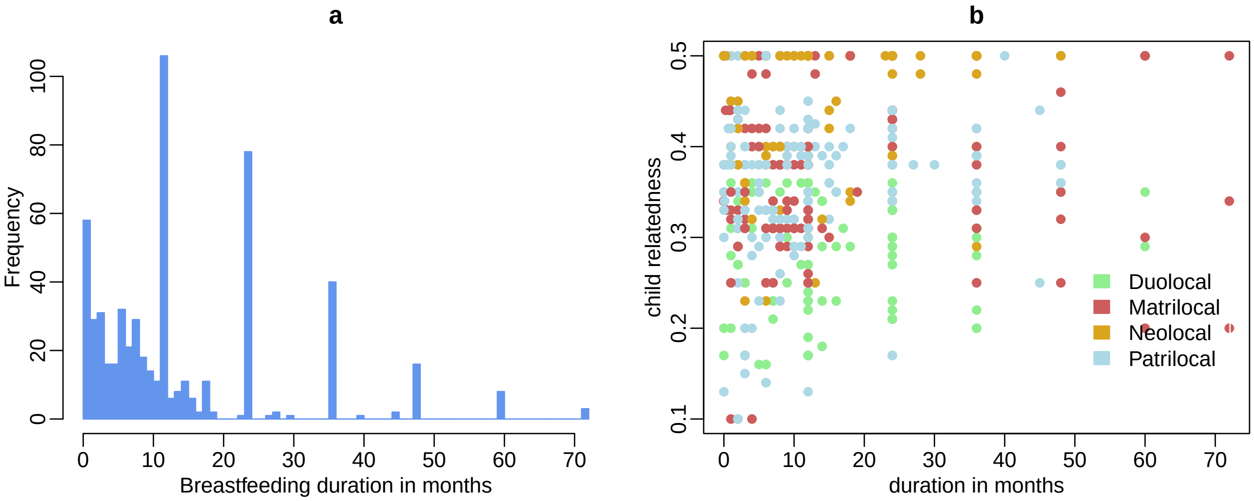

Figure 2: a - Histogram showing the duration of breastfeeding in our sample. Note the heaping at values corresponding to yearly marks. b - Duration of breastfeeding by child relatedness, color coded by residence pattern.

- Child relatedness: one of the main predictors, estimated genetic relatedness of the focal child to the rest of their household given the reported family relations (parents are on average 0.5 related to their children, grandparents 0.25 and so on; the relatedness for the parents is similarly calculated, see notation in the main text). We expect longer duration of breastfeeding the higher the average genetic relatedness to the household, under the assumption that in a more related household the interests of the child (longer duration of breastfeeding) count more.
- Mother relatedness: see child relatedness for the calculation of this measure. The mother optimal breastfeeding duration is influenced by her cost in producing milk, her interest in her child’s well-being and the opportunity cost of not doing something else
- Father relatedness: see child relatedness for the calculation of this measure. Fathers’ interests are likely associated with a shorter duration of breastfeeding, as he is expected prefer having another baby sooner than the mother’s preference (breastfeeding inhibits the luteal cycle thus rendering women temporarily infertile).
- Village: Data was collected across the Zhaba, Lugu, Zhuoni, Maqu, and Shangrila regions, each comprising numerous distinct villages. Village is used as a proxy for geographical/ecological differences between these groups and for ethnicity, which is linked to cultural practices and prevalent subsistence strategies that can influence breastfeeding duration. The prevalence of residence patterns varies in each region, see SI Table 2, for example Duolocality is prevalent in Zhaba (53.4% of households), present in Lugu (16.5%) and completely absent in Zhuoni, Maqu and Shangrila, the last of which is prevalently matrilocal (47%), while the remaining two are largely patrilocal.
- Residence pattern: one between duolocal (each parent remains within their natal household, relatedness of the mother is highest, lowest for the father), matrilocal (the couple lives with the wife’s family, relatedness is high for the child and mother, low for the father), neolocal (the couple lives in a new household, relatedness is lower and similar for mother and father, high for the child) or patrilocal (the couple lives with the husband’s family, father and child have high relatedness, lowest for the mother). We assume that any cultural effect linked to residence pattern is clustered at the level of village (ethnicity), rather than residence pattern.

- Household size: The people you live with can greatly influence the amount of assistance you receive; in some cases, it also determines the number of potential competitors you may face. Therefore, the size of the household is crucial for breastfeeding practices, as it is associated with the level of direct support (such as bottle-feeding infants) or indirect support (such as relieving the mother of household chores so she can focus on breastfeeding) that the mother can receive during her breastfeeding journey. Household size ranges from 2 to 22, with a median 7.
- Birth order: Siblings compete for family resources, a competition that begins from birth. For instance, if a mother breastfeeds one child for an extended period, it may delay her ability to have another baby. The intensity of this competition varies between full and half-siblings, as noted by Trivers in 1974. Parents might exhibit a preference for the older offspring, a phenomenon known as primogeniture, which has been documented in one of the populations from the same database (Du et al. 2023). However, parents may also show a preference for the youngest child, particularly in contexts where child policies reduce the likelihood of having more children. In this paper we present this variable as either 1st born or >=2nd born. This is because we only included births after 2010 (to improve accurate recalling of breastfeeding information), by which point the area was interested by a fully implemented child policy (a maximum of 3 children per woman in this area). As a result, our data include only 4 births of a 3rd child, which were thus classified together with 2nd borns.
- Child sex: Parents may exhibit gender-biased parental investment, with preferences that vary according to ecological and social norms. In one of our studied populations, we have previously demonstrated that mothers tend to breastfeed daughters longer than sons (Du & Mace 2018). However, the patterns of gender-biased investment across five different populations remain unclear. To address this, we controlled for the gender of the offspring in our analysis, categorizing them into two groups: daughters/females and sons/males.
- Mother cohort: the middle and latter half of the 20th century saw a gradual decline of breastfeeding, which was replaced by formula feeding in many high-income contexts (Tomori et al., 2016). We controlled for mother birth time at 10 years cohort, which could capture how globalization influences the norm and the practices of feeding. In addition, several political factors might also influence the feeding practices, for example, child policy that was implemented in the early 1980s, and the compulsory education policy that was implemented at 1990s. We thus categorized mother birth into 10 years cohort: <=1980, 1980-1989 to >=1990
- Physical constraints: physical problems are one of the important reasons for terminating breastfeeding (Verronen, 1982; Page et al 2021), i.e. sore and cracked nipples, painful breasts and poor latching et al (Li et al., 2008) are commonly reported as important problems and act as a barrier to continued breastfeeding. Individual data on physical constraints was unfortunately not available for this analysis. In the DAG, this information falls within the unknowns labeled as U.
- Household wealth: higher household wealth is expected to be associated with longer breastfeeding if mothers' labour is needed in poorer households, or shorter if alternative food sources are a limiting factor for weaning. Detailed data on household wealth was unfortunately not available for this analysis. Similarly, ithis information falls within the unknowns labeled as U in the DAG.

Table 2: Descriptive statistics by ethnic group.

	LuGu (N=103)	MaQu (N=121)	ShangriLa (N=83)	ZhaBa (N=208)	ZhuoNi (N=65)	Total (N=580)
Residence						
Duolocal	17 (16.5%)	0 (0.0%)	0 (0.0%)	111 (53.4%)	0 (0.0%)	128 (22.1%)
Matrilocal	15 (14.6%)	27 (22.3%)	39 (47.0%)	37 (17.8%)	13 (20.0%)	131 (22.6%)
Neolocal	37 (35.9%)	35 (28.9%)	14 (16.9%)	35 (16.8%)	11 (16.9%)	132 (22.8%)

	LuGu (N=103)	MaQu (N=121)	ShangriLa (N=83)	ZhaBa (N=208)	ZhuoNi (N=65)	Total (N=580)
Patrilocal	34 (33.0%)	59 (48.8%)	30 (36.1%)	25 (12.0%)	41 (63.1%)	189 (32.6%)
Cohort						
<1980	11 (10.7%)	3 (2.5%)	1 (1.2%)	14 (6.7%)	5 (7.7%)	34 (5.9%)
>=1990	56 (54.4%)	60 (49.6%)	55 (66.3%)	140 (67.3%)	28 (43.1%)	339 (58.4%)
1980-1989	36 (35.0%)	58 (47.9%)	27 (32.5%)	54 (26.0%)	32 (49.2%)	207 (35.7%)
Birth order						
1st	38 (36.9%)	51 (42.1%)	57 (68.7%)	112 (53.8%)	20 (30.8%)	278 (47.9%)
2nd	65 (63.1%)	70 (57.9%)	26 (31.3%)	96 (46.2%)	45 (69.2%)	302 (52.1%)
Gender						
daughter	55 (53.4%)	55 (45.5%)	39 (47.0%)	106 (51.0%)	29 (44.6%)	284 (49.0%)
son	48 (46.6%)	66 (54.5%)	44 (53.0%)	102 (49.0%)	36 (55.4%)	296 (51.0%)
Household						
Big	27 (26.2%)	31 (25.6%)	30 (36.1%)	74 (35.6%)	20 (30.8%)	182 (31.4%)
Medium	66 (64.1%)	50 (41.3%)	50 (60.2%)	115 (55.3%)	44 (67.7%)	325 (56.0%)
Small	10 (9.7%)	40 (33.1%)	3 (3.6%)	19 (9.1%)	1 (1.5%)	73 (12.6%)
Duration						
Mean (SD)	14.6 (9.9)	19.0 (19.3)	8.0 (3.2)	16.5 (13.0)	7.3 (6.4)	14.4 (13.3)
Range	0.0 - 48.0	0.0 - 72.0	1.0 - 14.0	0.0 - 72.0	1.0 - 36.0	0.0 - 72.0
Mother						
Mean (SD)	0.3 (0.1)	0.3 (0.1)	0.3 (0.1)	0.4 (0.1)	0.2 (0.1)	0.3 (0.1)
Range	0.1 - 0.5	0.1 - 0.5	0.0 - 0.4	0.1 - 0.5	0.1 - 0.4	0.0 - 0.5
Child						
Mean (SD)	0.4 (0.1)	0.4 (0.1)	0.3 (0.1)	0.4 (0.1)	0.3 (0.1)	0.4 (0.1)
Range	0.2 - 0.5	0.1 - 0.5	0.1 - 0.5	0.1 - 0.5	0.1 - 0.5	0.1 - 0.5
Father						
Mean (SD)	0.3 (0.2)	0.3 (0.1)	0.3 (0.1)	0.1 (0.2)	0.3 (0.1)	0.2 (0.2)
Range	0.0 - 0.4	0.0 - 0.4	0.0 - 0.4	0.0 - 0.5	0.1 - 0.5	0.0 - 0.5

3.2 A digression on causes for weaning

The current section reports information on the causes women adduce for stopping breastfeeding, introducing further details over table 4 in the main text. Across the populations, the majority of causes are relative to social norms or opportunity costs (27% and 36% respectively). But once we split by residence pattern, opportunity cost becomes a much more prominent cause in patrilocal households (57%, see table 4 in main text).

Table 3: Reported reasons for weaning, categorized into physical costs, social norms, opportunity costs and other reasons.

category	Reasons for weaning	count	total (%)
Physical costs	Mastitis	1	7 (16 %)
	Constantly ill	2	
	Sterilization surgery	1	
	Not enough breast milk	3	
Social norm	I heard that the breast milk has become clear , lacking fat	1	12 (27 %)
	Family members say that the breast milk is no longer nutritious	3	
	The child keeps crying because the milk is not good	1	
	Several of my friends weaned their children at this time	3	
	If the feeding time is too long, it's not easy to wean	1	
	Most people around me wean at this time	3	
Opportunity cost	It's too time-consuming, I can't do long-distance work	6	16 (36 %)
	Frequent breastfeeding can lead to breast engorgement , affecting farm work	2	
	Can't go out to work	5	
	Went to help with work at my sister's house for a while	1	
	Went off to work	2	
Other	The child sleeps with the grandmother, so he / she doesn't eat my breastmilk	1	9 (20 %)
	The child refuses to eat	5	
	Stopped breastfeeding after getting pregnant with the second child	2	
	I don't want to breastfeed	1	

3.3 Direct Acyclic Graph and causal inference strategy

Our causal inference strategy relies on estimating the relative effects of children's and parents' relatedness on breastfeeding duration. We considered a set of covariates that could influence the results, as described in the previous section. According to our proposed causal structure, shown in Figure 6 in the main text, a minimum set of controls for correctly estimating the direct effects of individuals' relatedness include only village, household size and mother's cohort in addition to our estimands (model 3). To estimate the total effect of residence strategy (model 2), we do not control for household size. In both models, we also control for sex of child, birth order of child, cohort of mothers and random effects for mothers' IDs, which help the estimate. The linear regression for the cox model 3 used to report the results of the effect of individual's relatedness on breastfeeding duration includes as predictors: child relatedness, mother relatedness, father relatedness, sex of child, household size, child birth order, cohort of mother, village and mothers' IDs as random effects (see section 4).

In order to estimate the total effect of residence pattern on breastfeeding duration, model 2, which summarizes the separate effects of the various relatedness structures, the minimum adjustment set (i.e. which control variables need to be considered to obtain a reliable causal inference) includes only village, to which we add sex of child, birth order of child, cohort and random IDs for mothers, to increase the precision of the estimate. The linear regression for the cox model used to report the results of the effect of residence pattern on breastfeeding duration includes as predictors: residence pattern, sex of child, child birth order, birth cohort of mother, village and mothers' IDs as random effects. Note that while household size is an appropriate control variable for the control model and for a model aiming to estimate the effect of mother, father and child relatedness on breastfeeding duration, it should not be included in a model that aims to estimate the total effect of postmarital residence strategy. It is indeed on the downstream path between postmarital residence strategy and breastfeeding duration.

The following section will help elucidate why these models are appropriate for testing the predictions for the hypotheses considered and provide additional material for inference.

3.4 Hypotheses and causal models

While we believe that the statistical models presented above report the correct estimates for our predictors, the causal interpretation of these estimates require careful consideration. Because of the genetic mechanism correlating children's and parent's relatedness to the rest of the family, we aimed at improving our ability to parse out between different predictions associated to the hypotheses. We recur to the use of simulations to address the problem of equifinality and better understand how different cox models are able to pick up on the differences between data associated to generative causal models.

We start by reviewing the main hypotheses, the causal models associated with these hypotheses, i.e. the expected directions of the effects of the variable, and the reasons why it can be difficult to compare them, before moving on to simulation, testing and interpretation.

Parent-offspring conflict: We expect the child's relatedness to have a positive effect on the duration of breastfeeding, while parents' relatedness would have a negative effect.

Sexual conflict: We expect mothers' relatedness to have a positive effect on the duration of breastfeeding, while father's would have a negative effect

This would result in longer breastfeeding expected in households where the child has higher than average relatedness and shorter where the father has higher relatedness. However, intermediate duration is consistent with both hypotheses, as we can see when we simulate them.

4 Survival analysis

We use tools from survival analysis to address the duration of breastfeeding in our sample. In particular, we employ semiparametric cox models, with a set of linear predictors defined depending on the inferential goal of the analysis, for which we define informative priors.

4.1 Cox Likelihood

The Cox proportional hazards model is used to estimate the effect of covariates on the hazard rate of an event, accounting for censored data. The likelihood is based on comparing the relative risks of individuals who are still at risk at the time of an observed event.

For each individual i with an observed event, the likelihood is given by the following partial likelihood:

$$L(\theta) = \prod_{i \in R(t)} \frac{\exp(\theta_i)}{\sum_{j \in R(t)} \exp(\theta_j)}$$

Where: - $R(t)$ is the risk set at time t_i, consisting of individuals who are still at risk at time t_i (i.e., have not experienced an event before t_i). - $\exp(\theta_i)$ is the risk for individual i, where θ_i is the linear predictor. - The denominator sums the risks of all individuals in the risk set at time t_i, ensuring that the likelihood reflects the relative hazards among those at risk.

In the model, the log of the sum of risks for individuals at risk is subtracted from the individual's own risk, capturing the proportional relationship between individuals' risks at each event time.

This formulation allows for the estimation of regression coefficients for covariates, accounting for censored data while modeling the hazard (expressed as log hazard coefficients) for each individual relative to others at risk.

4.2 Linear models

The linear predictor θ_i for each individual i is defined differently for each model employed.

Model 1:

$$\theta_i = \omega + \gamma_{\text{sex}[i]} + \kappa_{\text{ord}[i]} + \epsilon \cdot \sum_{y=1}^{\text{hsz}[i]} \delta_y + \zeta_{\text{coh}[i]} + \eta_{\text{vil}[i]} + \iota_{\text{mid}[i]}$$

Model 2:

$$\theta_i = \omega + \alpha_{\text{res}[i]} + \gamma_{\text{sex}[i]} + \kappa_{\text{ord}[i]} + \zeta_{\text{coh}[i]} + \eta_{\text{vil}[i]} + \iota_{\text{mid}[i]}$$

Model 3:

$$\theta_i = \omega + \sum_{k=1}^{K} \beta_k \cdot \text{rel}_{ik} + \gamma_{\text{sex}[i]} + \kappa_{\text{ord}[i]} + \epsilon \cdot \sum_{y=1}^{\text{hsz}[i]} \delta_y + \zeta_{\text{coh}[i]} + \eta_{\text{vil}[i]} + \iota_{\text{mid}[i]}$$

Where:

- ω is the intercept term.
- α is the effect associated with each residence strategy.
- β_k are the coefficients for each of the individuals' relatedness rel_{ik}, the relatedness of individual k between child, father and mother.
- $\gamma_{\text{sex}[i]}$ represents the effect of sex (a binary variable: male or female).
- $\kappa_{\text{ord}[i]}$ represents the effect of birth order (also a binary variable).
- ϵ is the coefficient for household size, which is modeled as a monotonically increasing categorical variable.
- δ_y modulates the household size-specific effects, which are parameterized by a Dirichlet prior and reflect the varying effects of household size. This adds a small increase of the total effect ϵ per each additional household members up to the household size y, allowing for non-linear variation of the outcome with household size (variables with monotonically increasing effects can be modelled by two parameters, δ,which represents the unit specific effect, and δ_y, or the sum of effects up to y units, the number of household co-residents for individual i).
- $\zeta_{\text{coh}[i]}$ represents the effect of mother cohort as a random effect.
- $\eta_{\text{vil}[i]}$ captures the village-level multilevel random effect.
- $\iota_{\text{mid}[i]}$ represents the mother-level random effect.
- K is 3, or the total number of relatedness parameters β_k, i.e. mother's father's and child's parameter.

4.3 Priors

The model assigns the following priors to its parameters:

$$\begin{aligned} \omega &\sim \mathcal{N}(0, 2) \\ \alpha, \beta, \gamma, \kappa, \epsilon, \zeta &\sim \mathcal{N}(0, 1) \\ \eta &\sim \mathcal{N}(0, \sigma_\eta) \\ \sigma_\eta &\sim \text{Exponential}(1) \\ \iota &\sim \mathcal{N}(0, 0.5) \\ \delta &\sim \text{Dirichlet}(2) \end{aligned} \tag{1}$$

These are simple informative priors designed to restrict the spatial search of the MCMC chain. Note that the intercept ω is assigned a different prior in the case of Model 3 in order to stabilize the model and does not hold inferential value. Values for η are pooled across villages by the standard deviation σ_η.

4.4 Full results from cox models

Here we report estimated log Hazard coefficients for the three main cox linear regression models.

Table 4: Results from Bayesian Cox regression models predicting factors associated with likelihood of weaning, censored at two years old. Log Hazard Coefficients (LHC, positive values mean higher hazard, associated with shorter breastfeeding duration), and 89% Percentile Intervals (PI). Model 1: the Control model (accounting for child sex, child birth order, mother's birth cohort, and household size). Model 2: residence pattern effect, with control model, except household size, plus post-marital residence. Model 3: includes, Control model plus child, mother and father's average relatedness to other household members. The Hazard Ratio (HR) is indicated; a value greater than 1 suggests a higher likelihood of breastfeeding termination, while a value less than 1 indicates a lower likelihood.

	Model 1 - LHC (89%PI)	Model 2 - LHC (89%PI)	Model 3 - LHC (89%PI)
Household size	1.2 (0.45 , 1.99)		0.7 (-0.22 , 1.58)
Daughter	-0.03 (-1.15 , 1.12)	-0.02 (-1.13 , 1.16)	-0.04 (-1.15 , 1.14)
Son	0.02 (-1.08 , 1.18)	0.05 (-1.06 , 1.23)	0.02 (-1.1 , 1.19)
1st child	0.05 (-1.09 , 1.17)	0.09 (-1.08 , 1.2)	0.09 (-1.04 , 1.24)
2nd child	-0.1 (-1.23 , 1.01)	-0.04 (-1.2 , 1.07)	-0.04 (-1.2 , 1.11)
Mother cohort <1980	0.05 (-0.92 , 0.99)	-0.04 (-1.01 , 0.88)	0.02 (-0.93 , 1.01)
Mother cohort 1980-89	0.01 (-0.97 , 0.98)	-0.03 (-1.02 , 0.89)	0.02 (-0.93 , 1.01)
Mother cohort >=1989	-0.03 (-1.01 , 0.98)	-0.01 (-1.05 , 0.93)	0.02 (-0.93 , 1.01)
Duolocal		-0.37 (-1.18 , 0.43)	
Matrilocal		0.03 (-0.8 , 0.84)	
Neolocal		-0.09 (-0.91 , 0.71)	
Patrilocal		0.47 (-0.36 , 1.31)	
Child relatedness			-1.34 (-2.4 , -0.27)
Mother relatedness			-0.84 (-1.84 , 0.18)
Father relatedness			0.63 (-0.18 , 1.41)

5 Approach

Because of the high degree of multicollinearity in the relatedness variables, we employ a simulation-based strategy: by simulating data from parameter sets consistent with the competing hypotheses considered here, we can assess whether the model can distinguish among them when applied to the synthetic datasets. By comparing simulated and observed posterior distributions, we examine whether the data-generating mechanisms implied by different hypotheses could be observationally indistinguishable, helping us assess risks of equifinality.

This approach resembles an approximate Bayesian computation, or likelihood-free inference (Beaumont, 2010), and complements the more traditional statistical analysis, allowing to address an additional inferential difficulty. Moreover, because the Cox proportional hazards model is semiparametric and does not specify the baseline hazard function, standard posterior predictive checks are not straightforwardly applicable (Gelman et al., 2020). This limits the model's internal capacity for self-validation through simulated outcomes based on posterior predictions. The approach based on simulated data allows to address this limitation, functioning as an external adequacy test of the model's ability to differentiate among plausible causal structures, given the data and its constraints.

5.1 Simulate relatedness

We simulate N = 500 children and assign them to one of the four possible residence types (Duolocal, Matrilocal, Neolocal and Patrilocal). We then generate for each child the relatedness of the mother, father and child itself. The relatedness of the parents is sampled from normal distributions that match the real data for the four residence types (means of 0.4, 0.36, 0.3 and 0.22 for the mothers and 0.06, 0.22, 0.30 and 0.38 for fathers respectively, with a standard deviation around 0.1). For children, instead, we generate a relatedness level by summing the parents' relatedness and dividing by two and add a random value sampled from a Gaussian distribution with mean 0.1 and SD 0.05, which simulates variation in household structure within the residence pattern and brings the generated distribution closer to the observed distribution for children's relatedness by household (see SI Figure 3).

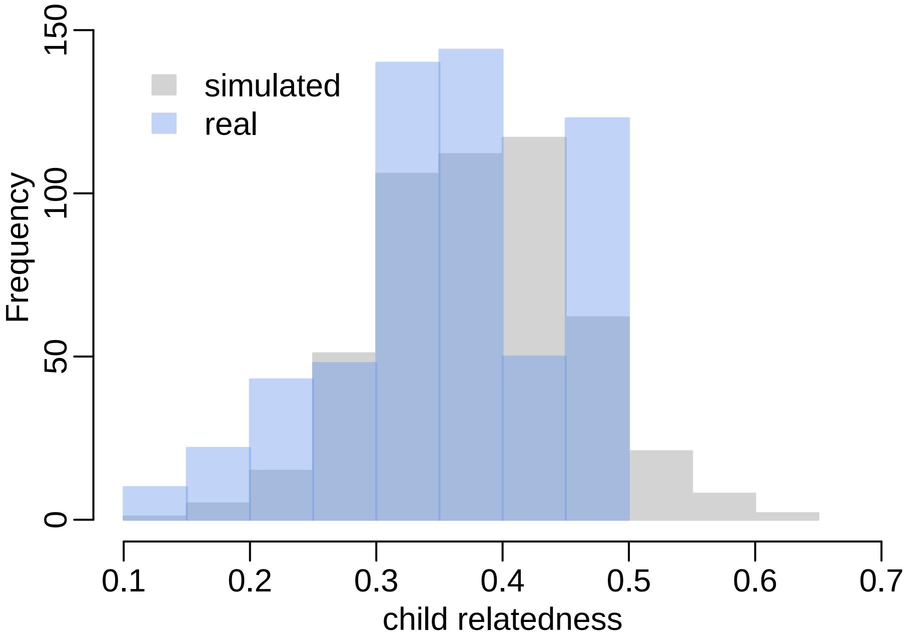

Figure 3: Real distribution of relatedness (grey) and simulated relatedness (blue).

Note that, because our simulation adheres to the generative process that produces the data in the real world, it inherently generates also a certain degree of multicollinearity observed in the real data. This happens even though we do not actively construct any correlation between mothers' and fathers' relatedness, because of the interdependencies of family members and residence strategy. Indeed, even though we simulated mother and father's relatedness independently, only from the distributions of these measures in the real data, the negative relationship emerges as a feature of these distributions. Calculating the correlation coefficients for children and parents' relatedness for both real and simulated data returns relatively similar results within the simulations and real data.

5.2 Generate simulated breastfeeding duration according to different causal models

We then generate duration of breastfeeding from these genetic relatedness (simulated) data we sample from a Poisson distribution which rate λ depends on a linear function of child and parent's relatedness (indicated in the equation below as C, M and D respectively). The parameters for the predictors χ, ψ and ϕ are selected depending on the two main alternative hypotheses and possible other scenarios, including a combination of

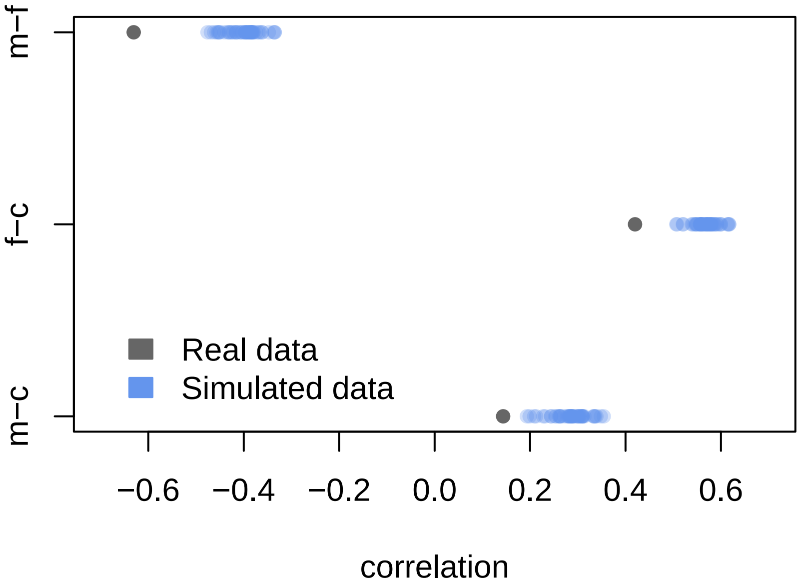

Figure 4: Multicollinearity in the real data (grey) and simulated (blue) calculated as a correlation matrix.

the two hypotheses (see SI table 5, which recapitulates table 1 in the main text plus an additional hypothesis considered here to add a case study).

$$Duration \sim \text{Poisson}(\lambda)$$

$$\lambda = \alpha + \chi C + \psi M + \phi D$$

Table 5: Hypotheses associated to causal models.

	Hypothesis	Child	Mother	Father
H1	Parents-offspring conflict	+	-	-
H2	Gender conflict	0	+	-
H3	Both	++	+	-
H4	No effect of parents	+	0	0

Note that the columns 'Child', 'Mother' and 'Father' indicate the expected direction of the effect for genetic relatedness as a predictor in the different hypotheses. According to the Parent offspring conflict hypothesis, the more a child is related to their household the longer they are breastfed, while it is the contrary for the parents, and so on. SI Figure 5 shows simulated duration of breastfeeding according to the parameters associated with the causal models above. The points are colored depending on residence strategy.

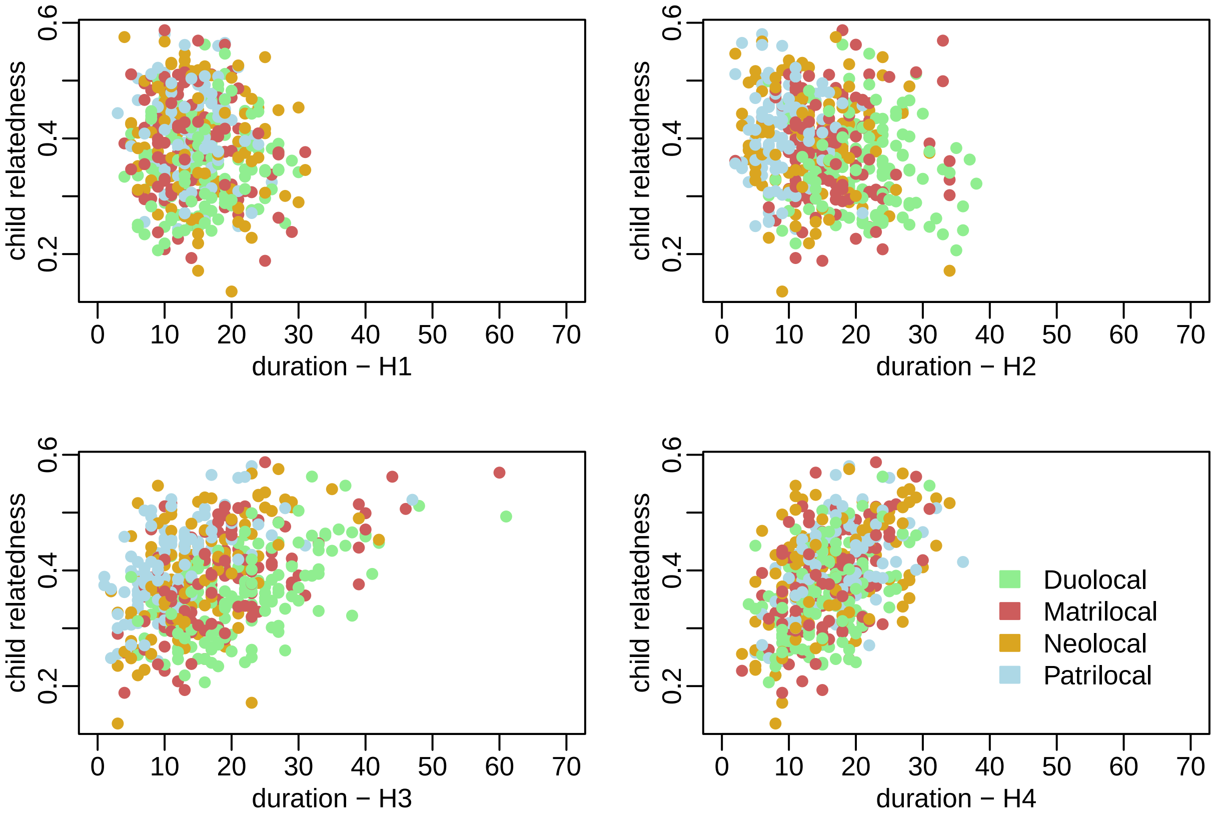

Figure 5: Simulated breastfeeding duration for four different hypotheses (causal models), color coded by residence pattern. Green stands for Duolocal, Red stands for Matrilocal, Yellow stands for Neolocal and Blue stands for Patrilocal.

5.3 What can we learn about the causal model from simulations?

The first objective is to use our simulations based on different causal models to qualitatively evaluate which of the dataset generated by each causal model produces parameter estimates from the cox model that are the most similar to those generated by the real data. The second objective is to find a set of generative parameters for our simulation that generates data producing the most similar results (once the cox regressions are fit on them), and then compare this 'most-likely parameters set' to our causal models.

5.3.1 Simulate data from causal models and compare results of simulated and real data

We start by running six combinations of cox regression models on the real data (see SI table 6 to see which sets of predictors and covariates were included; the last two correspond to models 3 and 2 in the main text respectively). From these models we obtain multiple estimates for the effect of parental and child's relatedness on the duration of breastfeeding (note that these effects are estimates for log hazard coefficients from the cox model, so that negative numbers mean a reduction of risk, and a positive effect on breastfeeding duration). We then run the same six cox model (including only the main predictors, as we did not simulate the covariates) on data simulated according to our causal models. This allows us, as a first step, to observe the ability of the cox models to qualitatively recover the effects of the main predictors and make inferences.

Table 6: hypotheses associated to causal models (note that the column 'Panel' indicates the panel in SI Figure 6, below, that reports the results relative to each regression).

model	main predictors	covariates	panel
child	child relatedness	sex + birth order + family size + age + birth cohort + village	a
mother	mother relatedness	same as above	b
father	father relatedness	same as above	c
parents	mother relatedness + father relatedness	same as above	d
everyone	child relatedness + mother relatedness + father relatedness (model 3)	same as above	e
residence pattern	household type (post marital residence)	sex + birth order + age + birth cohort + village	f

The large grey dots in SI figure 6 refer to the results from the datasets shown in SI figure 5, while the smear of smaller dots is given by 50 datasets simulated with different parameters. These represent parameter estimates of cox regression models for each causal model (listed as H1 to H4) estimated by the different cox regressions. Panel a) shows data relative to a model where we include only the child's relatedness as a predictor. Let's look at each hypothesis one at a time. In the first row we observe the estimated effect of the child's relatedness calculated on data simulated according to H1. Note that the simulation included *postitive* effect of the child's relatedness on breastfeeding duration, so we would expect a negative effect, i.e. the more the child is related to the rest of the family, the longer will breastfeeding be. But if we include only the child's relatedness as a predictor, the negative effect of the parents' relatedness overcomes that of the child's relatedness, and the parameter estimated will be positive: a counterintuitive result, but unavoidable given the connection between the parents' and child's relatedness. Data simulated according to H2, where the child's relatedness has no direct effect, also produce an estimation that the child's relatedness will negatively affect breastfeeding duration. Once we move to H3 and H4, on the contrary, the child's relatedness has a positive effect. Remember that in both cases the data was simulated with a consistent positive effect of the child's relatedness, only including some effect for parents in H3 (positive for mother, negative for father) and no parental effect in H4. In panel b, are shown the results from a model that estimates only the effect of maternal relatedness, and again, let's look at the grey dots. The model applied on data generated according to H1 correctly estimates a negative effect of maternal relatedness on breastfeeding duration, or a positive estimated parameter from the cox model. Similarly, H2 and H3 pick up on the positive effect of mother's relatedness, however they provide different effect sizes, even though the Poisson simulation used the same parameter. This is because in H3 there is also a positive effect of the child's relatedness, which correlates to maternal relatedness and hence is picked up by the model. Data generated according to H4 still produce a positive effect of maternal relatedness, even though there was none in the simulation: this is because maternal relatedness is connected to the child's relatedness, which in turn has positive effect on breastfeeding duration. By this point it should be clear that simply interpreting the regression coefficients for these models will be unlikely to provide a reliable inference on the causal model generating the real data because of equifinality. Only the model including the three relatedness measures is able to recover the original relations between the factors (positive effect of the child's and mother's, negative of father's relatedness).

Moreover, we compare the results of all these six cox regressions on the real data to results obtained with data generated according to different causal models. We qualitatively compare the cox parameters estimated from the real data, shown by a light blue dot in panels a-c, and by lighter colors in panels d-f, to the estimates based on data simulated according to each causal model (H1-H4), shown in grey in panels a-c, in darker colors in panels d-f (note that the smear of points shows parameter estimates for 50 different simulations for which were used different sets of parameters, generated by sampling from a Gaussian distribution with mean 2 and SD 1 and multiplying according to the causal model, e.g. $\beta = 4, \gamma = 2, \delta = -2$, for H3). We then qualitatively look at which of the casual models produces data that, once analyzed with the different cox models, *looks the most like* the real data *across* the different statistical cox models. This allows us to address equifinality issues beyond the correct estimates for the parameters.

The model including only the child's relatedness, in panel a), shows a positive effect of the child's relatedness (the cox parameter estimated is negative) for the real data and for H3 and H4, which suggests that H1 and H2 do not match the real data. The model that estimates only the effect of maternal relatedness, in panel b), shows a negative effect of maternal relatedness only in H1, while the real data, and H2-H4 are consistent with a positive effect of maternal relatedness on breastfeeding duration. Panel c) shows the results of a model including only the father's relatedness as a predictor. The real data, as well as hypotheses H1-H3 predict a negative effect of paternal relatedness (H4 was generated with no effect of paternal relatedness, but because the child's relatedness has a positive effect, if we include only the father's relatedness, this will appear to have a positive effect because it is correlated to the child's relatedness). If we include a predictor for each of the parent's relatedness, in panel d), we can look at the effect of each parent once we *control for the effect of the other parent's relatedness*. We can see that with the data generated according to H1, which posits a negative effect of both parents, the effect of their relatedness is markedly negative, while in the real data mother's effect is positive and father's effect is only slightly negative. H2 posits a marked negative effect of fathers (positive estimated parameter in the cox regression), and positive of mothers, which is what we observe in the real data, albeit with a smaller effect size. H3 generates a markedly positive effect of the mother's relatedness and close to zero effect for the father's relatedness, which is qualitatively similar to the results from the real data in this model. H4 produces a positive effect for both parents' relatedness (even though in the generative simulation we included no effect of parents, again, this is caused by the positive effect of the child's relatedness, which is picked up by both parents). As indicated by the analysis of the DAG represented in Figure 7 in the main text, the model including predictors for all members of the family is the one better able to disentangle the relative effects of each of their relatedness: it correctly picks up on the positive effect of the child's relatedness, in contrast to the negative effect of that of the parents in H1; it correctly estimates the effect of the child's relatedness close to zero, that of mother's relatedness to be positive, and father's relatedness to be negative, as generated by H2; it picks up on the positive effect of both child and mother's relatedness, with the former having a more positive effect, while fathers have a negative effect, for H3; and similarly positively correlates the child's relatedness to breastfeeding duration for data generated according to H4, while the parent's relatedness is close to zero. Comparing the results from the real data to those of the different models, H3 seems to generate data more closely fitting the real results.

Summing up, while multiple causal models *could* have generated results similar to those from the real data in some of the cox regression sets (i.e. equifinality), when all the models are observed together, and focusing on the linear model presented in panel e), model 3 from the main text, which includes predictors for all family members, H3 seems to be the causal model more closely matching the results obtained from the real data.

5.3.2 Estimate the parameter set most closely matching the real data

A second contribution to inference comes from a search in the parameter space for a combination of parameters that more closely match the results from the real data. To do so, we simulate 100 datasets from a random set of parameters where the intercept, the parameter for the child's and parents' relatedness are sampled from a Gaussian distribution with mean 0 and SD 3. We calculate the mean difference between the coefficients estimated from the real data and the coefficients estimated from each dataset for the different cox models (described in SI table 6), and select the set of parameters with the best match to the real data. We repeat the process 250 times, and calculate the mean value of these parameters, as well as the 5th and 94th percentiles. These are reported in table 1 in the main text. This approach resembles an Approximate Bayesian Computation method where the ABC rejection algorithm is based on the Log Hazard Coefficients resulted from the Cox models.

As we can see, the parameters generating data whose results in a cox model are the most similar to the real data indicate a similarly positive effect for child and maternal relatedness, and a mostly negative effect for paternal relatedness, which is coherent with the predictions of H3.

6 References

Attané I, Courbage Y. (2000). Transitional stages and identity boundaries: the case of ethnic minorities in China. Population Environment. 21(3):257-280

Bai, PP, Mancini, M., Du, J., Mace R. (2021). Matching local knowledge and environmental change with policy changes in rangeland tenure. Human Ecology, 49(1),341-352. https://doi.org/10.1007/s10745-021-00235-y

Beaumont, Mark A. 2010. 'Approximate Bayesian Computation in Evolution and Ecology'. Annual Review of Ecology, Evolution, and Systematics 41(Volume 41, 2010):379–406. doi:10.1146/annurev-ecolsys-102209-144621.

Du, J., Mace R. (2018). Parental investment in Tibetan populations does not reflect stated cultural norms, Behavioral Ecology, 29(1), 106-116, https://doi.org/10.1093/beheco/arx134

Du, J. (2017). Family and Group Dynamics in a Pastoralist Society, PhD Thesis, Department of Anthropology, University College London.

Du J., Huang YM., Bai PP., Zhou LQ., Myers S., Page AE., Mace R. (2023). Post-marital residence patterns and the timing of reproduction: evidence from a matrilineal society. Proceedings of the Royal Society B:Biological Science.29020230159, http://doi.org/10.1098/rspb.2023.0159

Fan, CF. (2005). Political and cultural transmission in the origin of winterworm summer herb: economic anthropology studies of caterpillar fungus society in Animaqing Area, Tibetan Studies, 4(2),37-47,

Fortunato, L. (2012). The evolution of matrilineal kinship organization. Proceedings of the Royal Society B:Biological Science, 279)1749), 4939-4945. https://doi.org/10.1098/rspb.2012.1926

Gelman, A., Vehtari, A., Simpson, D., Margossian, C.C., Carpenter, B., Yao, Y., Kennedy, L., Gabry, J., Bürkner, P.C. and Modrák, M., 2020. Bayesian workflow. arXiv preprint arXiv:2011.01808.

He QQ, Rui JW, Zhang L, Yi Tao, Wu JJ, Mace R. (2022). Communal breeding by women is associated with lower investment from husbands. Evolutionary Human Sciences. 4:e50. doi:10.1017/ehs.2022.47

Leanwangdui. (2003). Brief introduction to Chinese ethnic groups: The Tibetans in Shangri-La, Diqing. Beijing: The Ethnic Publishing House.

Mattison, SM. (2010). Economic impacts of tourism and erosion of the visiting system among the Mosuo of Lugu lake. The Asia Pacific Journal of Anthropology, 11(2),159–176. https://doi.org/10.1080/1444221100 3730736

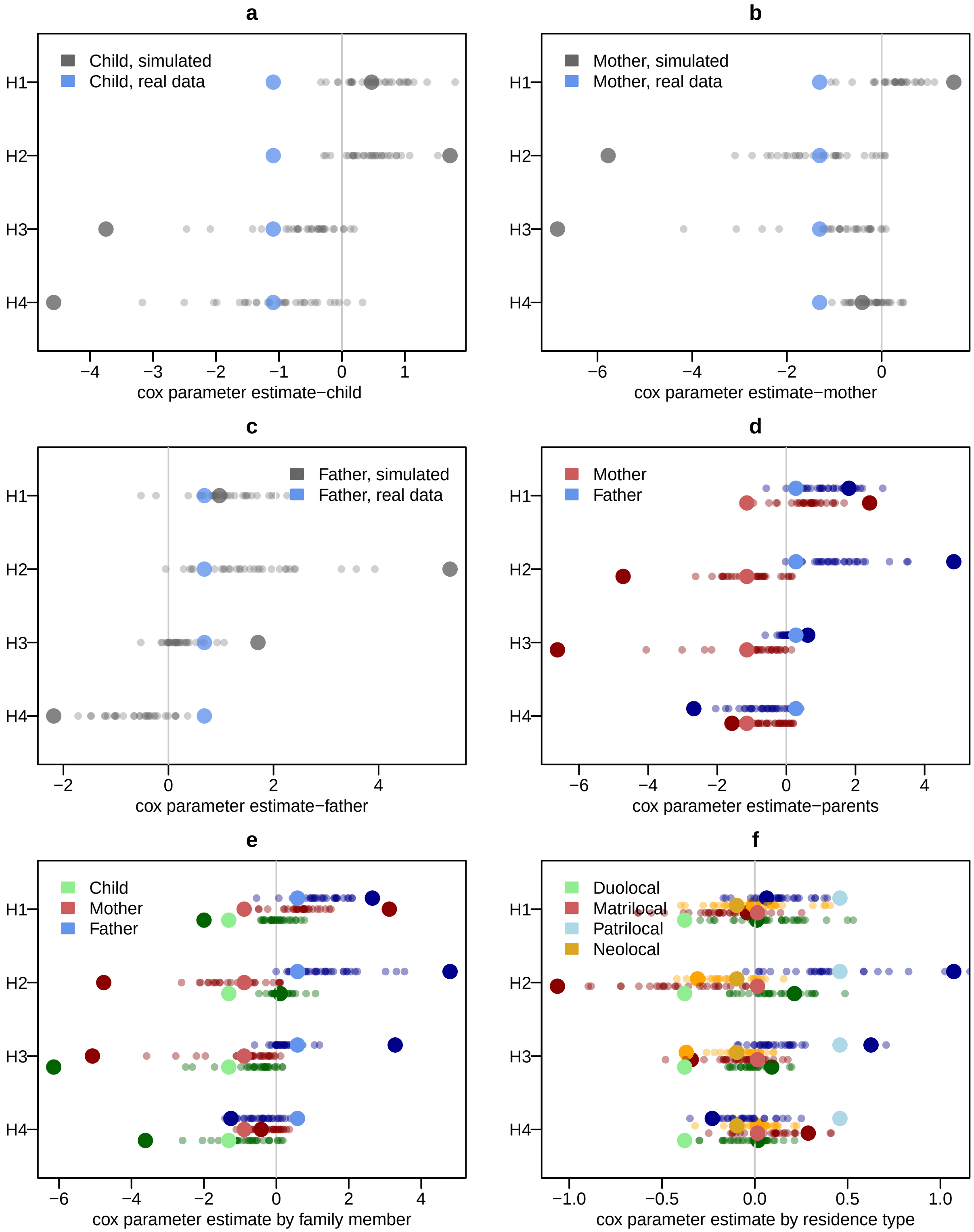

Figure 6: Multiple plots showing parameters estimated by cox models run on the real data (light blue in a-c, light colors in d-f), in comparison to similar models run on simulated data (each row in each model represents an hypothesis, larger grey/darker color dot is relative to one specific set of data, smear is from replication with 50 different parameter sets).

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Shih, CK. (2009). Quest for harmony: the Moso traditions of sexual union and family life. Redwood City (CA): Stanford University Press

Sinnwell, J. P., Therneau, T. M., & Schaid, D. J. (2014). The kinship2 R package for pedigree data. Human heredity, 78(2), 91-93.

Thomas, MG., Ji, T., Wu, JJ., He, QQ., Tao, Y., Mace, R. (2018). Kinship underlies costly cooperation in Mosuo villages. Royal Society Open Science, 5(2), 171535. https://doi.org/10.1098/rsos.171535CrossRefGoogle ScholarPubMed

Walsh, ER. (2001). The Mosuo Beyond the Myths of Matriarchy: Gender Transformation and Economic Development, PhD Thesis, Department of Anthropology, Temple University.

Wang B. (2018). Development of water-oriented tourism based on Xiaozhongdian reservoir. China Water Resour. , 34–35. (doi:CNKI:SUN:SLZG.0.2018-16-023)

Wang J. (2021).A Study on the Changes of Intermarriage among Tibetans in Shangri-La from the Perspective of the Transformation of Livelihood Mode. J. Qiqihar Univ. Soc. Sci. Ed. , 84–88.

Wright, S. (1922). Coefficients of Inbreeding and Relationship. The American Naturalist, 56(645), 330–338. https://doi.org/10.1086/279872

Wu, Q. (2013). Tradition and modernity: cultural continuum and transition among Tibetans in Amdo [PhD dissertation]. Helsinki (Finland): University of Helsinki.

Xing, HY., Wang, X. (2023), Interembedding and integration: The construction of ethnic communities in economic interactions—An investigation based on the cordyceps trade in the northwestern tibetan region, Journal of Shanghai Institute of Socialism,2023(3),60-75. https://doi.org/10.3969/J.ISSN.1672-0911.2023.03.060

Zhou S. (2010). Annals of Xiaozhongdian town,Shangri-La.

Zhou LQ., Ge EH., Micheletti AJC., Chen Y., Du J., Mace R. (2018). Monks relax sibling competition over parental resources in Tibetan populations, Behavioral Ecology, 33(6), 1070–1079, https://doi.org/10.1093/beheco/arac059