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Causes and consequences of adult sex ratio imbalance in a historical U.S. population

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The responsiveness of individuals to partner availability has been well-documented across the literature. However, there is disagreement regarding the direction of the consequences of sex ratio imbalance. Specifically, does an excess of males or females promote male–male mating competition? In an attempt to clarify the role of the adult sex ratio (ASR) on behaviour, here we evaluate both competing and complimentary expectations derived from theory across the social and biological sciences. We use data drawn from a historical, nineteenth century population in North America and target several life-history traits thought to be affected by partner availability: age at first birth, relationship status, completed fertility and longevity. Furthermore, we assess the role of various contributors to a population’s ASR. We find that both the contributors to and consequences of sex ratio imbalance vary over time. Our results largely support predictions of greater male pairbond commitment and lesser male mating effort, as well as elevated bargaining power of women in response to female scarcity. After reviewing our findings, and others from across the literature, we highlight the need to adjust predictions in response to ASR imbalance by the: (i) culturally mediated mating arena, (ii) variable role of demographic inputs across time and place, (iii) constraints to behavioural outcomes across populations, and (iv) ability and accuracy of individuals to assess partner availability.

This article is part of the themed issue ‘Adult sex ratios and reproductive strategies: a critical re-examination of sex differences in human and animal societies’.

1. Introduction

The adult sex ratio (ASR) has long been recognized as a key population-level determinant of behaviour [1]. Early work, across both human and non-human animals, showed the importance of partner availability on the patterning of relationship outcomes [2,3]. More recent work highlights the significance of ASR variation on the intensity of sexual selection and violence across populations [4]. Thus, the responsiveness of individuals to local mate availability has been well-documented across time and animal taxa. However, while the relative scarcity of either sex is expected to structure optimal individual reproductive strategies, there is disagreement across the literature regarding the direction of the consequences of sex ratio imbalance. Specifically, will male–male antagonistic competition intensify or attenuate in response to female scarcity? In an attempt to clarify the role of the ASR on behaviour, here we evaluate both competing and complementary expectations derived from theory across the social and biological sciences. We use data drawn from a historical population in North America, including periods of natural fertility and the demographic transition, to answer unsettled questions regarding reproductive strategies in populations with either ‘too many men’ or ‘too many women’.

Behavioural flexibility in reproductive strategies has been well documented in response to a variety of individual variables (e.g. age, sex and social status; reviewed in [5] for humans), yet after decades of research the role of the sex ratio is still debated [6]. This is despite partner availability being a fundamental demographic characteristic affecting mating options across populations [7]. This lack of progress may be driven in part by two key factors: (i) the most prominent theoretical approaches offer intuitive yet conflicting predictions and (ii) parallel lines of inquiry and argument have developed independently within the social and biological sciences. Consequently, this has led to entrenched positions across the theoretical divide and the lack of cross-pollination essential for the advancement of scientific inquiry. To help advance our understanding, here we present and evaluate predictions from competing approaches regarding optimal behaviour in response to ASR imbalance.

(a) Two approaches to the study of sex ratios

Briefly, we outline two sets of theoretical frameworks that are largely shared across the social and biological sciences yet are often, and unknowingly, applied separately. The study of sex differentiated reproductive behaviour in the evolutionary sciences generally relies on Trivers' parental investment (PI) theory for explaining behavioural differences between the sexes [8]. At the centre of this theory is the argument that, because males benefit more from mating multiply than do females (largely due to sex differences in reproductive investment), selection typically favours mate-seeking and competitive behaviour in males. And, this antagonistic competition among males over partners only increases as the relative number of available females decreases [9]. These expectations derived from a PI model are in-line with a socio-demographic model generally referred to within the social sciences [10,11]. It is well documented that men are more violence-prone and competitive than women [12]. Accordingly, it is expected that as the number of men increases relative to women, rates of family and social instability will increase as well (due primarily to the growing number of unattached, bachelor males; [11,13]). Thus, there is the general expectation from these frameworks (collectively referred to as PI throughout for convenience) that a relative abundance of males will elevate levels of conflict (particularly between males over partners), reduce pairbond stability and decrease paternal investment.

Reformulations within sexual selection theory reconsider PI predictions drawn from sex differences in optimal mating rates and costs to reproduction [6,14–16]. A key assertion of these critiques is that under most conditions, the profitability for males to invest in mating effort (i.e. the pursuit of and/or competition over multiple partners) increases when there are more, not fewer mating opportunities available. For example, those males that pursue an intensive mating effort strategy when mates are rare may find themselves spending longer periods in between reproductive events than if they were to acquire and maintain a single relationship. Thus, when males are in abundance, and surrounded by competitors, they should reduce, not increase, mating effort [17]. This prediction is in-line with mating market (MM) theory that too takes a frequency-dependent approach to behaviour [18,19]. The number of males and females in a population is argued to be structured as a

mating market, which is subject to economic principles of supply and demand. The rarer sex has more bargaining power and can leverage their scarcity to realize their preferred mating strategy, while the more common sex must cater to the preferences of the rarer sex in order to acquire a mate. Thus, according to these frameworks (collectively referred to as MM throughout following the convention above), mating behaviour is seen as a response to sex-structured pay-offs to partner availability. The general expectation is that when males are rare they behave more promiscuously, offering little PI and are still able to obtain partners. However, when females are in short supply, males will be more willing to commit to a single partner and, depending on the culture or species under study, adopt behaviours consistent with female relationship preferences.

(b) Consequences of 'too many males'

Outcomes in support of both approaches can be found across animal taxa. In other species, *both* male- and female-biased sex ratios have been shown to be associated with elevated male–male aggression and male–female harassment, resulting in the disruption of pairbond formation and female reproductive output [20–22]. The support for one framework over the other is likewise mixed in humans, with findings highlighted in a recent review on the role of sex ratio imbalance on the cross-cultural patterning of violence [4]. Homicide, for example, is both more *and* less common across studies of male-biased populations. Obviously, confusion regarding the role of the sex ratio on behaviour is warranted given the conflicting results in the literature. The theory, from both frameworks, appears intuitive and contrasting predictions have been supported empirically across a variety of systems. Subsequently, while seemingly straightforward to assess, results from both human and non-human studies raise the question, *does male excess at the population-level drive elevated male–male mating competition and pairbond instability, or not?*

Here we attempt to answer this question in three ways: first, often overlooked is that the ASR itself is a composite measure that emerges as a result of three inputs commonly studied by demographers: secondary sex ratios, sex biases in mortality and sex-biased migration [7]. Important to note is that these inputs may play variable roles in generating ASR imbalance across time and populations. For example, migration of adults can lead to considerable imbalance across populations as men and women leave home at different rates in search for work [23]. In addition, the effects of stochastic sex-biased births and deaths can play transient, yet powerful roles on partner availability—particularly in small populations [24]. Thus, it has been hypothesized that an individual source of ASR variation may be a better predictor of behaviour than partner availability alone [7,25]. While recent work highlights the variable importance of different demographic inputs on ASR imbalance, this work has not been applied systematically across animal taxa [7,25] and rarely to humans (see [24], for a longitudinal examination of the causes of ASR imbalance in a small-scale society).

Second, we assess which sex ratio influences behaviour. Specifically, is it the ASR an individual experiences during childhood or adulthood that structures his/her reproductive decisions? This is an important distinction. Paying attention to the ASR while still a juvenile could serve to prepare an individual for mate acquisition as an adult, and may

Table 1. Contrasting PI and MM predictions of reproductive outcomes in a population with a male-biased ratio. Specific measures are in parentheses.

	PI	MM
marriage involvement		
(men)	lower	higher
(women)	lower	higher
male mating competition		
(male mortality)	higher	lower
reproductive timing		
(men)	no prediction	later
(women)		earlier
male investment		
(female fertility)	lower	higher
(female mortality)	higher	lower

accordingly influence his/her developmental pathway [26]. For example, whether or not males across several beetle species develop competitive weaponry depends on the ASR imbalance they experience as juveniles—when males ‘expect’ to compete as adults they prepare accordingly (*Orthophagus* spp.; [27]). In humans, a long juvenile period devoted to learning is argued to have evolved, in part, due to the skill-intensive niche we occupy and the variable nature of social organization and mating systems across cultural groups [28]. Thus, there are possible developmental consequences to residence as a juvenile in a population with a skewed sex ratio. Alternatively, individuals may facultatively adjust their reproductive strategies as adults in response perceived partner availability [23]. Humans, in addition to learning in childhood, update their behaviour throughout the life-course based on both socially learned information and individual experience [29]. For example, recent laboratory-based studies find that mate choice preferences vary in response to perceptions of partner availability manipulated through experimental priming [30]. Accordingly, here we examine reproductive outcomes across individuals in response to the ASR experienced both in one’s youth and adulthood simultaneously.

Third, once we have identified the variables responsible for ASR imbalance (Part I) and the ASR of relevance to individual behaviour (Part II), we will assess how the ASR and its contributors influence outcomes related to reproduction (Part III). This strategy will allow us to distinguish the effects of ASR separately from the forces affecting it. Furthermore, our competing frameworks (PI versus MM) have contrasting predictions of reproductive outcomes in response to ASR imbalance that allow us to evaluate their support with data (table 1). For example, PI models commonly expect greater male mating effort in response to partner scarcity, while MM models expect the opposite. Specifically (with empirical measures in parentheses), we explore what best predicts relationship involvement (marriage), male mating competition (male survival), female bargaining power (age at first birth) and paternal investment (female survival and fertility).

Here we evaluate both competing and complementary expectations derived from theory across the social and biological sciences regarding reproduction in populations with an excess of males or females. To answer open questions

regarding the causes and consequences of sex ratio imbalance, we draw our data from a historical nineteenth century population in North America.

2. Material and methods

(a) Population and data description

Our data were sourced from the Utah Population Database (UPDB). The UPDB consists of vast genealogical records originally obtained from the Utah Family History Library and includes individual-level US Census data as well as birth and death information contributed both by genealogical records and by the Utah Department of Health, all spanning the last two centuries. We focus on the time periods 1880 and 1900 for measuring our population-level variables, which are then used to predict individual-level outcomes (that may extend well into the twentieth century; e.g. survival, fertility). Between 1880 and 1900, there was rapid growth in Utah—the population nearly doubled in size (from 143 963 to 276 749; [31]) and the region transitioned from a US territory to a state. While population growth was driven in part by high fertility (μ completed fertility = 6.3, s.d. = 3.6; $n = 26\,175$ individuals in our sample born 1861–1880), it was also due to high rates of immigration, which was often male-biased [32]. Most men were involved in farming during this time; however, mining and economic opportunities in growing urban areas were also available. This resulted in a state-level male-biased ASR (0.537 in 1880; calculated as the number of adult males/(male + females)).

We use individual-level decennial US Census data linked to the UPDB to capture information on individuals ($n = 33\,940$; 17 208 men and 16 732 women) and their population of residence in 1880 and 1900 (1890 data were destroyed and are unavailable for nearly all of the USA). Our population-level measures (e.g. ASR) are calculated from the enumeration district (an administrative census unit within a county or township that closely approximates a neighbourhood, which we simply refer to as ‘district’ throughout) in which individuals reside. Accurate estimates of the ASR are necessary to explore its effect(s) on behaviour. Uncounted individuals can lead to considerable bias in ASR measures, particularly in small and/or ephemeral populations [7]. Accordingly, we focus our analysis on districts with a population of 100 or more men and women (aged 20–50) and an ASR of 0.75 (i.e. three times as many men as women) or less. With districts of this size and structure, we have greater confidence that most of the men and women have been captured in the decennial census. Excluded districts are those that generally have transitory populations and/or rapid change driven by migratory individuals (uncounted and highly mobile) whose information may be unrecorded.

Another challenge, among humans in particular, is to refine the definition of the ASR for the population under study [32]. Which ages to include in a sex ratio range are currently debated and quite variable across studies [4]. Women have a constrained reproductive window compared with men due to menopause. However, while a man’s reproductive tenure can be quite long, it is often culturally defined through mating system. In polygynous societies, or those where serial monogamy is practiced, males may remain reproductively active well past female reproductive senescence [33]. However, in other groups where monogamy is normative, the fertility window for males is probably very similar to that of women [23].

In late nineteenth century Utah, monogamy was the most common marriage type (only 0.2% of men in our sample were polygamous, an estimate consistent with previous work; [34]), with divorce being extremely uncommon (only 0.3% of individuals ever divorced). Additionally, women had their first child, on average, at 23 years of age. Thus, to generate the sex ratio measure used in our analysis, we selected an age range that

includes all men and women aged 20–50. Because most individuals were exclusively monogamous, men stopped reproducing when their wives did. Thus, isometric ASR limits for men and women seem most appropriate for our sample because a man's fertility window largely matches that of his partner. We chose the lower bound of the age window (20 years of age) so that our measure would be inclusive of the time women were involved in courtship before marriage and the upper bound (50 years of age) to include women who remain fertile in their mid to late 40s and so are still part of the reproductive pool.

(b) Description of variables and order of analysis

We begin with a population-level analysis exploring the factors associated with ASR imbalance (Part I). Here, we include data from 109 districts in 1880 (μ population size = 432, s.d. = 225) and 206 districts in 1900 (μ population size = 509, s.d. = 242). ASRs across the districts in the two time periods are male-biased on average (0.537 in 1880 and 0.526 in 1900). This population-level excess of males is unsurprising given male-biased migration into Utah for economic opportunities. Nonetheless, there is considerable variation in ASR across our sample (e.g. from 0.390 to 0.715 across the 206 districts in 1900). In addition to the role of migration on ASR imbalance, we are also interested in the effects of sex biases in birth and death rates. However, because we are working with historical data, we must evaluate some of these demographic measures somewhat indirectly, largely due to small sample sizes in districts and the rarity of certain events (e.g. infrequent adult mortality in small districts). The following list includes our district predictors of ASR imbalance.

- (i) *Child sex ratio* (CSR), calculated as the proportion of boys to girls aged 0–19 within a district. This is a composite measure inclusive of juvenile births, deaths and migration, and is used to assess the relationship between an excess of either sex in childhood and adulthood.
- (ii) *Local births*, calculated as the percentage of children 0–19 born in Utah within the district. This is used as a measure of migration—where Utah births are low, rates of migration are likely to be high.
- (iii) *Widowhood*, calculated as the per cent of women whose husbands died within the district. A high percentage indicates relatively high male mortality.
- (iv) *Widowerhood*, calculated as the per cent of men whose wives died within the district. A high percentage indicates relatively high female mortality.
- (v) *Farmer*, calculated as the per cent of men who are farmers within a district. A higher percentage indicates male economic opportunities and *male-biased* immigration potential.
- (vi) *Polygamy*, calculated as the percentage of men who have multiple wives simultaneously out of all married men within the district. Higher percentages indicate female-biased immigration potential. (Note: here we use polygamy to refer to what is technically polygyny, but we do so to remain consistent with UPDB usage.)

Next, we evaluate the role of the ASR in both childhood (1880) and adulthood (1900) on reproductive outcomes (Part II). To do so, we identified individuals ($n = 39\,440$) who were captured in the 1880 census as children (0–19 years of age) and then later as adults in 1900 (20–39 years of age). Using the 1880 and 1900 district ASRs for individuals, we then assess which ASR better predicts reproductive outcomes. The outcomes are age at first birth, longevity, marital status and completed fertility. Our final step is to then include the most relevant ASR (from Part II) and its predictors (from Part I) into our statistical models constructed to predict individual outcomes (Part III).

Table 2. Model output for predictors of ED ASR in 1880. This analysis includes districts with a population of at least 100 men and women, resulting in an ASR range of 0.40–0.73 ($\mu = 0.53$, s.d. = 0.06; $n = 109$).

predictor	estimate	s.e.	p-value
intercept	4.5117	0.6161	<0.0001
farmer	0.3156	0.2842	0.2668
local births	−3.8027	0.6432	<0.0001
widowhood	−2.4440	1.0165	0.0162
widowerhood	2.4658	1.6565	0.1366
polygamy	−6.0734	1.6275	0.0002
CSR	0.4990	0.2199	0.0233

(c) Statistical analyses

We used SAS v. 9.4 for all analyses. For our first analysis (Part I), we use generalized linear models (PROC GENMOD) with district-level ASR (both 1880 and 1900) as the outcome variable and district predictor variables (i)–(vi) listed earlier. For our second analysis (Part II), we assess the role of district ASR (1880, 1900) on four reproductive outcomes. For age at first birth and longevity, we estimate Cox proportional hazard rates (PROC PHREG). For outcome marital status, we apply logistic regression (PROC LOGISTIC). For completed fertility, we use a mixed-effect model (PROC MIXED). For our third analysis (Part III), we follow the strategy of analysis two (Part II), but include variables from analysis one (Part I) that significantly predict the ASR. Below we discuss these analytical approaches in greater detail.

3. Results

(a) Predictors of the adult sex ratio

Here we begin by examining possible components of a district's ASR (Part I). As outlined above, we include six independent variables and evaluate their association with the ASR in 1880 and 1900. Beginning with the year 1880, we find that across 109 districts, four of the six predictors are statistically significant: local births, widowhood, polygamy and CSR (table 2). We show that: where a larger percentage of children are born locally (less population-level movement), the ASR is more female-biased; where the percentage of women who are widows is higher (and where we infer male mortality is as well), the ASR is more female-biased; where more men are polygamous, the ASR is more female-biased; and where the CSR is more male-biased so is the ASR. In sum, from these results, we show that in 1880, a male-biased ASR was associated with higher levels of migration, lower male mortality, lower levels of polygamy and a male-bias in the CSR.

We next explore whether these results hold for 1900. We find that across districts, again four of the six predictors are statistically significant: local births, widowhood, widowerhood and polygamy (table 3). Thus, in 1900, we add the percentage of men who are widowers (inferred to signal higher female mortality) but no longer observe a significant influence of CSR. Consequently, we show that the significance of various inputs to ASR composition vary across time.

(b) Reproductive outcomes

Our next models examine the role of various individual and district-level predictors on reproductive outcomes (age at first

Table 3. Model output for predictors of district ASR in 1900. This analysis includes districts with a population of at least 100 men and women and an ASR less than 0.75, resulting in an ASR range of 0.39–0.69 ($\mu = 0.52$, s.d. = 0.07; $n = 206$).

parameter	estimate	s.e.	p-value
intercept	1.6013	0.2699	<0.0001
farmer	0.1896	0.1762	0.2819
local births	−0.4669	0.2358	0.0477
widow	−3.5271	0.3764	<0.0001
widower	5.1985	0.7449	<0.0001
polygamy	−3.5728	1.3553	0.0084
CSR	0.1771	0.1286	0.1685

birth, longevity, marital status and completed fertility). We begin by constructing statistical models with district ASR in 1880 and 1900 as predictors to assess the role of a particular year's ASR on individual reproductive outcomes for those who were children in 1880 and adults in 1900 (Part II). To avoid repetition, we include our model summaries in the electronic supplementary material. We do this because the 1900 district ASR is significantly associated with all outcomes, while the 1880 district ASR is not (electronic supplementary material, tables S1–S4).

Accordingly, for our final set of analyses, we focus on the ASR and significant district-level predictors from 1900 (local births, widowhood, widowerhood and polygamy) and their association with reproductive outcomes (Part III). We begin by looking at the outcome age at first birth and estimate Cox proportional hazard models for individuals from sexual maturity (14 years of age) to age at first birth, censored at age 50 ($n = 25\,268$). We stratify the population by individual birth year due to later ages of first birth over time and include district-level random effects to account for unmeasured heterogeneity. We find that three out of the four district-level predictors are significant (table 4). Where local births proportions are high, individuals are having children at earlier ages (hazard rate = 4.56). Where widowhood and widowerhood rates are high, individuals are having children at later ages (hazard rates = 0.148 and 0.142, respectively). Next, we look to the ASR and its interaction with sex. As the ASR increases, women's age at first birth decreases and men's age at first birth increases. Specifically, men in male-biased ASRs are having children at later ages than men in female-biased ASRs, and this relationship is reversed for women.

We next look to the outcome longevity and estimate Cox proportional hazard models for individuals for whom we have a death or last living date ($n = 33\,940$) and again stratify the population by birth year and include random effects for district. This analysis yields two significant results (table 5). First, and unsurprisingly, men do not live as long as women (hazard rate for sex: 1.228). Second, individuals living in more polygamous districts generally live longer (hazard rate for polygamy: 0.062). We find no other significant predictors for lifespan.

We next consider marital status. Because this is a binary variable (married/unmarried) we apply logistic regression and include all individuals for whom marital status is known in 1900 (married: $n = 22\,891$; unmarried: $n = 11\,054$)

and a control for birth year. We find that three out of the four district-level predictors are significant (table 6). Where local birth proportions are high, individuals are more likely to marry. Where widowhood and widowerhood rates are high, individuals are less likely to marry. Next, we look to the ASR and its interaction with sex. We show that as the ASR increases, women are more likely to be married and men are less likely. Specifically, men in male-biased ASRs are less likely to be married than men in female-biased ASRs, and this relationship is reversed for women. We also explore the outcome variable ever-married to be additionally inclusive of individuals who were single in 1900, but marry later in time (electronic supplementary material, table S5). We find that all results discussed above hold save polygamy, which is positively associated with ever-marrying.

Lastly, we examine the outcome completed fertility. We apply a mixed-effect model and include all individuals who are not lost to follow-up before the age of 50, a random effect for district and a control for birth year. We find that all four district-level predictors are significant (table 7). Where local birth proportions are higher, individuals are having more children. Individuals are having fewer children where widowhood and widowerhood rates are high. Where polygamy is common, individuals are having more children. We then look to the ASR and its interaction with sex. As the ASR increases, women are having more children and men are having fewer. Specifically, women in male-biased ASRs are having more children than women in female-biased ASRs and this relationship reverses for men.

4. Discussion

Through our analysis of optimal reproductive strategies in response to partner availability, we find general support for MM predictions. We find no evidence that male–male contest competition is elevated in response to a male-biased ASR, instead women seem to have greater relational bargaining power and men appear to be investing more in a partner and children. However, we also find that men are less likely to be pair-bonded when women are rare. Below we situate our findings within the literature on the causes and consequences of ASR imbalance, as well as discuss how our results cast doubt on contemporary alarmist predictions for populations with an excess of men

First, the role of various inputs on the ASR varies over time. Indicators of mortality, migration and CSRs are all important predictors of ASR. However, their association with ASR varies by year, with some losing their statistical significance. Thus, the demographic processes affecting group-level composition are temporally variable within a population. Consequently, the selective environment individuals face both within a lifetime and across generations is not uniform, possibly generating behavioural variability in response to similar ASR measures over time.

Second, the ASR of relevance for individual reproductive outcomes is the ASR of adulthood (1900 district ASR). We found that the ASR of childhood (1880 district ASR) was not significantly associated with any of the outcomes assessed here. This was somewhat surprising given the importance of the long period of juvenility devoted to learning in humans [35]. However, when the environment experienced in childhood does not necessarily match what

Table 4. Parameter estimates and summaries for the effects of Sex, ASR, the ASR \times Sex interaction, and additional district-level measures on the age at first birth ($n = 25\,268$) using Cox proportional hazards model and stratifying by birth year.

parameter	estimate	s.e.	χ^2	<i>p</i> -value	Hazard
sex (male)	−0.73606	0.01370	2888.4714	<0.0001	0.479
ASR	0.41206	0.05677	52.6760	<0.0001	1.510
ASR \times sex (male)	−0.46638	0.05664	67.7935	<0.0001	0.627
local births	1.51915	0.15962	90.5823	<0.0001	4.568
widow	−1.91036	0.29288	42.5443	<0.0001	0.148
widower	−1.95091	0.60162	10.5155	0.0012	0.142
polygamy	0.70928	0.81578	0.7559	0.3846	2.033
random effect:					
district	0.01468	0.002502			

Table 5. Parameter estimates and summaries for the effects of sex, ASR, the ASR \times sex interaction and additional district-level measures on lifespan ($n = 33\,940$) using Cox proportional hazards model and stratifying by birth year.

parameter	estimate	s.e.	χ^2	<i>p</i> -value	Hazard
sex (male)	0.20538	0.01278	258.4282	<0.0001	1.228
ASR	0.03007	0.04604	0.4265	0.5137	1.031
ASR \times sex (male)	0.03957	0.05404	0.5363	0.4640	1.040
local births	0.05010	0.11381	0.1937	0.6598	1.051
widow	0.18071	0.20090	0.8091	0.3684	1.198
widower	−0.65609	0.42128	2.4254	0.1194	0.519
polygamy	−2.77348	0.56033	24.4998	<0.0001	0.062
random effect:					
district	0.003312	0.001102			

Table 6. Parameter estimates and summaries for the effects of sex, ASR, the ASR \times sex interaction and additional district-level measures on the marital status (married = 22 891; single = 11 049) using logistic regression.

parameter	estimate	s.e.	<i>p</i> -value
intercept	479.4	6.0626	<0.0001
birth year	−0.2557	0.00324	<0.0001
sex (male)	−1.0664	0.0299	<0.0001
ASR	1.6020	0.1118	<0.0001
ASR \times sex (male)	−1.4747	0.1289	<0.0001
local births	1.8069	0.2138	<0.0001
widow	−3.7126	0.3674	<0.0001
widower	−5.7511	0.7662	<0.0001
polygamy	−0.5794	1.0082	0.5655

will be experienced in adulthood (as is possibly the case here across districts due to rapid population change), learning is useful for promoting flexible behavioural responsiveness to later life conditions [28]. Thus, flexibility in reproductive decision-making allows for adaptive responses of individuals within populations that experience variable socio-ecological conditions over time [37]. However, in some populations

Table 7. Parameter estimates and summaries for the effects of sex, ASR, the ASR \times sex interaction and additional district-level measures on completed fertility ($n = 26\,175$) using mixed-effect models.

effect	estimate	s.e.	<i>t</i> -value	<i>p</i> -value
intercept	219.60	7.1430	30.74	<0.0001
birth year	−0.1172	0.003800	−30.83	<0.0001
sex (male)	−0.1414	0.04307	−3.28	0.0010
ASR	1.4989	0.2568	5.84	<0.0001
ASR \times sex (male)	−0.6173	0.1811	−3.41	0.0007
local births	7.5853	0.7346	10.33	<0.0001
widowhood	−7.1583	1.4381	−4.98	<0.0001
widowerhood	−8.2261	2.8415	−2.90	0.0038
polygamy	22.6595	4.0713	5.57	<0.0001
random effect:				
district	0.5122	0.06649		<0.0001

and species where the environments of childhood and adulthood are better aligned, cues early in life may reliably signal developmental pathways necessary for later optimal

behaviour. Still other individuals may face trade-offs when attempting to forecast future conditions, particularly when the development of a trait or behaviour must occur in childhood (e.g. the facultative development of sexually dimorphic traits), yet conditions faced in the adult environment are uncertain [27]. Thus, the ability of individuals to respond to ASR imbalance probably varies within and across species and thus so too should predictions given the system under study.

Third, even after including the significant components of ASR structure into our models, the ASR was still significantly associated with three out of the four reproductive outcomes. As mentioned earlier, the ASR is a summary measure and variation is generated through sex biases in births, mortality and migration that can be quite variable across time and place [24]. Thus, only looking at the ASR itself may cause researchers to ignore important components of the selective arena that generate behaviour [7]. Indeed, this could be one reason for the highly variable findings across animal taxa, where researchers only assess the effects of partner variability on behaviour. Here, however, we find, even after controlling for significant predictors of ASR, the ASR itself predicts reproductive outcomes, a critical finding from our analysis. This may be because the optimal heuristic for individual adaptive behaviour in late nineteenth century Utah was to respond to ASR itself, regardless of which inputs generated imbalance in partner availability. In populations with high levels of growth, migration and/or turnover, population characteristics may be quite variable over time and individuals may not be able to track accurately all inputs (e.g. sex biases in births and mortality). Thus, the ASR may be a very useful rule of thumb used to evaluate optimal reproductive strategies, particularly in a 'noisy' ecological context [38]. Accordingly, variation in responses to ASR imbalance could be additionally driven by perceptions of partner availability, which may vary in accuracy across individuals [39].

This does not, however, altogether resolve questions regarding variability in findings across studies. MM models expect that men will be increasingly willing to commit to a single relationship in response to partner scarcity, while PI models expect that under these same conditions, males will compete more aggressively for the limited number of partners available. Below we summarize our findings from each test of a reproductive outcome to offer a degree of resolution to the conflicting state of the literature.

(a) Timing of reproduction

We find that age at first reproduction increases for men and decreases for women in response to a male-biased ASR. Within our study population, reproduction happens, primarily, within the confines of marriage; therefore, male excess increases the demand among men for access to a sexual partner. Accordingly, in-line with MM predictions, we interpret male commitment to securing a single partner, in response to their rarity, decreasing the age at which women begin their reproductive career. Moreover, women's relative bargaining power increases with their rarity, resulting in older ages for men at first reproduction. Older men are more likely to be economically and socially established and so are, at least by these metrics, better partners [40]. Research on mate choice in Western populations clearly show preferences of women for partners with indicators of investment potential [41], and that choosiness intensifies with male

abundance (i.e. when women have a greater number of potential partners to choose from they become increasingly discriminating; [30]); although see studies of non-Western populations for alternate preferences [42,43].

A complication to straightforward interpretations offered thus far, however, is that a recent study of a contemporary Western population finds age at first birth to be lower for women in female-biased populations [44]. While seeming to conflict with our findings, the authors interpret later ages at first birth to also signal greater relationship commitment by men. In their population, reproduction is not limited to marriage, and earlier ages of first birth are generally indicative of greater promiscuity and/or sexual risk-taking. Thus, both older and younger ages at first birth can be inferred to support MM models, depending on cultural institutions structuring norms of intimate relationships. Accordingly, the accuracy of a particular interpretation offering support for one approach over the other depends on the population-specific context that takes into account aspects of the culturally mediated mating arena.

(b) Lifespan

We do not find that the risk of death for Utah men or women increases in response to a male-biased sex ratio. PI frameworks generally predict that conflict and violence between males will intensify in response to partner scarcity, resulting in increased rates of mortality through male-male contest competition and the harassment of females [20,45]. However, we find no evidence of elevated male mating effort increasing male and female mortality. Nonetheless, we do not interpret this result to offer clear support for MM predictions because we find longevity to be unassociated with ASR imbalance. We see two interpretations for this lack of association. One, this could indicate that men do not compete violently or through risky behaviours for partners in this population. Two, because mortality is, just as the ASR, influenced by many factors, using it as metric for male mating effort may not be ideal. Instead, assessing the specific sources of sex-biased mortality may be more appropriate. These data are infrequently available in historical datasets; however, they are available for many contemporary populations. For example, recent research on the association between ASR and male mating effort-related violence and mortality finds that, for example, rates of homicide are elevated in response to partner abundance and not shortage, in-line with MM predictions [46].

(c) Marital involvement

Here we find that men are less likely and women are more likely to be married in response to a male-bias. In line with MM predictions, women are more commonly involved in committed relationships in response to their rarity. Our results support recent work on the subject that finds similar associations in the contemporary USA [10]. However, Schacht & Kramer [10] also reported that men are more likely to marry, while here we show the opposite. How should these differences be interpreted? Again, as mentioned earlier, sexual access to a partner in our population generally requires marriage. Therefore, regardless of ASR, men seek a monogamous partner. Thus, we highlight the importance of paying attention to the culturally mediated mating arena and that, at least here, male marital involvement may not

be a very useful indicator of support for any one framework. However, in other populations, where sexual access to partner is not bound by marriage and women are largely free to choose partners (e.g. contemporary USA), marriage rates for men across ASR values may be a better indicator of male relationship commitment [10].

The excess of unmarried men in male-biased populations has raised concerns regarding the intensity of violence, particularly in India and China, because men are more likely to be both victims and perpetrators of violence than women [11,45,47–49]. However, research in the area does not necessarily find that places with more men are more violent [4,50]. Paying attention to male relationship preferences, and how they are conditioned differently across individuals, populations and cultures, may provide useful insight regarding violence. For example, recent research shows that in parts of China with a male excess, bachelor males are not more risk-prone or competitive; instead, they are more shy, withdrawn and likely to be depressed in response to their inability to marry, despite familial expectations and demands [51]. Thus, expecting greater violence simply in response to male excess is probably misguided. What may motivate male dispositions to violence against one another over partners is of course probably driven by partner availability, but also socio-ecological conditions under which men's mating psychology is short-term oriented—as may be the case in areas with male-biased economic opportunities and high turnover (e.g. mining camps). Thus because the underlying motivations of violent behaviours may be quite variable, violence may not simply be more or less common in response to male scarcity or surplus. Accordingly, future research, following recent work, may find it productive to target specific violent behaviours whose individual motivations may be as a result of partner availability as well as other social and ecological variables [4].

(d) Completed fertility

We find that completed fertility increases for women and decreases for men in response to a male-biased ASR. Because women in Western settings show a clear preference for resource providers, and human offspring require assistance from helpers in addition to the mother to reach independence, here we interpret female fertility as an indicator of male investment. MM approaches expect males in male-biased populations to focus on behaviours necessary to acquire and maintain a single relationship. This could take many forms, from male mate guarding to paternal investment. Accordingly, higher fertility of women when they are relatively rare is a potential indicator of men's greater commitment to a partner and shared offspring. However, because this finding could also be due to a higher proportion of women remaining unmarried and not having children in places with an excess of women (i.e. when men are rare a numerical argument could be the simplest explanation for lower female fertility rather than facultative adjustment of male investment). To investigate this, we only look to women who are married and find that the ASR still remains a significantly positive predictor of female fertility (electronic supplementary material, table S6). Thus, women's higher fertility in response to their scarcity may be driven, in part, by elevated male investment.

5. Conclusion

In reviewing our findings, and others from across the literature, we highlight the degree to which results vary across studies and populations—consequently, confusion is warranted regarding our current understanding of the relationship between ASR and behaviour. Here, however, our results can largely be interpreted in support of MM models. As we argue, seemingly conflicting results across studies could be offering support for the same prediction. In particular, we highlight the role of the culturally defined mating arena as an overlooked mediating variable between ASR and reproductive outcomes in humans. For example, in the historical population under study here, reproduction occurred primarily within the confines of marriage. However, in the contemporary USA, where sexual mores are relaxed, many individuals are free from this constraint (e.g. non-marital fertility rates are at 40% [52]). Thus whether or not a particular indicator, such as male marital status, is a useful measure of MM predictions depends on the population under study. Moreover, responses to ASR imbalance should be expected to vary because of the (i) changing roles of specific inputs generating imbalance across time and space, (ii) individual and species-level ability to facultatively respond to partner availability and (iii) discrepancies across individuals within and among populations in their ability to accurately assess the ASR. Accordingly, we hope to make clear that behavioural outcomes across populations and species that vary in ASR should not be expected to be uniform. Furthermore, disagreement in the literature regarding the relationship between partner availability and reproductive behaviour is both useful and necessary for the refinement of theory, and key for the maturation of our behavioural models. We argue that predictions, while derived from theory, must be tailored to a particular population and pay attention to feedbacks between partner scarcity, sex-structured pay-offs to mating strategies, mating system and, particularly among humans, the social and cultural setting.

Ethics. The research was approved by the University of Utah Institutional Review Board (IRB #00043524) as part of the 'Early Life Conditions, Survival, and Health: A Pedigree-Based Population Study' (PI Smith).

Data accessibility. The UPDB is a unique research resource that enhances the value and furthers the advancement of research in studies linking early life circumstances to health and behavioural outcomes later in life. Special attention is given to protect individuals and their information contained within the UPDB and the organizations that contribute data while also allowing access to researchers. Accordingly, the Utah Resource for Genetic and Epidemiologic Research (RGE), established in 1982 by Executive Order of the Governor of Utah, administers access to the UPDB through a review process of all proposals using UPDB data. The protection of privacy and confidentiality of individuals represented in these records has been negotiated with agreements between RGE and data contributors. Data from the UPDB are available only for approved health-related research studies and access is project-specific and granted after review and approval by an RGE oversight committee and the University of Utah's IRB. This process allows researchers with approved protocols to use the data, a process that has proven effective and successful as evidenced by hundreds of approved studies that have relied on the UPDB.

Authors' contributions. R.S. and K.R.S. designed the research and wrote the paper.

Competing interests. We have no competing interests.

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