Social status mediates the effect of the adult sex ratio on mating and parenting strategies

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Summary

Evidence from animal species indicate that a male-biased adult sex ratio (ASR) can lead to higher levels of male parental investment and that there is heterogeneity in behavioural responses to mate scarcity depending on mate value. In humans, however, there is little evidence of the effect of ASR on relationship stability and parental investment and even less how they vary by an individual's mate value. In this paper we use detailed census data from a developed population (Northern Ireland) with a high local sex ratio skew to test the association between the ASR and relationship stability and parental investment by social status (education and social class) as a proxy for mate value. We find evidence that in female-biased areas women with low education are less likely to cohabit with a partner than highly educated women, but in male-biased areas low educated women do as well as their highly educated peers. For men there is no evidence that the sex ratio is associated with likelihood of a stable pair-bond, regardless of education. In contrast, we find evidence that among high status men, parental investment is high regardless of ASR, but among low status males, parental investment increases markedly with the ASR. We discuss these results in the light of recent reformulations of parental investment theory.

Keywords: adult sex ratio, mating, parental investment, census, heterogeneity.

Introduction

The adult sex ratio (ASR) has important consequences for mating-related behaviours. When one sex has many potential partners and the other has few, the mate-limiting sex can increase demands on prospective mates. Various responses in mating behaviours to a skewed ASR have been observed across species; male-biased sex ratios are associated with higher levels of copulation and faster sperm depletion in fruit flies and snow crabs (1,2), higher levels of mate-guarding in spiders, crustaceans and water striders (3,4), and increased male allocations to parenting rather than mating effort, lower levels of polygyny and divorce (mate switching) in various species of shorebirds (5). In humans, there is evidence that female-biased sex ratios are associated with earlier reproduction, higher rates of single motherhood, higher preference for short-term sexual relationships, and higher number of sex partners in both males and females (6–12). However, inconclusive or contradictory evidence that suggests the opposite relationship between the ASR and mating related behaviours also exist, e.g. that violence is lower when men are in excess (13), and that male mortality from violence and risk-taking is not higher when men are plentiful (14). With regards to reproduction a female-biased sex ratio might either lead to lower (11) or higher (15) ages of first birth. The empirical evidence that is pointing in different directions, along with contrasting theoretical frameworks, mean that ASR research is contradicting and currently without consensus (15).

Scholars addressing questions regarding the impact of the ASR come from different disciplines and theoretical traditions, and until recently, often published without much exchange between parallel streams of work. On one hand, predictions based on evolutionary parental investment (PI) theory, stipulate that male competition should increase under male-biased sex ratios, and that there should be weaker pair-bonds, less parental investment from fathers and more male-male violence as a result (16). But parental investment theory based on sex roles of coy females and competitive males thought to have evolved as a response to anisogamy, is increasingly outdated. It commits the 'Concord fallacy' which is that parents should not invest based on past, but on future fitness gains

from alternative strategies (17). Recent evolutionary modelling work predicts that there should be higher male competition for males under female-biased, rather than male-biased sex ratios (18). A crucial point is that under a male-biased sex ratio males have to spend longer time out of the mating pool after deserting a mate, potentially rendering it more advantageous to stay in the pair-bond.

In line with this reformulated parental investment perspective, mating market theory proposes that the sex in oversupply should respond to the demands of potential mates. Taking a mating market approach, one consequence of a male-biased sex ratio might be that rather than engaging more in contest competition, males who seek a mate might invest in income generating activities. Those men who already have a mate might increase their chances of a staying in the pair-bond by investing in any existing offspring. An assumption here is that females are free to choose their partners, and that females value resource provisioning more than displays of physical prowess or contest competition. While it might seem obvious that individuals should seek to meet the demands imposed by potential mates, it is often overlooked that what those demands are might vary depending on both the local sociocultural context and individual characteristics.

One potential explanation for the varying results in the literature is the fact that ASR studies come from varying ecological and cultural contexts. The consequences of sex ratio imbalances are being examined in a range of societies (several of which are presented in this issue), from hunter and gatherer populations where population sizes are small and ASR highly fluctuating (19), historical populations with strict marriage norms where reproduction took place within the confines of marriage (15), to modern day societies with urban-rural divides, high economic inequality such as China (20), or where the ASR differs between racial groups such as in the US (21). Human behavioural ecologists recognise that local costs and benefits that impact individual reproductive strategies can come in the form of sociocultural norms (as well as vice versa with local costs and benefits also generating the norms) (22). For instance, being mate-limited in societies that have strong social sanctions against divorce will have quite different consequences compared to ones where mate monopolisation is weak and pair-bonds are unstable. Another factor that varies between societies is the degree to which women are dependent on men for resources and whether they are able to request male engagement in childrearing. Paying greater attention to what Schacht and Smith (15) refer to as the 'culturally mediated mating arena' can help unpack the reasons why ASR responses are not uniform across societies.

Contrasting results of the ASR from different populations might in part be due to the fact that characteristics within populations vary. If we only examine the population average responses to the ASR, variation in magnitude or direction might go unnoticed. The aim of this paper is to address the question whether individuals *within* populations react differently in response to the ASR based on their mate value and status. The rationale is as follows; what strategy to choose to woo a prospective mate, or the payoffs from staying in a pair-bond versus deserting one's mate, should depend on an individual's particular traits and his or her mating value. An individual who is likely to be successful in a contest interaction due to greater physical prowess might opt for violence when competition for mates is high, whereas someone who has potential to attract mates through resources might instead invest in provisioning activities or increase the level of parental investment. It is also possible that individuals pursue the same type of strategy, but that the degree of mating effort varies with individual attractiveness. An example is black striped pipefish, where smaller females compete more vigourously under a female-biased sex ratio, whereas larger females, who are more desirable as mates, do not alter their behaviour when the sex ratio becomes more

female-biased (23). We have previously shown that single men in the current study population (Northern Ireland) are more likely to be involved in fatal violence and accidents than partnered men if they have low socioeconomic status (SES) but for high SES men risk of death was not predicted by whether he was in a pair-bond or not. In other words, although some single men who try to secure a mate might compete through violence or risk-taking behaviours, this might be less common among men who can compete with resources (24).

Within human evolutionary sciences, it is well-established that men with more resources are more desirable as long-term mates, have more stable pair-bonds and invest more in their offspring than men with fewer resources (25,26), possibly because these men gain more in terms of offspring outcomes per unit of investment than men without such resources (27). Because an individual with higher status and resource access is more attractive to the opposite sex, he/she might have higher bargaining power on the mating market and in a pair-bond. Thus, both socioeconomic factors (here proxied by level of education and social class) and the local ASR shift the conditions of individuals with potential implications for mating and parenting behaviours. Because the assumptions of ASR dynamics lie in bargaining power, it is important to test how an individual's characteristics interact with the pressures imposed by the local sex ratio, and to consider behaviours of both individuals who are seeking mates, and those who are in established pair-bonds as we do in this study.

Overall the ASR literature tends to place greater emphasis on the behavioural responses of men, than of women. This male-centric view might have its basis in the belief that it is undesirable behaviour of men that contributes to societal problems, which would grant a greater emphasis on male behaviour. A growing body of evidence now challenges this view (13). Because it is difficult to know what underlies a relationship between the ASR and mating behaviour (behaviour or men, women or both?) (28), and because responses that are associated with a female-biased or male-biased sex ratio might not be symmetrical, behaviour of both sexes should be examined in unison.

Aims of the study
We use detailed migration data to show how the sex ratio skew arises and then consider how the ASR affects pair-bonding and parental investment for individuals of different SES. Our study population, Northern Ireland, is well-suited to studying the effect of the ASR because there are several female-biased and several male-biased areas. This balance of local ASR areas is important but is unusual among other studies examining ASR at a local level.
This study has at least three key strengths, i) we explore three different mating related behaviours (likelihood of being in a stable pair-bond, separation and parental investment) that offer complementary insights into sex ratio response, ii) we use detailed census data with a wide ranging ASR measured at the local ward-level, and iii) we explicitly consider individual heterogeneity in ASR responses by socioeconomic factors, and examine behaviours of both single and coupled individuals and males and females simultaneously.
Below we lay out our predictions regarding the effects of SES, the ASR, and the interaction between the two on pair-bonding (cohabitation and separation) and male parental investment. Differences between the predictions are in bold for emphasis.

Predictions
The effect of SES on pair-bonding
1) If individuals with **high SES** are more desirable as mates, and have higher payoffs from investing in their offspring, they **should be more likely to be in a long-term pair-bond** (be cohabiting/have lower likelihood of separation) than low SES men.

The effect of ASR on pair-bonding

2) If females have higher fitness payoffs from being in a stable pair-bond than males, and females have higher bargaining power under male-biased ratios, then **males should be more willing to commit to a pair-bond for longer when the sex ratio is male-biased** (i.e. both sexes should be more likely to be cohabiting/have lower likelihood of separation).

The effect of ASR on pair-bonding should depend on SES

3) If a skewed sex ratio means that the mate-limited sex relaxes demands on prospective mates, and having high status and access to resources is one such demand, **the effect of the ASR on pair-bonding** (higher cohabitation/lower separation) **should be stronger for individuals with low SES** than high SES.

The effect of ASR on male parental investment should depend on SES

4) If a male-biased sex ratio increases female demands for male parental investment, and low SES males have more to gain from staying in the current pair-bond (as they are less likely to be successful on the mating market), **the positive effect of the ASR on parental investment should be stronger for low SES men** than high SES men.

2. Data and Methods
Data
The Northern Ireland Longitudinal Study (NILS) links administrative data including the national Census to vital events, such as birth and migration. NILS comprises circa 28% of the Northern Irish population, randomly selected by 104 birthdays. A range of individual covariates are linked from the Census. We also make use of the detailed migration data in order to establish how local sex ratio skews are generated. Any missing data were imputed by the Census. For a more detailed description of the NILS, see (29).

Dependent variables
Cohabitation
To test the effect of the ASR on cohabitation (a proxy for a stable pair-bond), we use data on relationship status (cohabiting versus non-cohabiting) of NILS members on Census day on the 29th of April 2001. Our cohabitation measure includes, but is not restricted to, married individuals as living together can be considered a stable pair-bond. The sex of census members is not known here, and our analyses thus include all individuals regardless of the sex of their partner. Analyses are restricted to individuals aged 25-59 years in 2001. The lower age cap is imposed because we are examining interactions with highest educational level. Therefore we can only include individuals who have completed their education trajectory. Moreover, by excluding the under 25s we avoid including teenagers and young adults who might not yet wish or be able to live with a partner. Age is capped at 59 years because we are interested in individuals of roughly reproductive age and do not wish to include potential widows and widowers.

Separation
The 2001 and 2011 Censuses are used to examine risk of transitioning from a pair-bond to singlehood during this ten year period. The transitioning to singlehood (henceforth separation) is a good measure for pair-bond stability as it enables us to estimate the risk of ending up without a partner among those who previously managed to establish a pair-bond. The same age range, 25-59 years in 2001, is used for the reasons described above.

Parental investment

To examine the level of parental investment as a function of the ASR, we use data on whether the father of a child is cohabiting with its mother (registered at the same address) at the time of birth of that child. Deserting one's partner already prior to the birth of the child is a clear sign of disinvestment and cohabitation is therefore a useful measure of minimum parental effort. We have data on 28955 mother-father pairs for women who had a first birth between years 2001 and 2013 (for ages, see table 4). In a fifth of these births the father was not registered at the same address as the mother at the time of the birth. Data on the father's address is available regardless of whether the father was named by the mother on the birth certificate, which limits bias. The ASR used in parental investment models is based on the mother's residential ward at the time of the birth.

Independent variables
All individual independent variables are taken from the NILS and linked from the 2001 Census. Among our sample of 25-59 year olds, 60% live in urban areas, 43% are Catholic, 55% Protestant and 2% report having no/other religion. 39% have no qualifications, 20% GCSE (General Certificate of Secondary Education, taken at age 16, 15% GCSE+, 7% A-level, and 19% have a university degree. In the United Kingdom, students take examinations in a range of subjects at GCSE level after 5 years of secondary education; after an additional two years of study, students may take A-Level examinations (required for university entrance). Father's social class (NS-SEC) is based on the 2002 classifications: "higher managerial and professional occupations", "lower managerial and professional occupations", "intermediate occupations", "small employers and own account workers", "lower supervisory and technical occupations", "semi-routine occupations", "routine occupations" and "never worked or long-term unemployed" (see table 4). In the analysis on parental investment we control for father's age and father's age squared, as this might otherwise confound any effects of the father's social class. Mother's age and social class could not be used due to collinearity.

Methods
For our three outcomes, cohabitation, separation and parental investment, we run multilevel logistic regressions where individuals (or as in the case of parental investment, couples) (level 1) are clustered within wards (level 2). The random intercept for ward controls for unmeasured variation at the local ward-level. For cohabitation and separation models, interaction terms between the ASR and an individual's highest level of education are used to determine whether the effect of the local ASR varies between individuals with different status. For parental investment models, we use data on father's social class, as this is a more detailed measure than highest educational level and is more variable over the life course. (Note that only educational level was available for the analyses on cohabitation and separation). Akaike information criterion (AIC) was used to infer model fit where a decrease in AIC of more than 2 units implies a better fit. Maximum likelihood was used as estimation method, and for the figures we display the predicted probabilities. All analyses were performed in Stata 14.

Adult sex ratio
To construct the ASR we use data from the Northern Ireland Neighbourhood Information Service (NINIS) on ward-level population by sex and age (calculated as the ratio of men to women, 16-39 years). A ward is an administrative area that comprises c. 2900 individuals, of which there are 582 in Northern Ireland. We use the 16-39 age range as we are interested in individuals of roughly reproductive age. Note that the ASR based on individuals aged 16-64 years is correlated to our measure at r=0.94 (p<0.001) and the ASR of 16 and over at r=0.83 (p<0.001). The ASR of 16-39 year olds in 2001 and 2011 was correlated at r=0.60 (p<0.001).

ASR was categorised into quartiles because this was a better fit than other categorisations (e.g. tertiles, quintiles and sixtiles), and because it allows for easier interpretation. See table 1 below for ranges and means.

	1st quartile	2nd quartile	3rd quartile	4th quartile
Range	0.64-0.93	0.94-0.98	0.99-1.05	1.06-2.08
Mean(sd)	0.87(0.05)	0.96(0.01)	1.02(0.02)	1.15(0.17)

Table 1. Ward-level adult sex ratio in 2001 (age 16-39 years).

Insert Figure 1 about here.

What causes the adult sex ratio skew?

A skew in the ASR can arise because of unequal sex ratios at birth, sex differences in mortality, or in migration patterns. In addition, factors such as incarceration rates of males might lead to skewed sex ratios in some human populations (30). Because levels of incarcerations are low in Northern Ireland at the time of the study, and male deaths are not as dramatic as in for example US populations, and the sex ratio at birth is not skewed, sex biased migration is a more plausible explanation for the variation in ASR. Using data on migration within Northern Ireland we find that women are significantly more likely to out-migrate from certain types of areas and that this has impact on the ASR. Overall, 51.8% of women out-migrate from their ward at least once during the study period, compared to 47.6% of men. Importantly, women are more likely than men to move out of rural areas, areas with higher ward-level deprivation, areas with lower population density and areas with a male-biased sex ratio (see Electronic Supplementary Material, table S1). Women are most likely to migrate if never married, whereas men are most likely to migrate when separated or divorced (see Electronic Supplementary Material, figure S1). Lastly, by examining the ASR of the 'source' and 'sink' wards, we can conclude that women who move from male-biased areas migrate to areas that are *more* female-biased areas than the areas men migrate to (see Electronic Supplementary Material, table S2 and S3).

RESULTS

Cohabitation and separation

The tables below show the percentage of cohabiting individuals and separations between 2001 and 2011 by ASR quartiles in 2001 (table 2) and highest educational level (table 3). Circa 67% of women in the most female-biased areas were cohabiting compared to 81% of women in the most male-biased areas. Approximately 23% of men and women in the most female-biased areas experienced separation, compared to circa 16% in the most male-biased areas. About 15 and 16% of men and women with the highest level of education separated compared to circa 21% and 23% of those with the lowest level of education.

		1st quartile	2nd quartile	3rd quartile	4th quartile
Cohabitation	Men	77.2%	81.0%	80.1%	78.0%
	Women	66.7%	75.4%	77.9%	80.5%
Separation	Men	22.7%	18.4%	17.8%	16.3%
	Women	23.3%	19.3%	18.9%	16.4%

Table 2. Cohabitation and separation by ASR, individuals aged 25-59 years in 2001, men n=69117, women n=71685.

	Degree	A-level	GCSE+	GCSE	No qual.

Cohabitation	Men	81.0%	76.3%	79.7%	78.1%	79.5%
	Women	74.9%	75.8%	78.7%	74.3%	73.2%
Separation	Men	15.3%	17.2%	17.9%	19.7%	20.5%
	Women	16.4%	18.0%	17.5%	19.3%	22.5%

Table 3. Cohabitation and separation by education, individuals aged 25-59 years in 2001, men n=69117, women n=71685. No qual.- no qualifications.

In multilevel logistic regressions we find evidence that men with higher education are more likely to cohabit with a partner (figure 2a). This offers some support for our first prediction but the relationship is not dose-dependent; men with no qualifications are less likely than men with any other educational level to be cohabiting with a partner, but other groups appear similar. Notably, the results show no significant effect of the ASR among men of any educational group (figure 2a). Thus, neither prediction 2, that men should be more likely to be in a stable pair-bond under male-biased sex ratios, nor prediction 3, that the effect of ASR should be stronger among men with lower education, is supported for males (see ESM, table S4).

We find evidence that women without any formal education are less likely to be cohabiting with a partner compared to more educated women under female-biased sex ratios. But under male-biased sex ratios, there is no significant difference in the probability of cohabiting with a partner between women of different educational levels (figure 2b, and ESM table S4). In other words, there is a positive effect of the ASR on female cohabitation (supporting prediction 2), and this effect is strongest among women with low levels of education (supporting prediction 3). Prediction 1, that high education should be associated with higher probability of being in a pair-bond, is only partially supported.

Insert Figure 2a-b.

In the models on separation, there is evidence that men and women with at least a university degree are less likely to end up as single compared to peers with no qualifications. Second, separation is more likely to occur at female-biased sex ratios among individuals with both the highest and lowest levels of education (figure 3a and 3b). Third, the effect of the ASR is only marginally stronger for individuals with the lowest educational category (no qualifications). Thus while our first two predictions are supported, there was only tentative support for the third.

Insert Figure 3a-b.

Parental investment

Table 4 and 5 show the percentage of fathers who are cohabiting with the mother at the birth of their child. There is a large difference in parental investment with the father's social class: 42% of fathers who have never worked/are long-term unemployed are cohabiting with the mother, compared to 96% of fathers who have a higher managerial or professional occupation (table 4). In female-biased areas, 39% of fathers who have never worked/are long-term unemployed cohabit with the mother, compared to 52% of their peers in the most male-biased areas (table 5).

			Father's age	Mother's age
Father's social class	*n*	*Cohabitation*	mean (sd)	mean(sd)
Never worked/long-term unemployed	927	42%	27.5(7.4)	24.3(6.0)
Routine occupations	4776	74%	31.1(6.5)	28.4(5.7)
Semi-routine occupations	4033	74%	30.4(6.5)	27.9(5.7)

Lower supervisory and technical	3400	78%	30.9(6.3)	28.7(5.6)
Small employers and own account work	466	77%	32.1(6.6)	29.3(5.8)
Intermediate occupations	2981	86%	32.3(6.3)	30.2(5.3)
Lower managerial and professional	4284	91%	33.3(5.9)	31.0(5.0)
Higher managerial and professional	3848	96%	34.2(5.3)	32.2(4.5)

Table 4. Father's social class by father's and mother's age, n=28955.

Father's social class	1stquartile	2nd quartile	3rd quartile	4th quartile
Never worked/long-term unemployed	38.8%	41.4%	41.4%	51.7%
Routine occupations	65.4%	73.4%	77.7%	80.7%
Semi-routine occupations	66.6%	75.4%	78.3%	76.6%
Lower supervisory and technical	70.1%	79.3%	80.1%	80.6%
Small employers and own account work	67.6%	78.0%	78.7%	82.9%
Intermediate occupations	80.0%	87.1%	87.4%	89.6%
Lower managerial and professional	87.3%	92.6%	92.4%	92.2%
Higher managerial and professional	94.9%	96.1%	96.2%	95.5%

Table 5. Percentage of men cohabiting with the mother at the time of the birth of their child, by father's social class and adult sex ratio of mother's residential ward, n=28955.

Figure 4 shows the results of a multilevel logistic regression with the predicted probabilities of the father cohabiting with the mother at the time of the birth of the child, by father's social class and the ASR of the mother's residential ward. As predicted, fathers with higher social class are more likely to exhibit parental investment and overall there is a positive effect of ASR on parental investment. Moreover, men of low social class, but not men of high social class, are more likely to live with the mother of their child in a male-biased area than in a female-biased area. These results thus offer support for prediction 4.

Insert Figure 4.

Individual and ward-level variance
We calculate the variance partition coefficient (VPC) to examine the percentage variance of the total variance in the outcome that can be attributed to the ward-level (31). For cohabitation the ward-level was responsible for 4.6 and 5.2% of male and female cohabitation respectively. The corresponding figures for separation was 1.7 and 1.2%, for men and women respectively, whereas for parental investment the variance explained by the ward-level was 10.7%. The remaining variance is attributable to differences between individuals.

DISCUSSION

We have explored the effect of the ASR on mating and parenting behaviours in a developed population with a wide range in the local sex ratio. The results demonstrate that the effect of the ASR on cohabitation, separation and parental investment is contingent on sex and on social status and resources, but differs between reproductive and parenting outcomes. These findings are novel as the literature to date has put little emphasis on the fact that any facultative responses to the ASR might vary both in type and magnitude based on an individual's resources and bargaining power. Moreover, previous studies have often used ASR on country or state-level and in the case of parental investment, measured population averages of single parenthood, rather than the parents' cohabitation at the time of the birth of their child (7,32). Below we discuss these results and compare them to previous findings, speculate on the underlying explanations and offer suggestions for future research.

Our data reinforce the idea that males might invest in behaviours that strengthen the pair-bond rather than compete more violently when there are plenty of males(13,14). Instead, it is possible that men who want to woo or keep a partner when competition is high signal their intention to invest and become more engaged in childrearing. While there was some support for the prediction that men with high SES should be more likely to cohabit, there was no evidence that the effect of ASR on male cohabitation varied with male SES. This was surprising as we had predicted that females would relax demands on prospective mates under female-biased sex ratios. These results contrast with those of Pollet and Nettle (32), who found that the effect of SES on marriage success was stronger in male-biased states in a historical US sample, possibly as a result of higher female demands on male provisioning in areas where men are plentiful. It is difficult to say whether the differences between Pollet and Nettle and our study stem from differences in methodology, the coarse nature of their US state-level ASR, and/or if they are due to differences in sociocultural context. In the historical US childbearing occurred within the confines of marriage whereas in present day Northern Ireland, social sanctions of divorce are less stark, childbearing out of wedlock or even among parents who are not cohabiting is common, and some state benefits are available for single parents if needed. While it is intuitive that women can drive a harder bargain when men are plentiful the results here are not so straightforward. We do however find a similar pattern to that reported from historical US for couples *with children* in the parental investment model, and for female cohabitation. We return to discuss possible reasons for these differences after reviewing the results of the other models.

For women we find a positive effect of the ASR on the likelihood of cohabitation and that a male-biased ASR increased the likelihood of cohabitation particularly for women with low SES. One interpretation is that men in female-biased areas are low investors and that women in such areas, and especially women with the lowest SES and lowest bargaining power, are better off not being partnered at all. Females can benefit from mating with multiple men (33,34) and could do better by not committing to a single partner if he is a burden rather than someone who will reliably provide care. It is the low SES women in areas where women are plentiful who have the lowest probability of cohabitation in this population. We have previously shown that it is women in female-biased areas and those with low SES who start reproducing early, often without the support of a partner (11). It is worth mentioning that abortion is illegal in Northern Ireland, and so risky sexual behaviours, arguably more common in female-biased areas (21), might lead to early parenthood for these women more often than if abortion was legal and accessible.

Turning to the women with high SES, it was somewhat surprising that these women, who, if SES implies higher status, might find it easier that low SES women to find a partner, were not

cohabiting to a larger extent. But high SES women might not necessarily be the first choice for a man in a female-biased area, as he might struggle to meet her higher demands on investment. Rather than lowering their demands, high SES women might favour a strategy where they delay family formation until a higher quality mate is around and in the meantime focus on their career. This resonates with some experimental evidence that when women are exposed to cues of a female-biased sex ratio, they are more likely to prefer career investments over family formation (35) and evidence that birth rates of the over 30s are higher in female-biased areas only in more affluent wards whereas birth rates at younger ages are higher in female-biased deprived wards in England and Wales (36).

Some of the asymmetries between the male and female models are likely to be explained by the fact that men in female-biased areas could opt for younger women, possibly younger than the age cut-off at 25 years that we used in these analyses. Females in female-biased areas might accept a male with relatively low SES (even in male-biased areas) if these costs are outweighed by the perceived benefits associated with an older age male. Lastly, because of homogamy, i.e. that individuals tend to assort with mates similar to themselves based on for example SES, it might be over-simplistic to assume that the sex in oversupply will lower their standards to be able to marry someone from the opposite sex if this means having a partner with lower SES than oneself. In the face of homogamy an extension of the overall ASR based on the general population to an SES specific ASRs might yield higher predictive power. All our data captures absolute characteristics of individuals, but demands on mates *relative* to one's own characteristics might also change when mates are scarce.

Separation and parental investment
The results on separation confirm patterns from previous studies that divorce is more common among individuals with low education and under female-biased sex ratios. However, the difference in the effect of the ASR on separation based on education was very slight and only marginally stronger among those with low education. If this effect reflects a true relationship, it could be because males with low education start behaving more like highly educated men and stay with partners longer when competition for mates is high. By necessity, the relationship between the ASR and the separation risk cannot differ in the two sexes as 'it takes two to tango', or in this case, separate, and by definition, cohabiting couples reside in the same ward prior to separation. In order to understand the dynamics that precede separation, behaviours that can be indicative of effort/disinvestment in the relationship can be examined. Time spent on household chores has been linked to relationship satisfaction and likelihood of separation (37) and can be meaningfully compared for women and men to map negations within the pair-bond.

Men with low levels of resources, who would generally be more likely to desert or be deserted by a woman, seem to opt for a strategy of more parental investment when there are many other men around. Interestingly, these results show that even among relatively high status individuals there is an effect of the ASR on male parental investment. In female-biased sex ratios, men with intermediate occupations are less likely than higher managerial/professional men to live with their offspring, but in male-biased sex ratios, these men have 'caught up' with men with the highest social class. As our measure captures a base-level parental investment, future work should examine whether this pattern holds for more detailed parental investment measures. Another interesting question is whether parental investment responses are symmetrical. In shorebirds parental investment is higher in males at male-biased sex ratios and higher among females at female-biased sex ratios (38) but other animal evidence suggesting non-symmetrical responses in e.g. divorce rates also exist (39). Females might start investing more in offspring in female-biased areas as a means

to remain a competitive mate, or they might respond to other demands their partners might have, for example increase investment in physical appearances. Our measures of education and social class as proxies for mate value and social status is just one dimension of mate desirability and many others might also be worth investigating (e.g. physical attractiveness, personality traits etc.).

In Northern Ireland sex biased migration patterns are the root cause of the sex ratio imbalances. We found that area factors predicted sex differences in migration, in that women were more likely to migrate from areas that were scarcely populated and deprived. But there was also evidence that sex differences in migration was related to an individual's stage in the life course (marital status). We only had data on internal migration, but it is possible that young men and women with the highest income generating potential leave Northern Ireland to seek economic opportunities elsewhere. In societies where individuals have multiple options for employment and residence and the geographic distances between rural villages and cities are small the ASR skew over time will diminish over time. If women are more likely to migrate to urban areas to seek education or employment, low levels of mates in certain areas could lead to more men following the women. Thus, in the long run ASRs might stabilise or at least not increase. Whether this is a strategy that men pursue might vary depending how skewed the sex ratio is, and with structural and economic opportunities of men in new areas.

As more detailed data from a range of populations are now being used, the question of how stable ASRs are, and the mechanisms by which it affects behaviour are starting to be investigated. There was some change in the ASR over the two waves in our data but this variation might be small in comparison to fluctuations experienced up until adulthood. In a comparison of the ASR during juvenility and present ASR, Schacht and Smith (15) found that childhood ASR did not impact on reproductive outcomes. What time frame that is relevant and when the environment is most important for an individual's subsequent behaviour, is a broader question within developmental biology and psychology (40). To answer this question future analyses ought to be conducted on longitudinal data, incorporating migration, to capture an individual's varying ASR in both time and space.

When interpreting the interaction between SES and ASR, one has to bear in mind that low SES individuals in male-biased areas might differ in some way compared to low SES individuals in female-biased areas. For example, individuals in rural areas might be faced with a more conservative community, where deserting a partner would be associated with stronger social sanctions than in cities. Furthermore, mate monopolisation might be stronger in rural areas if communities are more tight-knit and anonymity lower. For the ASR to influence the degree of sexual selection that is operating in a population, mate monopolisation has to be strong (41). This assumption might be questioned in developed populations where both sexes spend a considerable amount of time outside the home in employment, and there are plenty of opportunities to meet potential new partners.

We have assumed that the ward is a meaningful boundary at which to measure the sex ratio. Although there are other means to find a partner than within one's local ward, individuals tend to marry similar individuals who are likely to live nearby (42) and characteristics from an individual's local ecology might serve as cues to one's prospect of finding a mate even outside the ward. Because Northern Ireland has high levels of residential segregation, the sense of local community is strong. Drawing on this, we recently tested perceptions of local neighbourhoods in Belfast. We found that most individuals perceived themselves to live in slightly female-biased areas even when they lived in areas

where males clearly outnumbered females (43). While it is not necessarily assumed that individuals are consciously aware of the local ASR, these results raise questions about the mechanisms by which the ASR affects human behaviour. The magnitude of the ASR is important as threshold effects might exist so that the strategies pursued by the mate-limited sex might be different when there is some or very high likelihood of being without a mate. In some of our analyses, there appeared to be a non-linear relationship between the ASR and reproductive behaviours, which grants further study of when and how the ASR skew matters.

Findings presented here are in line with theoretical models and some empirical evidence from non-human species that show that male-biased sex ratios should be associated with higher efforts to stay in the current pair-bond (18). We show that there is heterogeneity in this effect and that the impact of mate scarcity varies with social status. Other factors related to the reproductive value of the individual, such as age or parity, might also be associated with heterogeneity of the ASR, as mate scarcity would have different fitness implications for individuals who have had many offspring compared to those that have had few or none. Moreover, we have shown that it is important to evaluate different types of behavioural responses because considering only one type of mating behaviour might lead to an incomplete picture of the effect of ASR on mating and parenting dynamics. To add to our understanding of ASR imbalances, future analyses should be longitudinal, capture multiple outcomes per individual, as this would allow assessing whether multiple strategies are pursued in the face of mate scarcity, or whether individuals tend to increase investment in one particular strategy. Whether men or women dictate terms in a population could vary with social institutions, how flexible marriage and pair-bonds are, and how mate monopolisation occurs. While a skewed sex ratio produces a scenario where the more plentiful sex ought to cater to the preferences of the rarer sex, an individual's optimal strategy under conditions of mate-scarcity varies with social status, and that these patterns are not necessarily symmetrical for males and females.

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Table and figure legends.

Table 1. Ward-level adult sex ratio in 2001 (age 16-39 years).

Table 2. Cohabitation and separation by ASR, individuals aged 25-59 years in 2001, men n=69117, women n=71685.

Table 3. Cohabitation and separation by education, individuals aged 25-59 years in 2001, men n=69117, women n=71685. No qual.- no qualifications.

Table 4. Father's social class by father's and mother's age, n=28955.

Table 5. Percentage of men cohabiting with the mother at the time of the birth of their child, by father's social class and adult sex ratio of mother's residential ward, n=28955.

Figure 1. Map of the ward-level ASR in 2001 in Northern Ireland. White- 1st quartile (ASR 0.64-0.93), light blue – second (ASR 0.94-0.98), blue- 3rd quartile (ASR 0.99-1.05), dark blue – 4th quartile (ASR 1.06-2.08).

Figure 2a-b. Predicted probability of cohabitation by highest level of education and adult sex ratio among men (a) and women (b) between the ages of 25-59 years. Multilevel logistic model, controlling for age, age squared and religion (Catholic, Protestant, none/other) with individuals men n= 87110, women n=95673 (level 1) clustered within wards (n=557).

Figure 3a-b. Predicted probability of separation by highest level of education and adult sex ratio among men (a) and women (b) between the ages of 25-59 years. Multilevel logistic model, controlling for age, age squared and religion (Catholic, Protestant, none/other) with individuals men n=69117, women n=71685 (level 1) clustered within wards (n=557).

Figure 4. Predicted probability of parental investment (male cohabitation with the mother at the birth of the child) by male social class and adult sex ratio of mother's residential ward. Couples (level 1, n=28955) are clustered within wards (level 2, n=570).