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ORIGINAL ARTICLE

Why empresses have more sons? Maternal instant social condition determines it

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Abstract

Sexual selection echoed by the sex ratio is a critical issue in evolution and reproductive biology studies, and the second sex ratio (sex ratio at birth, SRB) is an important evaluation indicator for sex regulation. However, broad debates on sex ratio at birth exist due to the lack of a clear spatiotemporal genealogical database. This study explicitly tests the Trivers and Willard's hypothesis stating that parents with good social conditions tend to show a male-biased SRB. Using a database of Chinese imperial families from 211BC to 1912 (2142 years) which avoids the spatiotemporal confusion of data thanks to its clear boundaries and long timespan, we found that a proportion of males at birth was 0.54. In particular, the results indicate that the empresses generated a significantly higher male-biased SRB than the concubines within the imperial harems (0.61 vs 0.53), while the SRB of concubines was not higher than ordinary people (0.53 vs 0.52). A significant difference of SRB before and after empress coronation (0.48 vs 0.65) was detected, indicating that the change to a higher social status is the leading cause of a biased SRB. These findings suggest that mothers with privileged *instant social conditions* tend to generate more boys than girls. In other words, a higher maternal social rank during the conception period, instead of rich resources, forms the primary mechanism regulating the SRB.

Significance statement

Adaptive sex ratio has been a debatable topic difficult to clearly verify since the publication of Trivers and Willard Hypothesis in 1973, which proposes that parents who have good conditions should produce more male offspring. The one reason is that the validity and sample size of the databases used contained unavoidable confounding noise, both genealogically and genetically. To overcome these issues, we specifically compiled a historical database of Chinese imperial families, which are characterized by a confined mating harem and unique eunuch system, guaranteeing biological and genetic purity with precise genealogical relationships and genetic linkages between the parents and the offspring. Thus, this is an extraordinary effort to clarify the hypotheses proposed by TWH and other hypotheses.

Keywords Trivers and Willard hypothesis · Sex ratio at birth · Maternal · Instant social condition

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Yan-Peng Li, Wei Ding and Zhi-pang Huang contributed equally to this work.

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Introduction

Sex ratio is a useful parameter for analyzing the dynamic process of sexual selection and social structure (Darwin 1859; Fisher 1930a, b; Hamilton 1967). The secondary sex ratio (sex ratio at birth) is regarded as the key parameter to understand the theory of sex allocation, because primary sex ratio (at conception) is difficult to determine. Theoretically, a sex ratio of offspring is an equilibrium, provided both sexes receive equal parental expenditure and investments. However, a disequilibrium widely exists in reality, either caused by natural selection (Hamilton 1967) or by arbitrary social interference (birth control), such as the One-Child policy in China between the 1980s and 2015 that caused a skewed sex ratio at the birth (SRB) due to induced abortion of female fetuses (Nie 1999; Wang 2012). From an evolutionary perspective, a deviation of the sex ratio may improve inclusive fitness under natural selection and environmental adaptation principles (Hamilton 1967; Trivers and Willard 1973). A series of studies has indicated that a biased SRB could be closely related to the following facts/factors: resource availability and competition pressures of the parents (Clark 1978; Silk 1983; Dittus 1998), maternal social status (Simpson and Simpson 1982; Symington 1987; van Schaik et al. 1989; Tanvez et al. 2008; Grech 2019), climate changes (Berkeley and Linklater 2010), war impacts (Polasek et al. 2005; Helle et al. 2009; Ellis and Bonin 2016), socioeconomic status (Catalano 2003; Luo et al. 2017), and natural disasters (Petersen 1972).

Thus, several hypotheses have been proposed for a dynamic SRB. The predominant one is the Trivers and Willard Hypothesis (TWH), which suggests that *parents in better condition would be expected to show a bias toward male offspring* (Trivers and Willard 1973). This proposition triggered extensive debates with published findings on different animal taxa, including birds (Clutton-Brock et al. 1985; Müller et al. 2002; Liker et al. 2013), mammals (Clark 1978; Brown 2001; Brown and Silk 2002; Sheldon and West 2004; Goswami et al. 2006; Cameron et al. 2007; Berkeley and Linklater 2010; Douhard 2017), insects (Trivers and Hare 1976; West and Sheldon 2002; Reece et al. 2004; Gardner et al. 2007), fishes (Ospina-Alvarez and Piferrer 2008), and humans (Polasek et al. 2005; Garenne 2008; Helle et al. 2009; Ellis and Bonin 2016; Douhard 2017). However, these efforts have aroused further controversies, with both consensus with the TWH (Cameron 2004; Cameron et al. 2007; Berkeley and Linklater 2010; James 2012) or against the TWH (Simpson and Simpson 1982; Gomendio et al. 1990; Hiraiwa-Hasegawa 1993; Leimar 1996; Brown and Silk 2002; West and Sheldon 2002; James 2012). Several scholars, nevertheless, declare that a definitive solid hypothesis does not actually exist (Simpson and Simpson 1982; West and Sheldon 2002; James 2012), and that alternative results were caused by sample size disparity (Palmer 2000; Brown 2001). As a result, different hypotheses have been proposed after the TWH. Among them, resource availability to females may be the key factor for SRB regulation (Clark 1978; Silk 1983), or so may environmental stress (Catalano 2003). The hormone hypothesis points to high hormone levels in females for increased male offspring (James 1980a, b, 1996), while the energy hypothesis suggests that maternal glucose levels at the time of the conception can regulate the SRB of offspring (Cameron 2004; Rosenfeld and Roberts 2004). We believe that the above inconsistencies were due to the neglection of the basic research conditions necessary to integrally test and perfect the TWH. These conditions are the following:

(1) A precise definition of the subject's condition (controlling factors) is needed, which is not provided by the TWH. In studies about humans, factors such as income, education level, physique, social rank, occupation, and age were proposed (Garenne 2008; Helle et al. 2009; James 2012; Ellis and Bonin 2016; Kolk and Schnettler 2016; Luo et al. 2017; Grech 2019). In studies focusing on other animals, the condition is measured by social rank, physique, habitat, climate, resource occupancy, etc. (Clark 1978; Simpson and Simpson 1982; Clutton-Brock et al. 1985; Brown and Silk 2002; Berkeley and Linklater 2010).
(2) A well-defined study boundary is required. The SRB is an important parameter of reproductive behavior, and the influence of SRB may only occur in certain spatial scales, such as a local reproductive unit or a group (Stevens 1955; Silk 1983). Thus, a specific subject's condition could be confounded: a person who makes 1000$ per month can be considered a high-income earner in an underdeveloped country, but a low-income one in a developed country. As for the social status, a mayor is supposed to have the highest rank in his city, but he is one of the subordinates of the provincial governor (Dittus 1998; IMF 2015; Luo et al. 2017). Moreover, results can also be influenced by the temporal scale (James 1980a, 1986, 2012). So, an explicit spatiotemporal measurement is needed to define the subject's condition.
(3) A necessary premise of TWH is that there should be a significant sex difference in reproductive capacity (Trivers and Willard 1973), which is limited in the monogamous system of most human societies (Polasek et al. 2005; Helle et al. 2009; James 2012; Kolk and Schnettler 2016; Morita et al. 2017; Grech 2019). Data uncertainty due to extramarital affairs need to be concerned when null hypotheses is based on parental factors.
(4) Some conclusions from wild animals may be distorted due to poor field observation, lack of continuous following up datasets, and unclear social status (Brown 2001; Cameron 2004; James 2012; Douhard 2017; Grech 2019).

Thus, in order to obtain more solid results, it is critical to use a consistent spatiotemporal database tracing back a long genealogical history. The Chinese imperial family history covers 2142 years starting with the first emperor of the Qin dynasty in 221 BC to the last emperor of the Qing dynasty in 1912 AD (Zhao 1977; Sima and Zhang 1982; Bo 2011). This is a relatively long period representing and ideal and unique material to fulfill such a requirement and effectively test the TWH. The imperial harem was an enclosed polygynous reproductive system with clear spatiotemporal boundaries, well protected from the influences by the outside (Zhu 1998; Zhang 2009; Miao 2017). The characteristic male-multi-female mating system coupled with high social, political, and economic status gave the emperor the highest reproductive potential and allows us to trace an authentic and genetically pure biological relationships between father, offspring, and mothers (empress and concubines) (Zhu 1998; Zhang 2006), which was also guaranteed by the use of the eunuch system within the harem (Wilson and Roehrborn 1999; Tougher 2008). Furthermore, the strict hierarchy of the sociopolitical structure among the mates, in particular between the empresses and concubines, is ideal to test the hypotheses related to SRB, especially in deciding whether parental or maternal part is playing a pivotal role in sexual selection (Zhu 1997; Wan 2004; Miao 2017). Also, compared with genealogical studies on ordinary citizens, the records from imperial families were fully documented by a strict historian system, which guarantees the reliability of the data (Wang 2008). Therefore, compared to monogamous or promiscuous systems where relationships and socioeconomic conditions are confused, the Chinese imperial harem provides an ideal dataset for this study, with long timespan and accurate information (Zhu 1998; Zhang 2006; Liu 2010; Zhao 2018).

Thus, based on such an advantageous database, the primary purpose of this study is to analyze the spatial–temporal imperial mating system development to test the TWH as well as other hypotheses. We focused on whether a male-biased sex ratio at birth (MSRB) appears in a mating system with higher social status and ample resources, and who is the especially the primary determinant of MSRB, father or mother, and then what is a decisive condition, the higher social rank or rich resources.

Materials and methods

Dynasties studied

The Chinese imperial society started from the Qin dynasty in 221 BC when the first emperor, Qin Shi Huang, united the six kingdoms, and ended with the Qing dynasty in 1912 AD (Zhao 1977; Sima and Zhang 1982; Bo 2011). The 2132 years-lasting imperial periods in Chinese history were featured by a centralized monarchy political and administrative system, in which more than twenty dynasties existed (Fan 1965; Bo 2011). All aspects of the imperial life were recorded by a series of historical books, such as “Hanshu,” “Hou Hanshu,” “Tangshu,” and “Qing History Draft” (Ban 1962; Fan 1965; Tuo and ALuTu 1974; Zhang 1974; Song et al. 1975; Zhao 1977; Sima and Zhang 1982; Liu 2010).

Considering the integrity and robustness of the historical records, we preliminary selected the following ten dynasties: Qin, Xi Han, Dong Han, Xi Jin, Sui, Tang, Bei Song, Yuan, Ming, and Qing. Among them, we narrowed down the final dataset to the dynasties that lasted more than 100 years, namely the Xi Han, Dong Han, Tang, Bei Song, Ming, and the Qing (Fig. 1). In total, 1597 years representing 74.91% Chinese imperial history were covered, with the shortest dynasty being the BeiSong (167 years) while the longest one which was Qing (296 years) (Ban 1962; Fan 1965; Tuo and ALuTu 1974; Zhang 1974; Song et al. 1975; Zhao 1977; Sima and Zhang 1982; Liu 2010).

A dynasty in China always encountered civil wars; foreign incursions, occupations, and devastating rebellions were frequent during the beginning or late period of every dynasty creating upheavals and transformations. During the middle stage, the society was the most stable and prosperous, with the economy and agriculture developing steadily. Such as the ‘HanWu Flourishing Age’ of the Xi Han dynasty (Fan 1965), the “ZhenGuan Flourishing Age” of the Tang dynasty (Song et al. 1975), and the “KangQian Flourishing Age” during the Qing dynasty (Zhao 1977). Based on this information, we divided each of the six dynasties into two stages according to their heyday and low point (Table 1).

It was not possible to record data blind because our study got data via history record.

Hierarchical structure of Chinese imperial families

The ancient Chinese imperial society was a monarchy system in which the emperors held supreme autocratic authority, not being challenged by any written laws, legislature, and customs. A clear social hierarchy structure existed (Fig. 2) with absolute authority to control the powers (Sima and Zhang 1982). Emperors governed the whole nation through the Mandate of the Heaven under the legacy of “Pu Tian Zhi Xia Mo Fei Wang Tu,” indicating that all the land and belongings of the nation were governed by the emperors and shared by their families, in particular social resources (Sima and Zhang 1982). Their family details were accurately documented as genealogical records (Huang and Zeng 2016).

Each imperial family living in the palace followed a rigid hierarchical frame featured by a reproductive harem where the emperor was married to the empress (the first lady) and multiple concubines (Zhu 1998). The empress held the highest position in the harem’s administration and management and was in charge of the internal governance of the palace (Zhu 1998; Zhang 2009). The concubines were additional mating partners functioning as offspring producers for the emperor. Besides, an emperor could also mate with the Palace maids. Such a mating system and environment

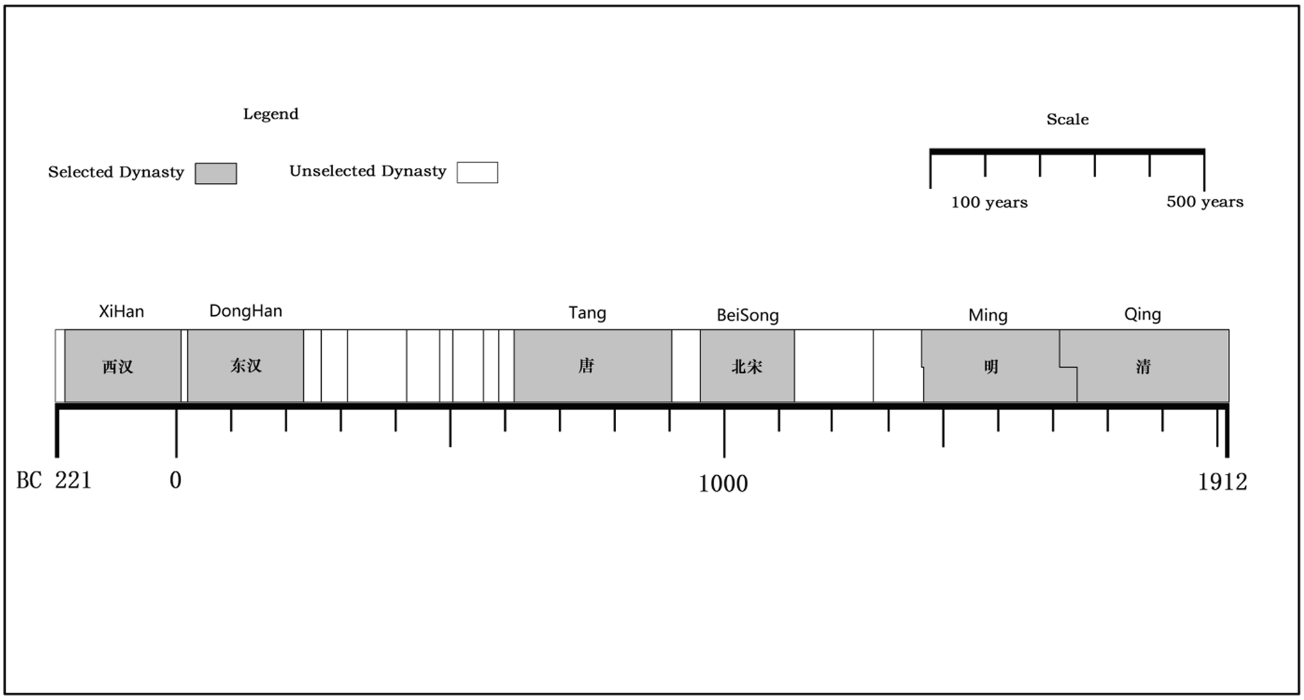

Fig. 1 Timeline of Chinese imperial dynasties from 221 BC to 1911 AD. The gray-colored are the dynasties that lasted more than 100 years, which were included in this study

guaranteed an emperor to reach his highest potential of generating offspring.

Data for emperors: among the requirements and tasks, emperors had to supremely rule the whole dynasty for more than 1 year, be aged more than 14 years, and be able to produce offspring (Diamond 1976; DeLamater and Friedrich 2002). Of the six dynasties analyzed, there were 76 emperors who meet requirements listed above. Their average age was 24.10 ± SD 12.36 at the time of coronation. The average period of their regime was 19.40 ± SD 13.42 years, and the average number of female mates they owned was 10.91 ± 15.02 (range 1–92, $N=76$), of which 1.31 ± 0.68 were empresses (0–3, $N=74$), and 13.31 ± 15.83 were concubines (0–89, $N=54$). In total, they produced 1083 offspring, with an average of 14.25 ± 13.91 for each (0–65, $N=76$) (Table 2).

Data for empresses: an empress was the highest-ranked mate of the imperial harem, similar to the queens in western society (Zhang 2009). A total of 97 empresses (excluding when this title was only conferred posthumously) belonging to 76 emperors were selected and analyzed in this study. Sixty-four empresses gave birth to 107 male and 68 female offspring. We found accurate canonization time records for 53 empresses that we used to analyze the SRB differentiation before and after the canonization. Forty males and 44 females were produced before canonization, while 32 males and 17 females after canonization (Table 3).

Data for concubines: more than 732 concubines belonging to 76 emperors were recorded and included in the analyses. They generated 483 males and 426 female offspring. They had lower social and political status than the empresses but higher than ordinary people. They respected the empresses by expressing courtesy whenever they met, as they did to the emperors. In addition, the empresses and concubines differed in several aspects, including title, clothing style, bedroom size, treatment, resource supply, medical care, and children's education — empresses were privileged (Zhu 1997, 1998; Zhang 2009).

For example, during the Qing Dynasty, an empress could dispose of ten servants for her daily life, an annual salary and other treatments amounting to 37.30 kg silver, 3000-m silks and satins, 2000-m cloths, and 90 mink skins, enough threads of the golds, silver, woolen, cotton, and other necessary items. A list of standardized daily consumption for an empress included 15 kg pork, one plate of mutton, chicken, and duck, separately, 3 kg rice, 5.5 kg noodles, 5.5 kg fruits, cooking oil, and vegetables. Such supplies increased hugely on the occasion of festivals and birthdays. In turn, the goods received by a concubine were limited to two servants, 1.12 kg silver and 266.64-m silk fabrics each year, and a daily meal of 1.07 kg pork, some rice, and vegetables. Another remarkable difference between empresses and concubines was

Table 1 The information of the heyday of Xi Han dynasty, Dong Han dynasty, Tang dynasty, Bei Song dynasty, Ming dynasty, and Qing dynasty

Dynasty	Total number of emperor	Duration (yrs)	Heyday									Low point							
			Appellation	Emperor number	Reigning time	The number of imperial offspring						Emperor number	Reigning time	The number of imperial offspring					
						Emperor		Empress		Concubine				Emperor		Empress		Concubine	
						Male	Female	Male	Female	Male	Female			Male	Female	Male	Female	Male	Female
Xi Han	14	215	汉武盛世 Han Wu Flourishing Age 昭宣中兴 Zhao Xuan Flourishing Age	3	95	11	8	2	3	9	5	11	120	44	10	7	6	37	4
Dong Han	9	196	明章之治 Ming Zhang Flourishing Age 永元之隆 Yong Yuan Flourishing Age	3	51	19	18	3	0	16	18	6	145	22	15	14	3	8	12
Tang	17	276	贞观之治 Zhen Guan Flourishing Age 开元盛世 Kai Yuan Flourishing Age	2	69	44	50	4	5	40	45	15	207	156	141	17	8	139	133
Bei Song	9	167	仁宗盛治 Ren Zong Flourishing Age	1	42	3	13	0	0	3	13	8	125	72	68	15	14	57	54
Ming	15	294	永宣盛世 Yong Xuan Flourishing Age	3	36	16	15	7	6	9	9	12	258	84	62	16	9	68	54
Qing	12	296	康乾盛世 Kang Qian Flourishing Age	3	137	63	38	7	4	56	34	9	159	56	55	15	10	41	45
Total	76	1597		15	430	156	142	23	18	133	124	61	1167	434	351	84	50	350	302
Offspring's SRB						0.52		0.56		0.52				0.55		0.63		0.54	

the reward received when the newborn babies survived the first month: 37.3 kg silver and 3333-m cloth for the empress while concubines would receive only 1.87 kg silver and 333.3-m cloth (Zhang 2009).

Moreover, the eunuch system applied in the palace guaranteed no male servant had the sexual influence on the emperor's reproductive potential and purity — biologically and genetically, all the kids in the harem are offspring of the emperors (Wilson and Roehrborn 1999; Tougher 2008).

Chinese historical recording system

The official historical written record system in China started at the dawn of the Chinese civilization (2717 BC). Historians working around the emperors were involved in significant events and routine administration, imperial family affairs, and recorded the emperor's words and deeds at any time. Chinese historians had a good tradition of "writing the truth without fear or favor" (Liu 2010; Zhao 2018). Sima Qian, who wrote "史记 / Historical Records," became the historians' moral and virtue model. In other words, such objective records ensure the reliability of historical records used for this study.

Data collection

The dataset was compiled by including the emperor's birthday and inauguration date, sex, and birth date for each of his kids. His empress and concubines ranked in a hierarchical family with different titles (Liu 2010; Zhao 2018). The emperors and empresses who had been conferred a posthumous title and had no offspring were excluded. All the data were verified through the "General Draft of Qing History" and "Twenty-Four Histories" (Ban 1962; Tuo and ALuTu 1974; Zhang 1974; Song et al. 1975; Liu 2010; Shun and Shun 2010) (Tables 2, 3).

SRB definition

The portion of males/offspring at birth time theoretically tends to be 0.5 (Hamilton 1967). To detect male or female bias in the sex ratio at birth (SRB), we used the following equation:

$$\mathrm{SRB} = \frac{\text{number of male offspring}}{\text{number of male and female offspring}}$$

An SRB value of 0.50 indicates a perfect balance between the number of male and female offspring. If the value is larger than 0.50, SRB is regarded as male-biased (MSRB). In this study, three different SRBs are used: $\mathrm{SRB}^{\mathrm{emperor}}$ for the emperor, $\mathrm{SRB}^{\mathrm{empress}}$ for the empress, and $\mathrm{SRB}^{\mathrm{concubines}}$ for the concubines.

Data analysis

The significance of male-biased SRBs was evaluated with a Binomial Test that includes four types.

(1) The difference between $\mathrm{SRB}^{\mathrm{emperor}}$, $\mathrm{SRB}^{\mathrm{empress}}$, and $\mathrm{SRB}^{\mathrm{concubines}}$, separately:

$$Z = \frac{p' - p_0}{\sqrt{p_0 q/n}}$$

where p′ = SRB, p0 = 0.50 (equal number between males and females), q = 1–p0, n = sample size.

(2) The difference between $\mathrm{SRB}^{\mathrm{emperor}}$, $\mathrm{SRB}^{\mathrm{empress}}$, $\mathrm{SRB}^{\mathrm{concubines}}$, and the average Chinese SRB in the 1960s and 1970s the first available census data under the current government regime before the One-Child Policy, which was 0.514 (Nie 1999; Wang 2012).

(3) SRB difference before and after the canonization of the empresses, similar to (2) but only compared between the two groups.

(4) SRB difference between each dynasty's heyday and low point, similar to (3).

Analyses were conducted using R Statistics version 1.1.442 (R Development Core Team 2016).

Results

MSRB in the imperial family

Seventy-six emperors produced 1084 offspring (mean ± SD: 14.45 ± 13.87, range 0–65); ninety-seven empresses generated 175 kids (mean ± SD: 2.02 ± 1.97, range 0–7); and more than 732 concubines had 909 children. An emperor had 7.15 times more kids than his mates (Table 2).

According to Table 2, the $\mathrm{SRB}^{\mathrm{emperor}}$ was significantly male-biased ($N = 1084$, 590 males and 494 females, 0.54 vs 0.50, $Z = 2.92$, $p = 0.002$). The same ratio for empresses ($\mathrm{SRB}^{\mathrm{empress}}$) was 0.61 (107 males and 68 females), which appears to be significantly male-biased as well ($N = 175$, 0.61 vs 0.50, $Z = 2.95$, $p = 0.002$). Concubines had an $\mathrm{SRB}^{\mathrm{concubine}}$ of 0.53 (483 males and 426 females), also male-biased at a significant level ($N = 909$, 0.53 vs 0.50, $Z = 1.89$, $p = 0.032$).

The difference between SRB of empresses and concubines was also significant: 0.61 vs 0.53, ($N_{\mathrm{empress}} = 175$, $N_{\mathrm{concubine}} = 909$, $Z = 1.95$, $p = 0.026$).

Fig. 2 Imperial family structure and its managerial system depicted for the Qing dynasty. Harem was the main part of the Forbidden City which is a penalty zone for other fertile men except emperor and his sons. Lower-rank persons can not into upper strata of regions who live can only be carried out in specified areas

SRB differentiation between imperial families and ordinary people

The average Chinese SRB in the 1960s and 1970s, the first available census data under the current government regime before the One-Child Policy, was 0.514 (Wang 2012), a significantly smaller rate than those of the whole imperial families ($N=1084$, 0.54 vs 0.514, $Z=1.99$, $p=0.025$), and of the SRB^{empress} (0.61 vs 0.514, $N=175$, $Z=2.58$, $p=0.006$). However, a comparison between SRB^{concubine} and ordinary citizens did not reach a significant level (0.53 vs 0.514, $N=909$, $Z=1.04$, $p=0.155$).

SRBs before and after empress coronation

The SRB^{empress} before the coronation was not a male-biased SRB (40 males and 44 females, $Z=-0.44$, $p=0.67$) but became biased after the coronation (32 males vs 17 females, $Z=2.14$, $p=0.02$) (Table 2). This difference reached a significant level (0.48 vs 0.65, $N_{\text{before coronation}}=84$, $N_{\text{after coronation}}=49$, $Z=1.97$, $p=0.02$).

MSRB in the heyday of the dynasties

Emperor MSRB during the heyday was not significantly higher than that of the low point (heyday 0.52 vs low point 0.55, $Z=1.16$, $p=0.245$, $N_{\text{heyday}}=14$, $N_{\text{low}}=54$) (Table 1). The same statistical result applies to the scenarios of the empresses and concubines (empress: heyday 0.56 vs low point 0.62, $Z=1.14$, $p=0.253$, $N_{\text{heyday}}=16$, $N_{\text{low}}=37$; concubines: heyday 0.52 vs low point 0.54, $Z=0.279$, $p=0.780$, $N_{\text{heyday}}=14$, $N_{\text{low}}=53$).

Discussion

As expected, the results based on a consistent spatiotemporal database recording 2142 years of imperial biological history provided solid scientific evidence and baseline information to clarify some critical hypotheses related to the SRB, which were initially proposed by TWH and debated by others. They offer new evidence to define an instant social condition (ISC).

MSRB in imperial families

The results listed in Table 1 show that the SRB^{emperor} is 0.55, and those for the SRB^{empress} and SRB^{concubine} are 0.61 and 0.53, separately. Thus, the imperial family members, considered together and individually, generated larger MSRB. This phenomenon clarifies the hypothesis that a good social and economic condition results in MSRBs (Trivers and Willard 1973). The fact that empresses show significantly larger MSRB than concubines and ordinary Chinese implies that a

Table 2 Datum records of the emperors and their families of Xi Han dynasty, Dong Han dynasty, Tang dynasty, Bei Song dynasty, Ming dynasty, and Qing dynasty

ID	Dynasty	Emperor	Stage	Reigning time	Ascended Age	Offspring number						Number of empresses	Number of concubines
						Emperor		Empress		Concubine			
						male	female	male	female	male	female		
1	XiHan	刘执嘉/LiuZhiJia	Low point	-	-	4	1	1	0	3	1	1	0
2		刘邦/LiuBang	Low point	12	51	8	1	1	1	7	0	1	4
3		刘盈/LiuYing	Low point	8	16	6	0	0	-	6	0	1	-
4		刘恭/LiuGong	Low point	4	-	0	0	0	0	0	0	1	-
5		刘弘/LiuHong	Low point	5	-	-	-	-	-	0	0	1	-
6		刘恒/LiuHeng	Low point	23	23	4	2	2	1	2	1	1	2
7		刘启/LiuQi	Low point	16	32	14	3	1	3	13	0	2	5
8		刘彻/LiuChe	Heyday	55	16	6	6	1	3	5	3	2	8
9		刘弗陵/LiuFuLing	Heyday	14	8	0	0	0	0	0	0	1	1
10		刘询/LiuXun	Heyday	26	18	5	2	1	0	4	2	3	-
11		刘奭/LiuShi	Low point	17	27	3	2	1	0	2	2	1	-
12		刘骜/LiuAo	Low point	27	20	5	1	1	1	4	0	2	-
13		刘欣/LiuXin	Low point	7	20	0	0	0	0	0	0	1	-
14		刘衎/LiuKan	Low point	6	9	0	0	0	0	0	0	1	-
15	DongHan	刘秀/LiuXiu	Low point	33	30	11	5	10	3	1	2	2	-
16		刘庄/LiuZhuang	Heyday	19	30	9	11	0	0	9	11	1	-
17		刘炟/LiuDa	Heyday	14	18	8	3	2	0	6	3	1	-
18		刘肇/LiuZhao	Heyday	18	10	2	4	1	0	1	4	2	-
19		刘祜/LiuHu	Low point	20	13	1		0		1	0	1	-
20		刘保/LiuBao	Low point	20	11	1	3	1		0	3	-	-
21		刘志/LiuZhi	Low point	22	15	0	3	0	0	0	3	3	-
22		刘宏/LiuHong	Low point	22	13	2	1	1	0	1	1	2	-
23		刘协/LiuXie	Low point	32	9	7	3	2	0	5	3	2	-

Table 2 (continued)

ID	Dynasty	Emperor	Stage	Reigning time	Ascended Age	Offspring number						Number of empresses	Number of concubines
						Emperor		Empress		Concubine			
						male	female	male	female	male	female		
24	Tang	李渊/LiYuan	Low point	9	53	22	19	4	1	18	18	1	19
25		李世民/LiShiMin	Heyday	24	29	14	21	3	4	11	17	1	14
26		李治/LiZhi	Low point	35	22	8	3	4	1	4	2	2	-
27		李旦/LiDan	Low point	7	23	6	11	2	4	4	7	2	-
28		李隆基/LiLongJi	Heyday	45	28	30	29	1	1	29	28	1	37
29		李亨/LiXiang	Low point	7	46	14	7	2	0	12	7	1	11
30		李豫/LiYu	Low point	18	37	20	18	1	0	19	18	1	9
31		李适/LiShi	Low point	27	38	11	11	1	1	10	10	1	6
32		李纯/LiChun	Low point	16	28	20	18	0	0	20	18	0	4
33		李恒/LiHeng	Low point	5	26	5	8	1	0	4	8	1	4
34		李湛/LiZhan	Low point	3	16	5	3	0	0	5	3	1	-
35		李昂/LiAng	Low point	15	19	2	4	0	0	2	4	0	2
36		李炎/LiYan	Low point	7	37	5	7	-	-	5	7	0	6
37		李忱/LiChen	Low point	14	27	11	11	0	0	11	11	0	5
38		李漼/LiCui	Low point	15	27	8	8	0	0	8	8	0	4
39		李儇/LiXuan	Low point	16	12	2	2	-	-	2	2	-	1
40		李晔/LiYe	Low point	13	22	17	11	2	1	15	10	1	-
41	BeiSong	赵匡胤/ZhaoKuangYin	Low point	17	34	4	6	3	2	1	4	1	2
42		赵光义/ZhaoGuangYi	Low point	22	38	9	7	2	0	7	7	1	12
43		赵恒/ZhaoHeng	Low point	26	30	6	2	1	0	5	2	1	12
44		赵祯/ZhaoZhen	Heyday	42	13	3	13	0	0	3	13	2	14
45		赵曙/ZhaoShu	Low point	5	32	4	4	4	2	0	2	1	3
46		赵顼/ZhaoXu	Low point	19	20	14	10	1	1	13	9	1	5
47		赵煦/ZhaoXu	Low point	16	10	1	4	1	1	0	3	2	8
48		赵佶/ZhaoJi	Low point	26	19	31	34	2	7	29	27	2	34
49		赵桓/ZhaoHuan	Low point	2	26	3	1	1	1	2	0	1	2

Table 2 (continued)

ID	Dynasty	Emperor	Stage	Reigning time	Ascended Age	Offspring number						Number of empresses	Number of concubines
						Emperor		Empress		Concubine			
						male	female	male	female	male	female		
50	Ming	朱元璋/ZhuYuanZhang	Low point	31	41	26	16	5	2	21	14	1	21
51		朱允炆/ZhuYunWen	Low point	5	22	2	0	2	0	0	0	1	0
52		朱棣/ZhuLi	Heyday	23	43	4	5	3	2	1	3	1	20
53		朱高炽/ZhuGaoZhi	Heyday	2	47	10	7	3	1	7	6	1	10
54		朱瞻基/ZhuZhanJi	Heyday	11	28	2	3	1	3	1	0	2	12
55		朱祁镇/ZhuQiZhen	Low point	15	9	9	8	2	1	7	7	2	19
56		朱祁钰/ZhuQiYu	Low point	9	22	1	2	1	2	0	0	1	4
57		朱见深/ZhuJianShen	Low point	24	18	14	5	0	0	14	5	2	16
58		朱佑樘/ZhuYouTang	Low point	19	18	2	3	2	1	0	2	1	0
59		朱厚照/ZhuHouZhao	Low point	17	15	0	0	0	0	0	0	1	7
60		朱厚熜/ZhuHouCong	Low point	46	15	8	5	0	0	8	5	3	89
61		朱载垕/ZhuZaiHou	Low point	7	20	4	6	0	0	4	6	1	17
62		朱翊钧/ZhuYiJun	Low point	49	10	8	10	0	1	8	9	1	18
63		朱由校/ZhuYouXiao	Low point	8	16	3	2	1	0	2	2	1	8
64		朱由检/ZhuYouJian	Low point	18	19	7	6	3	2	4	4	1	5
65	Qing	塔克世/TaKeShi	Low point	-	-	5	1	3	1	2	0	1	2
66		努尔哈赤/NuErHaChi	Low point	11	58	16	9	4	0	12	9	1	14
67		皇太极/HuangTaiJi	Low point	17	36	11	16	1	3	10	13	1	13
68		顺治/SunZhi	Low point	19	6	8	9	2	0	6	9	2	35
69		康熙/KangXi	Heyday	62	8	36	20	2	1	34	19	3	63
70		雍正/YongZheng	Heyday	14	45	10	7	1	0	9	7	1	27
71		乾隆/QianLong	Heyday	61	29	17	11	4	3	13	8	2	39
72		嘉庆/JiaQing	Low point	25	37	5	9	3	3	2	6	2	15
73		道光/DaoGuang	Low point	31	39	9	10	1	3	8	7	2	21
74		咸丰/XianFeng	Low point	12	20	2	1	1	0	1	1	2	16
75		同治/TongZhi	Low point	14	6	0	0	0	0	0	0	1	5
76		光绪/GuangXu	Low point	35	5	0	0	0	0	0	0	1	2
Total			-	-	-	590	494	107	68	483	426	97	732

Table 3 The list and offspring's information of the empress of Xi Han dynasty, Dong Han dynasty, Tang dynasty, Bei Song dynasty, Ming dynasty, and Qing dynasty

ID	Dynasty	Emperor	Number of empresses per emperor	Empress's family name	Empress's offspring number			Number of offspring of empress			
								Before coronation		After coronation	
					male	female	total	Male	Female	Male	Female
1	XiHan	刘执嘉/LiuZhiJia	1	Wang	1	0	1	-	-	-	-
2		刘邦/LiuBang	1	Lv	1	1	2	1	1	0	0
3		刘盈/LiuYing	1	Zhang	0	0	0	-	-	-	-
4		刘恭/LiuGong	1	-	0	0	0	-	-	-	-
5		刘弘/LiuHong	1	Lv	-	-	-	-	-	-	-
6		刘恒/LiuHeng	1	Dou	2	1	3	-	-	-	-
7		刘启/LiuQi	2	Bo	0	0	0	-	-	-	-
				Wang	1	3	4	0	2	1	1
8		刘彻/LiuChe	2	Chen	0	0	0	-	-	-	-
				Wei	1	3	4	0	3	1	0
9		刘弗陵/LiuFuLing	1	ShangGaun	0	0	0	-	-	-	-
10		刘询/LiuXun	3	Xu	1	0	1	1	0	0	0
				Huo	-	-	-	-	-	-	-
				Wang	-	-	-	-	-	-	-
11		刘奭/LiuShi	1	Wang	1	0	1	1	0	0	0
12		刘骜/LiuAo	2	Xu	1	1	2	-	-	-	-
				Zhao	-	-	-	-	-	-	-
13		刘欣/LiuXin	1	Fu	-	-	-	-	-	-	-
14		刘衎/LiuKan	1	Wang	-	-	-	-	-	-	-
15	DongHan	刘秀/LiuXiu	2	Guo	5	1	6	0	0	5	1
				Yin	5	2	7	5	2	0	0
16		刘庄/LiuZhuang	1	Ma	0	0	0	-	-	-	-
17		刘炟 /LiuDa	1	Dou	2	0	2	-	-	-	-
18		刘肇/LiuZhao	2	Yin	-	-	-	-	-	-	-
				Deng	1	0	1	-	-	-	-
19		刘祜/LiuHu	1	Yan	0	0	0	-	-	-	-
20		刘保/LiuBao	-	Liang	1	-	1	-	-	-	-
21		刘志/LiuZhi	3	Liang	-	-	-	-	-	-	-
				Deng	-	-	-	-	-	-	-
				Dou	-	-	-	-	-	-	-
22		刘宏/LiuHong	2	Song	0	0	0	-	-	-	-
				He	1	0	1	-	-	-	-
23		刘协/LiuXie	2	Fu	2	0	2	-	-	-	-
				Cao	-	-	-	-	-	-	-

Table 3 (continued)

ID	Dynasty	Emperor	Number of empresses per emperor	Empress's family name	Empress's offspring number			Number of offspring of empress			
								Before coronation		After coronation	
					male	female	total	Male	Female	Male	Female
24	Tang	李渊/LiYuan	1	Dou	4	1	5	-	-	-	-
25		李世民/LiShiMin	1	ZhangSun	3	4	7	2	2	1	1
26		李治/LiZhi	2	Wang	0	0	0	-	-	-	-
				Wu	4	1	5	1	1	3	1
27		李旦/LiDan	2	Liu	1	2	3	1	1	0	1
				Dou	1	2	3	1	1	0	1
28		李隆基/LiLongJi	1	Wang	1	1	2	-	-	-	-
29		李亨/LiXiang	1	Zhang	2	0	2	-	-	-	-
30		李豫/LiYu	1	Shen	1	0	1	-	-	-	-
31		李适/LiShi	1	Wang	1	1	2	1	1	0	0
32		李纯/LiChun	0	-	-	-	-	-	-	-	-
33		李恒/LiHeng	1	Wang	1	0	1	-	-	-	-
34		李湛/LiZhan	1	Guo	0	0	0	-	-	-	-
35		李昂/LiAng	0	-	-	-	-	-	-	-	-
36		李炎/LiYan	0	-	-	-	-	-	-	-	-
37		李忱/LiChen	0	-	-	-	-	-	-	-	-
38		李漼/LiCui	0	-	-	-	-	-	-	-	-
39		李儇/LiXuan	-	-	-	-	-	-	-	-	-
40		李晔/LiYe	1	He	2	1	3	-	-	-	-
41	Beisong	赵匡胤/ZhaoKuangYin	1	He	3	2	5	-	-	-	-
42		赵光义/ZhaoGuangYi	1	Li	2	0	2	-	-	-	-
43		赵恒/ZhaoHeng	1	Guo	1	0	1	-	-	-	-
44		赵祯/ZhaoZhen	2	Guo	0	0	0	-	-	-	-
				Cao	0	0	0	-	-	-	-
45		赵曙/ZhaoShu	1	Gao	4	2	6	4	2	0	0
46		赵顼/ZhaoXu	1	Xiang	1	1	2	1	1	0	0
47		赵煦/ZhaoXu	2	Meng	0	1	1	0	1	0	0
				Liu	1	0	1	-	-	-	-
48		赵佶/ZhaoJi	2	Wang	1	1	2	0	0	1	1
				Zheng	1	6	7	1	6	0	0
49		赵桓/ZhaoHuan	1	Zhu	1	1	2	1	1	0	0

Table 3 (continued)

ID	Dynasty	Emperor	Number of empresses per emperor	Empress's family name	Empress's offspring number			Number of offspring of empress			
								Before coronation		After coronation	
					male	female	total	Male	Female	Male	Female
50	Ming	朱元璋/ZhuYuanZhang	1	Ma	5	2	7	5	0	2	0
51		朱允炆/ZhuYunWen	1	Ma	2	0	2	1	0	1	0
52		朱棣/ZhuLi	1	Xu	3	2	5	3	4	0	0
53		朱高炽/ZhuGaoZhi	1	Zhang	3	1	4	3	1	0	0
54		朱瞻基/ZhuZhanJi-	2	Hu	0	2	2	0	2	0	0
				Sun	1	1	2	0	1	1	0
55		朱祁镇/ZhuQiZhen	2	Qian	0	0	0	0	0	0	0
				Zhou	2	1	3	1	0	1	1
56		朱祁钰/ZhuQiYu	1	Wang	1	2	3	0	1	0	0
57		朱见深/ZhuJianShen	2	Wu	0	0	0	0	0	0	0
				Wang	0	0	0	0	0	0	0
58		朱佑樘/ZhuYouTang	1	Zhang	2	1	3	0	2	0	1
59		朱厚照/ZhuHouZhao	1	Xia	0	0	0	0	0	0	0
60		朱厚熜/ZhuHouCong	3	Chen	0	0	0	0	**0**	**0**	0
				Zhang	0	0	0	**0**	**0**	**0**	0
				Fang	0	0	0	0	0	0	0
61		朱载垕/ZhuZaiHou	1	Chen	0	0	0	0	0	0	0
62		朱翊钧/ZhuYiJun	1	Wang	0	1	1	0	0	1	1
63		朱由校/ZhuYouXiao	1	Zhang	1	0	1	0	0	1	0
64		朱由检/ZhuYouJian	1	Zhou	3	2	5	0	0	3	2

Table 3 (continued)

ID	Dynasty	Emperor	Number of empresses per emperor	Empress's family name	Empress's offspring number			Number of offspring of empress			
								Before coronation		After coronation	
					male	female	total	Male	Female	Male	Female
65	Qing	塔克世/TaKeShi	1	Xuan	3	1	4	-	-	-	-
66		努尔哈赤/NuErHaChi	1	Yehe Nara	4	0	4	0	0	4	0
67		皇太极/HuangTaiJi	1	BoErJiJiTe	1	3	4	0	1	0	2
68		顺治/SunZhi	2	BoErJiJiTe	0	0	0	0	0	0	0
				Dongjia	2	0	2	0	0	0	0
69		康熙/KangXi	3	HeSheLi	2	0	2	0	0	2	0
				NiuHuRu	0	0	0	0	0	0	0
				DongJia	0	1	1	0	1	0	0
70		雍正/YongZheng	1	UlaNara	1	0	1	1	0	0	0
71		乾隆/QianLong	2	ShaJiFuCha	2	2	4	1	2	1	0
				Nara	2	1	3	0	0	2	1
72		嘉庆/JiaQing	2	XiTaLa	1	2	3	1	2	0	0
				NiuHuRu	2	1	3	1	1	1	0
73		道光/DaoGuang	2	DongJia	0	1	1	0	1	0	0
				NiuHuRu	1	2	3	1	0	0	2
74		咸丰/XianFeng	2	Yehe Nara	1	0	1	1	0	0	0
				NiuHuRu	0	0	0	-	-	-	-
75		同治/TongZhi	1	ALuTe	0	0	0	-	-	-	-
76		光绪/GuangXu	1	Yehe Nara	0	0	0	-	-	-	-
Total			97	-	107	68	175	40	44	32	17

better maternal social status may greatly influence SRB. Thus, we conclude that the imperial SRBs are significantly male-biased, and the empresses have significantly larger MSRB than the concubines. That clarifies that the maternal condition plays a crucial role in influencing the SRB (Trivers and Willard 1973; Clark 1978; Simpson and Simpson 1982; Symington 1987; Hiraiwa-Hasegawa 1993; Brown and Silk 2002).

Condition for a higher MSRB

As indicated in the "Materials and methods", the early stage of a new dynasty was always the period recovering from warfare and other disasters. Its middle stage was generally regarded as the most prosperous period, followed by an ending stage replaced by another dynasty (Zhang 1974; Zhao 1977; Sima and Zhang 1982). During the heyday, resources were the most abundant, and the economy was booming. The result that imperial SRB in the heyday was not significantly higher than during low point periods (Table 1) implies that the abundance of resources may not be the leading cause influencing SRB.

Empresses and concubines were the emperor's mates and lived in the same harem, the former had a higher social rank than the latter. However, they both were supplied with enough resources, much better than ordinary people (Zhang 2009). The results found in this study indicate that only the $SRB^{empress}$ is significantly higher than the ordinary people (0.61 vs 0.514, $N=175$, $Z=2.58$, $p=0.006$), but not the $SRB^{concubine}$ (0.53 vs 0.514, $N=909$, $Z=1.04$, $p=0.155$). Thus, we propose that the key factor determining SRB is tightly associated with social status instead of the guaranteed resources; maternal social status plays an essential role in sexual selection.

An empress had the highest social status among the females in the nation. Such advantages have been reported to psychologically promote her hormone release and other reactions benefitting reproduction, but the $SRB^{empress}$ was significantly male-biased just after the coronation; this is consistent with the glucose hypothesis and hormone hypothesis (James 1980b, 1996, 2012; Cameron 2004; Cameron and Linklater 2007), implying that such an advantage around the conception period plays a pivotal role in deciding the SRB ratio. In other words, a temporal boundary must be taken into account in assessing SRB, such the *good condition* that the key factor was set in TWH appeared temporally. Thus, we proposed the *instant social condition* (ISC) to replace the current *condition* in SRB study that is ambiguous: ISC appears in the conception period and plays a vital role in sexual selection. In other words, a female with advanced instant social privileges may intend to generate an MSRB. Thus, we propose the sexual selection in humans is primarily decided by the *maternal ISC*.

Although TWH did not propose a *condition* of generating an MSRB, others have suggested it from different aspects such as income, education level, physique, social rank, occupation, and age (Garenne 2008; Helle et al. 2009; James 2012; Ellis and Bonin 2016; Kolk and Schnettler 2016; Luo et al. 2017; Grech 2019). As for wild animals, such a *condition* is measured according to social status, physique, habitat, climate, resource occupancy, etc. (Clark 1978; Simpson and Simpson 1982; Clutton-Brock et al. 1985; Brown and Silk 2002; Berkeley and Linklater 2010). The results found in this study can allow us to set up such an objective *condition — instant social condition*, which is backed by the fact that a female had a significantly higher MSRB after being inaugurated as the empress, and empresses generated significantly greater MSRB than the concubines. Furthermore, although concubines and dynasty's heydays were guaranteed enough resources and living conditions, they did not produce significantly greater MSRB than the ordinary people, and a greater MSRB did not appear in heydays than during low point periods of the same imperial families. Since a defined *condition* is indispensable in human biology study (James 1980a, 1986, 2012), the new concept of the *condition* described in this study would provide a particular reference.

Conclusion

With a spatiotemporal imperial genealogical database covering 2142 years of Chinese history, the results found in this study clarify the TWH — parents with higher social status and resources tend to have a male-biased sex ratio at birth (MSRB). Meanwhile, it indicates that the maternal side around the conception period plays a vital role in sexual selection, and most importantly, the condition for having an MSRB is her instant social condition instead of rich resources. Thus, this study provides robust evidence to interpret sexual selection mechanisms and regulations. However, there are still some issues needed to be clarified. Although social status plays a vital role in sexual selection during the conception period, we need to determine how long that advanced period should be before the conception.

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Data availability All data generated or analyzed during this study are included in this published article.

Declarations

Competing interests The authors declare no competing interests.

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