Offspring Sex-ratio in Humans – Does it depend on population size?

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Summary

Balanced sex ratio evolves by a process known as frequency-dependent selection of the minority sex. Efforts to test this theory have focused mainly on experimental populations. Heterogametic sex has greater influence over the sex of the offspring. We tested the prediction that a smaller human population should favor male offspring. Our findings reveal that size of the population has significant inverse correlation with male proportion. We also present evidence for frequency-dependent selection of the minority sex and evolution of balanced sex ratio in isolated human population.

Keywords

Sex ratio; Population size; Sex ratio adjustments

Fisher's principle explains the basis for 1:1 proportion of male and female individuals in natural populations.[1] The model is based on the presumption of equal investment in sons and daughters by parents. Every offspring is produced by equal genetic contribution of parents in sexually reproducing species. If one sex is rare, it will be overrepresented in subsequent generations until the sex ratio is balanced. This frequency-dependent model of selection is widely accepted. Fisher's theory accounts for widespread occurrence of sex-determining mechanisms, such as heterogamity, that ensures balanced sex ratio.[2] This phenomenon has been observed in Drosophila [3] and fish, [4] where populations with experimentally biased sex ratios evolved towards equal proportions of males and females over generations. The possibility that human populations may also exhibit frequency dependent selection has seldom been considered.

In humans, male is the heterogametic sex, and offspring's sex is determined by whether an X- or Y-chromosome bearing spermatozoon fertilizes the ovum. Thus man may have greater control over the sex of the progenies. As population has an innate tendency to grow, [5] a smaller human population may produce male biased progenies to achieve higher growth rate. This is true otherwise also, since men are always fertile while women have limited fertility. Males of most mammalian species can father children throughout their life while females can produce limited number of offspring in the similar time period. This complies with Trivers and Willard hypothesis for sex allocation which predicts that parents should increase the production of offspring sex with higher fitness benefits.[6] Here the ability of male to regulate population growth can be considered as fitness trait. Given better fitness of male when it

comes to population growth, we tested the hypothesis that the smaller human populations may be male biased.

It is difficult to analyze every human population for sex ratio trends as multitude of factors have been implicated to play role in population sex ratios.[7] Nevertheless, an isolated population existing away from the modern world can be considered a good sample for evaluation. To test our hypothesis, we analyzed the population trends on the Andaman Islands for one hundred years (1901-2001).[8] These islands are not connected with Indian mainland and are home to some of the most primitive tribes in the world, and recent studies indicate that these tribes are the very first descendents of the modern humans migrated out of Africa. Andamanese populations is isolated from main lands since 50-60 thousand years, and genetically resembles African population more than Asian populations.[9]

The population data for Andamanese was obtained from Directorate of Economics and Statistics, Andaman and Nicobar administration, Port Blair, and for mainland populations from Office of the Registrar General and Census Commissioner, Government of India.

The Andaman population was 18138 in 1901 which increased to 314084 in 2001 (Table1). The proportion of males was 84% in 1901 which steadily declined to 54% in 2001. There was a significant inverse correlation between total population size and proportion of males (squared correlation coefficient $r^2 = 0.61$, $p = 0.0021$).

During initial five decades (1901-1951), the proportion of males declined steadily from 84% to 67%, whereas the population size increase was negligible (1.2%), which can be attributed to disproportionately low number of females. However, during next five decades (1951-2001), the proportion of males continued to decrease further from 67% to 54%, approaching 1:1 ratio, with a concurrent large increase in population size (Table. 1). Beginning from the year 1901, a steady increase in population size and concurrent evolution of balanced sex ratio can be observed (Figure. 1). The proportion of males was 54% during 2001 and it will be interesting to see the results of next population census that will be conducted in 2011.

Looking at the trends in Andamanese, we analyzed the mainland populations of India to strengthen our findings. The key challenge was to select a population where we can be sure of no prevalence of sex specific abortion.[10] The abortions have been correlated with economic status and literacy in India.[11] However, there is a large tribal population (8% of Indian population) spread all over India which still lives isolated, and away from urban communities (92% are in rural areas).[12] The mainland tribes are classified under the category of scheduled tribes. The habitats of these tribes are declared as scheduled areas and rank lowest on all the socioeconomic scales.[16] Hence we assumed the effect on sex ratio due to sex specific abortion in these areas to be negligible. Tribal population limited to 135 areas spread across India (districts/blocks) was analyzed. Data collected from 2001 Indian population census was analyzed for scheduled areas *(*Table 2). For these areas, the population data was not available for previous decades. This data is not temporal and cannot be compared with Andamanese; however a comparison can be made between smaller and larger populations. Total population in scheduled areas was 2.6 million and ranged from mere 1094 to as big as 1.25 million. As

observed in Andamanese, a smaller population can be expected to have higher proportion of males, and as population size increases shift towards equal sex proportions may occur. As expected, we observed a similar trend in proportion of males and total population in scheduled areas. The proportion of males was higher in smaller populations and a steady decline was seen with increase in total population size (fig. 2).

This is the first evidence for Fisher's frequency dependent balancing of sex ratio in human populations. Extreme skew towards heterogametic sex (male in mammals, female in birds) has been observed in numerous declining and endangered mammalian and bird populations.[13,14,15] Analogous to this situation, the smaller tribes of Himalayan tracts have been documented to favor male births.[16] This skewing to favor heterogametic offspring seems like a strategy employed to reverse the population decline / prevent extinction. These phenomenons are in agreement with our hypothesis of production of male biased offspring in an effort to increase population size. A minor effect, if any, on sex ratio due to other environmental factors may exist, however, evolution of balanced sex ratio by frequency dependent selection seems to be the strongest factor.

The obvious question now will be 'how selective fertilization is given effect in humans? Various factors ranging from physiological to environmental have been shown to affect secondary sex ratio,[17] however, it would be interesting to explore physiological factors that may favor adjustment in sex ratio in human population, pre-fertilization or post-fertilization.

Conflict of interest statement

We declare that we have no conflict of interest.

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Table 1. Andaman population over a period of 100 years

Year	Population	Females	Males	% males
1901	18138	2985	15153	84
1911	17641	2903	14738	84
1921	17814	2269	15545	87
1931	19223	4963	14260	74
1941	21316	6441	14875	70
1951	18962	6227	12735	67
1961	48985	17463	31522	64
1971	93468	35593	57875	62
1981	158287	67837	90450	57
1991	241453	108348	133105	55
2001	314084	143756	170328	54

Table. 2. Population of scheduled tribes in scheduled areas from 2001 national census

	State	District	Block	Total population	Females	Males	Per cent males
1	Andhra Pradesh	Mehboobnagar	Achempeth	15652	7534	8118	51.87
2	Andhra pradesh	Adilabad	Adilabad	20761	10544	10217	49.21
3	Andhra Pradesh	Adilabad	Boath	13116	6498	6618	50.45
4	Andhra Pradesh	Adilabad	Utnoor	25594	12435	13159	51.41
5	Andhra Pradesh	Adilabad	Asifabad	8996	4652	4344	48.29
6	Andhra Pradesh	Adilabad	Sirpur	19219	9681	9538	49.63
7	Andhra Pradesh	Warangal	Muluq	12995	6290	6705	51.60
8	Andhra Pradesh	Warangal	Narsampet	8239	4090	4149	50.35
9	Andhra pradesh	Khammam	Yellandu	34607	17492	17115	49.46
10	Andhra Pradesh	Khammam	Palwancha	24598	11780	12818	52.11
11	Andhra Pradesh	Vishakapatnam	-	557572	279204	278368	49.93
12	Andhra pradesh	East godavari	-	191561	96304	95257	49.73
13	Andhra Pradesh	West godavari	-	96659	48761	47898	49.55
14	Jharkhand	Ranchi	-	1164624	579092	585532	50.28
15	Jharkhand	Palamu	Latehar	44478	22361	22117	49.73
16	Jharkhand	Palamu	Garu	20532	10083	10449	50.89
17	Jharkhand	East singhbum	-	1111322	557323	553999	49.85
18	Jharkhand	West singhbum	-	552187	274007	278180	50.38
19	Jharkhand	Dumka	-	701903	349542	352361	50.20
20	Gujarat	Surat	Uchchal	71084	35911	35173	49.48
21	Gujarat	Surat	Vyara	211611	106541	105070	49.65
22	Gujarat	Surat	Mahuva	112655	55759	56896	50.51
23	Gujarat	Surat	Mandvi	140800	70470	70330	49.95
24	Gujarat	Surat	Songadh	170464	85529	84935	49.83

25	Gujarat	Surat	Valod	64112	31895	32217	50.25
26	Gujarat	Surat	Mangrol	90370	44543	45827	50.71
27	Gujarat	Surat	Bardoli	99213	49607	49607	50.00
28	Gujarat	Narmada	Dediapada	137553	67800	69753	50.71
29	Gujarat	Narmada	Sagbara	74980	38189	36791	49.07
30	Gujarat	Bharuch	Valia	96179	47481	48698	50.63
31	Gujarat	Narmada	Nandod	159443	77129	82314	51.63
32	Gujarat	Bharuch	Jhagadia	115458	56188	59270	51.33
33	Gujarat	The dang	The dang	175079	87320	87759	50.13
34	Gujarat	Valsad	Dharmpur	165662	82582	83080	50.15
35	Gujarat	Navasari	Chikhli	205275	101810	103465	50.40
36	Gujarat	Valsad	Pardi	158786	78994	79792	50.25
37	Gujarat	Valsad	Umbergaon	115392	59213	56179	48.69
38	Gujarat	Dohad	Jhalod	319443	158433	161010	50.40
39	Gujarat	Dohad	Dohad	273469	136460	137009	50.10
40	Gujarat	Panchmahals	Santrampur	1688	769	919	54.44
41	Gujarat	Dohad	Limkheda	146764	73382	73382	50.00
42	Gujarat	Dohad	Devgadbaria	48185	23837	24348	50.53
43	Gujarat	Vadodara	Chotta udaipur	175480	87255	88225	50.28
44	Gujarat	Vadodara	Nasvadi	107547	52816	54731	50.89
45	Gujarat	Narmada	Tilakwada	29678	14229	15449	52.06
46	Gujarat	Sabarkantha	Khedbrahma	153704	75840	77864	50.66
47	Gujarat	Sabarkantha	Bhiloda	114007	57484	56523	49.58
48	Gujarat	Sabarkantha	Meghraj	51612	25832	25780	49.95
49	Gujarat	Sabarkantha	Vijayanagar	68545	34845	33700	49.16
50	Himachal Pradesh	Kinnaur	-	56268	28686	27582	49.02
51	Himachal Pradesh	Lahaul and spiti	-	24238	12286	11952	49.31
52	Himachal	Chamba	Pangi	15337	7649	7688	50.13

	Pradesh						
53	Himachal Pradesh		Brahmaur	19089	9360	9729	50.97
54	Madhya Pradesh	Jhabua	-	1211116	603431	607685	50.18
55	Madhya Pradesh	Mandla	-	511798	259432	252366	49.31
56	Chattishgarh	Sarguja	-	1076669	534812	541857	50.33
57	Chattishgarh	Bastar	-	866488	437534	428954	49.50
58	Madhya Pradesh	Dhar	Sardarpur	128947	63657	65290	50.63
59	Madhya Pradesh	Dhar	Dhar	149197	72568	76629	51.36
60	Madhya Pradesh	Dhar	Kukshi	263145	130978	132167	50.23
61	Madhya Pradesh	Dhar	Manawar	159337	79469	79868	50.13
62	Madhya Pradesh	Barwani	Barwaha	188155	92645	95510	50.76
63	Madhya Pradesh	Barwani	Rajpur	116536	57798	58738	50.40
64	Madhya Pradesh	Barwani	Sendhwa	209337	103824	105513	50.40
65	Madhya Pradesh	West nimar	Bhikangaon	64686	31917	32769	50.66
66	Madhya Pradesh	West nimar	Khargone	46393	22626	23767	51.23
67	Madhya Pradesh	West nimar	Maheshwar	48463	23837	24626	50.81
68	Madhya Pradesh	East nimar	Khalwa of harshad	1094	510	584	53.39
69	Madhya Pradesh	East nimar	Khaknar of burhampur	1596	754	842	52.77
70	Madhya Pradesh	Ratlam	Sailana	80887	39994	40893	50.56
71	Madhya Pradesh	Betul	Betul	193913	96859	97054	50.05
72	Madhya Pradesh	Betul	Bhainsdehi	208021	103172	104849	50.40
73	Madhya Pradesh	Seoni	Lakhnadon	130512	65516	64996	49.80
74	Madhya Pradesh	Seoni	Kurai	49887	25397	24490	49.09
75	Madhya Pradesh	Balaghat	Baihar	181101	92759	88342	48.78
76	Madhya Pradesh	Hoshangabad	Hosangabad	9436	4401	5035	53.36
77	Madhya Pradesh	Shahdol	Puspharajgarh	149567	74896	74671	49.93
78	Madhya Pradesh	Shahdol	Sohagpur	186952	92770	94182	50.38
79	Madhya	Shahdol	Jaisinghnagar	80330	40165	4016	50.00

	Pradesh					5	
80	Madhya Pradesh	Sidhi	Kusimi	41202	20330	20872	50.66
81	Chattisgarh	Jashpur	Jashpurnagar	89932	44921	45011	50.05
82	Chattisgarh	Raigarh	Kharsia	38098	19331	18767	49.26
83	Chattisgarh	Bilaspur	Gaurella	2989	1492	1497	50.08
84	Chattisgarh	Bilaspur	Kota	1880	888	992	52.77
85	Chattisgarh	Durg	Balod	2378	1198	1180	49.63
86	Chattisgarh	Rajnandagaon	Rajnandgaon	8219	4062	4157	50.58
87	Madhya Pradesh	Sheopur	Sheopur	33196	16242	16954	51.07
88	Madhya Pradesh	Chhindwara	Sausar	28823	14110	14713	51.05
89	Maharastra	Thane	Dahanu	215162	109171	105991	49.26
90	Maharastra	Thane	Talasari	107379	54665	52714	49.09
91	Maharastra	Thane	Jawahar	99932	50485	49447	49.48
92	Maharastra	Thane	Mokhada	60964	30283	30681	50.33
93	Maharastra	Thane	Shahapur	89997	44406	45591	50.66
94	Maharastra	Nasik	Peint	89926	44918	45008	50.05
95	Maharastra	Nasik	Surgana	137602	68629	68973	50.13
96	Maharastra	Nasik	Kalwan	108955	54478	54478	50.00
97	Maharastra	Nandurbar	Nawapur	203292	101950	101342	49.85
98	Maharastra	Nandurbar	Akkalkuwa	150654	76110	74544	49.48
99	Maharastra	Nandurbar	Akrani	129621	65229	64392	49.68
100	Maharastra	Chandrapur	Chandrapur	47303	22933	24370	51.52
101	Maharastra	Chandrapur	Rajura	34304	16855	17449	50.86
102	Maharastra	Jalgaon	Chopda	69893	33995	35898	51.36
103	Maharastra	Jalgaon	Yawal	51059	24848	26211	51.33
104	Maharastra	Nanded	Kinwat	58527	29013	29514	50.43
105	Orissa	Mayurbhanj	-	1258459	627336	631123	50.15
106	Orissa	Sundergarh	-	918903	460140	458763	49.93
107	Orissa	Koraput	-	585830	295528	290302	49.55
10	Orissa	Sambalpur	Kochinda	36108	17991	1811	50.18

8						7	
109	Orissa	Kendujhar	Kendujhar	74006	37058	36948	49.93
110	Orissa	Kendujhar	Telkoi	43895	21782	22113	50.38
111	Orissa	Kendujhar	Champua	53925	26841	27084	50.23
112	Orissa	Kendujhar	Barbil	36770	18246	18524	50.38
113	Orissa	Khandamal	-	336809	170566	166243	49.36
114	Orissa	Ganjam	-	90919	45070	45849	50.43
115	Orissa	Kalahandi	Thuamul rampur	37850	19305	18545	49.00
116	Orissa	Kalahandi	Lanjigarh	25638	13052	12586	49.09
117	Orissa	Baleshwar	Nilgiri	38270	19183	19087	49.88
118	Rajasthan	Banswara	-	1085272	537984	547288	50.43
119	Rajasthan	Dungarpur	-	721487	365724	355763	49.31
120	Rajasthan	Udaipur	Kherwara	202529	101517	101012	49.88
121	Rajasthan	Udaipur	Kotra	163903	81332	82571	50.38
122	Rajasthan	Udaipur	Sarada	138195	69270	68925	49.88
123	Rajasthan	Udaipur	Salumabr	111419	55876	55543	49.85
124	Rajasthan	Chittaurgarh	Pratapgarh	115636	56548	59088	51.10
125	Rajasthan	Sirohi	Abu road	84477	41420	43057	50.97
126	Assam	North cachar hill	-	128428	62466	65962	51.36
127	Assam	Mikir hills (karbi angalong)	-	452963	221977	230986	50.99
128	Meghalaya	East khasi hills	-	512152	261466	250686	48.95
129	Meghalaya	Jantia hills	-	287049	144451	142598	49.68
130	Meghalaya	East garo hills	-	241916	119551	122365	50.58
131	Meghalaya	West garo hill	-	397166	197183	199983	50.35
132	Meghalaya	South garo hills	-	96616	47597	49019	50.74
133	Tripura	North	-	150500	73439	77061	51.20
134	Tripura	South	-	289519	143445	146074	50.45
13	Tripura	West	-	387081	19099	1960	50.66

5					1	90	

Figure 1: Relation between population size and proportion of males in Andaman tribes over a period of 100 years. Each open circle represents proportion of males for one decadal census beginning from 1901. With each decade an increase in population and subsequent decrease in male proportion is obvious.

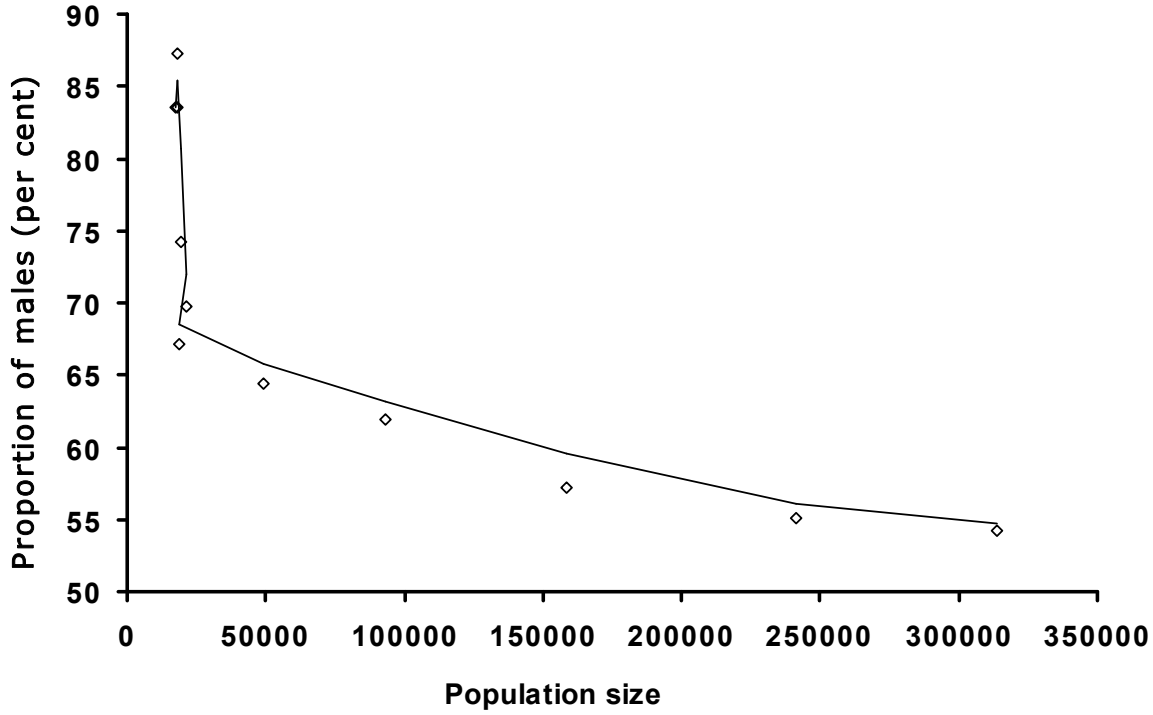

Figure 2: Relation between proportion of males and total population of tribes in scheduled areas. Each open circle represents one scheduled area. Note the change of value of proportion of males towards 50:50 as population size is increasing.