



Adaptive sex ratio variation in pre-industrial human (*Homo sapiens*) populations?

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Sex allocation theory predicts that in a population with a biased operational sex ratio (OSR), parents will increase their fitness by adjusting the sex ratio of their progeny towards the rarer sex, until OSR has reached a level where the overproduction of either sex no longer increases a parent's probability of having grandchildren. Furthermore, in a monogamous mating system, a biased OSR is expected to lead to lowered mean fecundity among individuals of the more abundant sex. We studied the influence of OSR on the sex ratio of newborns and on the population birth rate using an extensive data set ($n=14\,420$ births) from pre-industrial (1775–1850) Finland. The overall effect of current OSR on sex ratio at birth was significant, and in the majority of the 21 parishes included in this study, more sons were produced when males were rarer than females. This suggests that humans adjusted the sex ratio of their offspring in response to the local OSR to maximize the reproductive success of their progeny. Birth rate and, presumably, also population growth rate increased when the sex ratio (males:females) among reproductive age classes approached equality. However, the strength of these patterns varied across the parishes, suggesting that factors other than OSR (e.g. socioeconomic or environmental factors) may also have influenced the sex ratio at birth and the birth rate.

Keywords: birth rate; humans; operational sex ratio; secondary sex ratio; sex allocation

1. INTRODUCTION

Parents partition their reproductive effort into production of sons and daughters, and it has been proposed that when the fitness returns from male and female offspring differ, parents should facultatively adjust sex ratio at birth (SRB) to maximize their own reproductive success (Trivers & Willard 1973; Charnov 1982). Although there is firm support for this adaptive sex allocation theory from studies of sex ratio variation in insects and mites (Wrensch & Ebbert 1993), and studies of sex change in hermaphrodites (Warner 1975), the existence of biased sex allocation by skewing sex ratios has been (e.g. Fisher 1930; Williams 1979; Charnov 1982; Clutton-Brock 1982) and remains (Hiraiwa-Hasegawa 1993; Hardy & Krackow 1995) a controversial topic in taxa with chromosomal sex determination. However, an increasing number of empirical studies on birds (Ellegren *et al.* 1996; Svensson & Nilsson 1996; Komdeur *et al.* 1997) and on mammals (reviewed in Cassinello & Gomendio (1996)), including humans (Berezkei & Dunbar 1997), now suggest the true adaptive nature of sex ratio variation. The evidence for the adaptive nature of sex ratio variation in these studies derives from the fact that the observed sex ratio skew among families is correlated with inherited or environmental factors expected to result in higher fitness among the overproduced sex.

Furthermore, as pointed out by Fisher (1930), selection may also favour individuals biasing the offspring sex ratio in response to the ratio of reproductive males and females in the population, i.e. the operational sex ratio (OSR) (Werren & Charnov 1978; Charnov 1982). For example, in a population with a female-biased adult sex ratio, a parent that produces more sons will have more grandchildren compared with a parent who produces more daughters or even equal numbers of offspring of each gender. However, studies showing apparent facultative adjustment of offspring sex ratio in response to OSR in diploid organisms are scarce (Trivers 1985), involving, for example, a stinkbug (McLain & Marsh 1990) and a diploid aphid (Yamaguchi 1985). In particular, there is little evidence for adaptive sex ratio adjustment in vertebrates in response to OSR (Clutton-Brock & Iason 1986), presumably at least partly due to difficulties in detecting weak skews in sex ratios unless sample sizes are extensive.

This study investigates whether there were differences in OSRs and SRBs (males:females) among the local human (*Homo sapiens*) populations in rural, pre-modern (1775–1850) Finland, and whether the SRB was predictable from the OSR of a given population. Because parents can be expected to increase their fitness by biasing the sex ratio of their progeny towards the rarer sex in a population with a biased OSR, we predicted that proportionally more sons would be born when the OSR of a population was female-skewed. Furthermore, in a monogamous mating system an OSR of 1:1 could be expected to lead to the maximization of birth rate and thus population growth rate, because a biased OSR might reduce mating opportunities of individuals of the more abundant sex,

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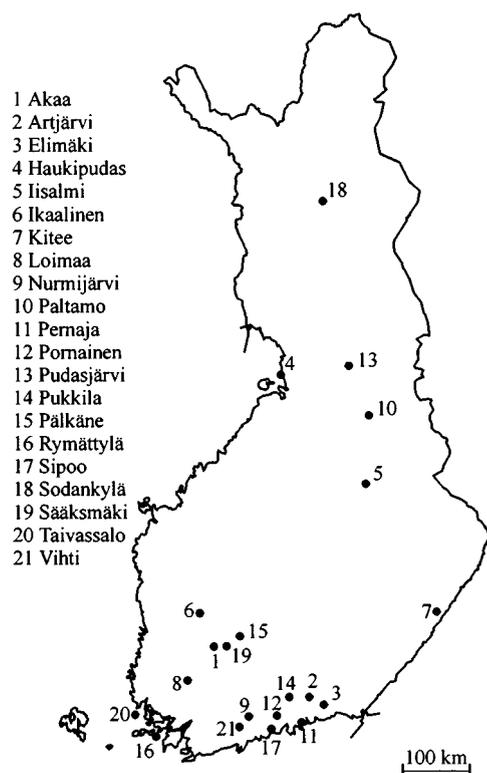


Figure 1. Location of the 21 study parishes in Finland. For the sake of simplicity, the approximate centre rather than the actual borders of each parish have been depicted.

resulting in some fertile females or males being unable to reproduce due to not having a mate (Beiles 1974; Clutton-Brock & Vincent 1991). Therefore, we also tested the prediction that a biased OSR leads to a lowered mean fecundity among individuals of the more abundant sex, and thereby to a decreased birth rate in the population.

2. MATERIALS AND METHODS

All analyses are based on the demographic records of Finnish populations maintained by churches since the early seventeenth century. Data from 21 parishes, situated around the country (figure 1), were included in the analyses, and they were chosen on the basis of the completeness of the data, and to cover a representative range of different environmental conditions experienced by pre-industrial populations. The study period covers the years from 1775 to 1850, therefore ending before industrialization and improvement in health care were likely to have had significant effects on the standard of living and survivorship. Despite the relatively small distances between some parishes located in southern Finland, permanent migration during the study era was rare as 90% of the marriages were contracted within villages or parishes (Nevanlinna 1972). Furthermore, high incidence of recessive genetic diseases endemic to many parishes indicates that, historically, migration among parishes has been restricted (Nevanlinna 1972).

Numbers of males and females belonging to the reproductive age cohort, sex ratio of newborn babies and birth rate of each parish were recorded as snapshots for every fifteenth year (i.e. cross-sectional data). In church books, the number of citizens recorded for each year indicates the number of females and males living in the parish at the end of the year. Individuals

Table 1. *MANCOVA* of the effects of parish, OSR and MR on SRB and BR in 21 local Finnish populations (1775–1850)

dependent	source	d.f.	<i>F</i>	<i>p</i>
SRB & BR	parish	20, 50	2.11	0.017
	OSR	2, 49	2.83	0.069
	MR	2, 49	3.02	0.058
	OSR × parish	20, 50	2.00	0.024
	MR × parish	20, 50	1.95	0.029

aged 15–50 years old were regarded as reproductive, and OSR was defined as the ratio of reproductive males to females (Emlen & Oring 1977; Parker 1983). Reproductive lifespan of human males is, however, difficult to estimate as males maintain their ability to sire offspring up to very old ages. However, Käär *et al.* (1996) have shown that the reproductive success of men depends heavily on their spouse. In addition, men living beyond the age of 50 were not very common during the studied period, and men reproducing after their fifties were even less common. Thus, the way in which we defined OSR is likely to characterize the actual situation in the populations rather well. As the population size of different parishes varied from an average of 1534 people living in Pornainen to the average of 11325 living in Ikaalinen, the number of births in a given year was divided by the number of reproductive females in a given population in that year to obtain a standardized birth rate for a given parish. This was also necessary because in all parishes (except in Elimäki, Pernaja and Paltamo), population growth was continuous during the study period, as indicated by significant positive correlations between population size (arranged into five-year periods) and time (Spearman rank correlation $r_s = 0.53–0.99$, $n = 16$ in each of the 18 tests, all significant at an α -level of 0.05 after sequential Bonferroni correction (Rice 1989)). In the three remaining parishes, population size fluctuated widely, with no obvious trends through time. Because the sex ratio of embryos (Stinson 1985) and infants (Lummaa *et al.* 1998) has been shown to be affected by environmental conditions, we also measured the overall mortality rate in a population to describe the quality of the local environment. Overall mortality was defined as the proportion of all people that died in a given year in each parish, and it was assumed that fewer people survived when conditions were poor.

The influence of OSR and mortality rate (MR) on SRB and birth rate (BR) was analysed first by using a multivariate analysis of covariance (MANCOVA), which allows correction of the significance levels for multiple tests when two or more response variables are tested from the same set of individuals (Scheiner 1994). In the MANCOVA model, parish was included as a factor, and OSR and MR as covariates. As the three-way interaction term, as well as the interactions between the covariates, were non-significant (OSR × MR × parish: $F_{18,31} = 1.56$, $p = 0.14$; OSR × MR: $F_{2,30} = 0.18$, $p = 0.84$), they were removed from the model. Therefore, the OSR of a population was not connected to local mortality rate. Because MANCOVA revealed significant, or marginally significant, effects for all of the independent variables in the model (table 1), we also used univariate ANCOVAs to study both response variables separately.

Our replicates within each parish (records collected every fifteenth year) might not represent strictly statistically independent observations, as the individuals in successive observation moments were partly the same. However, due to a relatively

Table 2. Mean number of reproductive-aged adults (15–50 years), mean number of infants born yearly, and mean OSR, SRB and BR in 21 Finnish parishes during 1775–1850

parish	adults <i>n</i>	infants <i>n</i>	OSR		SRB		BR	
			mean (s.e.)	min-max	mean (s.e.)	min-max	mean (s.e.)	min-max
Akaa	1279	72	0.95±0.01	0.92–0.99	0.94±0.08	0.73–1.22	0.110±0.008	0.09–0.14
Artjärvi	1095	62	0.93±0.02	0.90–0.99	1.32±0.15	0.88–1.79	0.109±0.009	0.08–0.14
Elimäki	2403	142	0.96±0.02	0.88–1.01	1.01±0.14	0.66–1.58	0.115±0.016	0.06–0.16
Haukipudas	963	65	0.98±0.01	0.95–1.01	0.82±0.02	0.72–0.89	0.134±0.008	0.11–0.15
Iisalmi	4381	283	0.98±0.02	0.95–1.00	0.97±0.13	0.77–1.20	0.134±0.018	0.11–0.17
Ikaalinen	5293	364	0.91±0.03	0.80–0.97	1.10±0.08	0.97–1.30	0.130±0.005	0.11–0.14
Kitee	3461	280	1.00±0.02	0.94–1.09	1.00±0.06	0.75–1.13	0.171±0.039	0.10–0.36
Loimaa	4043	255	0.92±0.01	0.90–0.98	1.01±0.03	0.89–1.07	0.120±0.004	0.11–0.13
Nurmijärvi	1655	116	0.96±0.01	0.93–0.99	1.02±0.07	0.72–1.21	0.141±0.012	0.12–0.20
Paltamo	2411	168	0.97±0.01	0.93–1.00	1.00±0.06	0.88–1.19	0.141±0.013	0.11–0.18
Pernaja	2835	147	0.99±0.05	0.93–1.08	1.07±0.13	0.85–1.29	0.104±0.012	0.09–0.13
Pornainen	733	41	0.88±0.03	0.80–0.98	1.07±0.11	0.78–1.03	0.107±0.009	0.07–0.13
Pudasjärvi	1693	113	0.99±0.01	0.96–1.01	1.10±0.14	0.85–1.72	0.136±0.005	0.12–0.15
Pukkila	778	52	0.89±0.02	0.87–0.94	0.93±0.11	0.72–1.14	0.128±0.013	0.10–0.16
Pälkäne	1624	93	0.90±0.01	0.85–0.95	1.00±0.08	0.83–1.39	0.109±0.004	0.09–0.13
Rymättylä	874	40	0.93±0.02	0.87–0.97	0.95±0.07	0.69–1.15	0.089±0.011	0.05–0.12
Sipoo	1981	110	0.93±0.01	0.88–0.98	1.20±0.10	0.91–1.48	0.106±0.008	0.08–0.12
Sodankylä	923	64	0.95±0.04	0.85–1.03	0.81±0.04	0.66–0.96	0.131±0.014	0.10–0.19
Sääksmäki	1657	83	0.96±0.01	0.92–1.00	0.99±0.12	0.70–1.43	0.097±0.009	0.06–0.13
Taivassalo	1748	83	0.86±0.02	0.77–0.92	1.01±0.11	0.79–1.52	0.092±0.010	0.06–0.13
Vihti	2581	150	0.90±0.01	0.84–0.93	0.95±0.05	0.80–1.15	0.109±0.004	0.09–0.12

high death rate in Finland during the study period (Gille 1949), individuals belonging to the reproductive age cohort probably changed rather extensively between the sampling occasions. Further, from a biological point of view, the response of humans to current environmental challenges during observation moments with 15-year intervals could be regarded as independent. For these reasons, we do not consider the structure of the data set as a major source of concern. Moreover, there was no evidence for systematic change in sex ratios during the study period as both OSR and SRB, arranged into five-year periods, were uncorrelated with time (OSR: Spearman rank correlation, $r_s = -0.42$ to 0.60, $n=16$ in each test, no significant p values after sequential Bonferroni correction; SRB: Spearman rank correlations, $r_s = -0.59$ to 0.60, $n=16$ in each test; no significant p values after sequential Bonferroni correction).

In all analyses, SRB, BR and MR were logarithm (natural) transformed to ensure normal distribution of observations. Residuals of all models were normally distributed and variances were homogeneous (Levene's test). The SAS statistical package (SAS Institute Inc. 1990) was used for all analyses.

3. RESULTS

(a) OSR versus SRB

There were significant differences in OSR among the different local populations (one-way ANOVA: $F_{20,93}=3.83$, $p=0.0001$), the average ratio (\pm s.e.) of reproducing males to females ranging from 1.00 ± 0.02 in Kitee to 0.86 ± 0.02 in Taivassalo (table 2). In no parish did the mean long-term OSR exceed 1.00, although some point estimates had values well above unity (table 2).

The mean SRB in the 21 study populations was 1.04 and thus well in line with the earlier studies showing that in humans an average of 106 boys are born for every 100

girls (Cavalli-Sforza & Bodmer 1971; Beiles 1974). However, for example, when the average ratio (\pm s.e.) of boys to girls was 0.81 ± 0.04 in Sodankylä, on average 1.32 ± 0.15 boys were born for every girl in Artjärvi (table 2). The overall effect of OSR on SRB was significant (tables 1 and 3), a female-biased OSR leading to a male-biased SRB in 14 out of the 21 parishes (figure 2a). The fact that SRB in a given population was independent of the local mortality rate (table 3) indicated that influence of poor environmental conditions was apparently a less important determinant of SRB than OSR.

(b) OSR versus BR

There was a significant difference in BR among the parishes (tables 1 and 3). In Kitee, an average of 0.17 ± 0.04 children were born yearly for every woman aged 15–50 years old, whereas only 0.09 ± 0.01 were born in Rymättylä (table 2). The magnitude, and even the direction of the association between BR and OSR, varied among the populations, as indicated by a significant OSR \times parish interaction (table 3). In 15 out of the 21 parishes, BR increased with increasing OSR (figure 2b). Furthermore, a high overall mortality rate in a given parish was associated with decreased birth rate, as indicated by a significant effect of MR on BR (table 3). However, this relationship also varied across the parishes, as shown by the significant parish \times MR interaction (table 3 and figure 2b).

4. DISCUSSION

In most of the local populations included in this study, males were produced in excess during times when the OSR (reproductive males: females) was female-biased.

Table 3. Results of the univariate ANCOVAs examining the effects of parish, OSR and MR on (a) SRB and (b) BR

dependent source		d.f.	MS	F	p
(a) SRB $r^2=0.58$	parish	20	0.047	1.17	0.318
	OSR	1	0.192	4.80	0.033
	MR	1	0.057	1.44	0.236
	OSR \times parish	20	0.054	1.35	0.193
	MR \times parish	20	0.027	0.67	0.838
	error	50	0.040		
(b) BR $r^2=0.77$	parish	20	0.076	2.07	0.019
	OSR	1	0.028	0.77	0.386
	MR	1	0.164	4.46	0.040
	OSR \times parish	20	0.070	1.91	0.033
	MR \times parish	20	0.072	1.95	0.029
	error	50	0.037		

This may suggest that the parents adjusted the sex ratio of their progeny in relation to the local OSR. It can be argued that it was probably advantageous for parents to overproduce the rarer sex in response to variation in OSR (Frank 1990), as the mating opportunities of the more abundant sex are decreased in a monogamous mating system and, hence, the reproductive value of offspring of this sex is lowered. To our knowledge, this is the first time a possible sex ratio adjustment in response to local OSR has been reported for mammals, and humans in particular. That adaptive sex allocation is feasible in humans was recently demonstrated by Bereczkei & Dunbar (1997). They showed that in the Hungarian Gypsy population, the expected fitness gain to parents through daughters (in terms of numbers of grandchildren) was greater than that through sons, and that the SRB was strongly female-biased (Bereczkei & Dunbar 1997), as predicted by sex allocation theory (Trivers & Willard 1973).

Overproduction of the rarer sex can only be regarded as adaptive if the overproduced individuals of the rarer sex form a breeding population with members of the originally abundant sex. This was not exactly the case in the studied populations. If the newborn surplus males reached a marriageable age in their mid-twenties, then the older women (previously surplus) were at least 15 years older by definition, and thus probably beginning to experience their climacterium. However, despite this time lag, the present situation might well have provided the only cue about the future mating opportunities in the population. In other words, we argue that if the OSR is currently biased, it may be that the best estimate of the OSR in the next generation, and hence of mating opportunities, is similar. We have also analysed our data to see whether the sex ratio of children born five years earlier (temporally the closest possible year in our data set), or the sex ratio of children aged 1–15 years, would predict the sex ratio of newborn infants. Our analyses revealed that neither of these possible cues for future OSR were significantly associated with the sex ratio of newborns (results not shown). Hence, it appears that the best cue for parents about the future OSR, or at least to which they seem to be responding to, might be the current OSR. It is also worth noticing that in our study

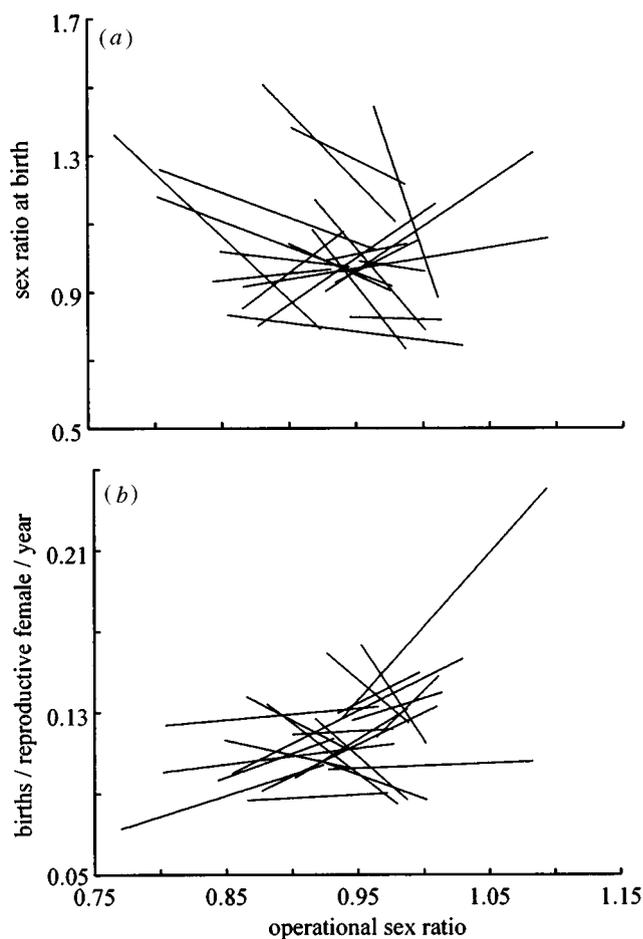


Figure 2. The relationships between (a) operational sex ratio and sex ratio at birth, and (b) operational sex ratio and birth rate in 21 local human populations in Finland (1775–1850). Lines represent regression lines for different parishes.

populations males were only very rarely over-represented among reproductive individuals, and the shortage of men has been common through centuries due to wars and recruiting to the army. Therefore, it might be advantageous for women to be more sensitive to female than male bias in the population, and adjust the SRB accordingly. Indeed, in line with our results, after both World Wars there was a short but distinctive rise in the SRB in countries involved in the conflicts (Russel 1936; MacMahon & Pugh 1954). Although satisfactory explanations for this phenomenon remain unclear (see Trivers 1985), the war-time sex ratio increase, together with our results connecting the actual bias in OSR and current infant sex ratio, provide an evidentiary basis for investigation of how such sex ratio adjustments could occur.

Although the negative correlation between operational and secondary sex ratio was not observed in all of our study populations, it is worth emphasizing that these exceptions do not necessarily contradict the idea of adaptive sex ratio adjustment in these populations. For example, even if more daughters than sons were produced in some parishes during times when the OSR was female-biased, it is possible that production of daughters was favoured by sociocultural and/or environmental factors. For instance, several mammalian studies have reported that mothers in good condition bias their sex ratio at birth in favour of males or in favour of females if

nutritionally stressed (reviewed in Cassinello & Gomendio 1996). This has been interpreted as adaptive and could be expected to occur in humans as well. If so, then this, together with the large sampling variance of our sex ratio estimates, could explain the deviating results from few parishes.

Our results confirm that the birth rate was at its highest in most of the local human populations when OSR was close to 1:1. The association between overall mortality rate and birth rate was also significant, birth rate being lowest in most of the populations at the time when mortality rate was at its highest. This may result from both a lowered conception rate and perhaps higher probability of abortion during a period of poor conditions. Nevertheless, the influence of OSR on birth rate was shown not to be a simple by-product of the effect of mortality, because OSR in a given population was independent of local mortality rate.

Finally, the cues that people might pick up to adjust the sex ratio of their offspring in response to adult sex ratios are difficult to study, as are the mechanisms translating those perceptions to differential production of sons and daughters. The role of infanticide as a determinant of infant sex ratio in our study was presumably very minor or non-existent, as this kind of behaviour was highly criminal and, if practised, severely punished. The theoretical segregational sex ratio of a diploid organism with chromosomal sex determination is 1:1, and the observed sex ratio at birth generally only slightly departs from this figure (Clutton-Brock & Iason 1986). Despite some recent progress in the field (James 1990, 1992, 1996; Krackow 1995), our knowledge about proximate mechanisms by which the sex ratio is adjusted remains obscure. Yet, as evidence for adaptive modification of sex ratios in vertebrates with chromosomal sex determination exists (e.g. Ellegren *et al.* 1996; Svensson & Nilsson 1996; Bereczkei & Dunbar 1997; Komdeur *et al.* 1997; this study), future studies are needed to understand the processes.

To conclude, our results suggest that humans adjusted the sex ratio of their offspring in response to the local OSR in such a way as to maximize the reproductive success of their progeny, i.e. by producing more sons when males were rare. In addition, the results demonstrate that a biased sex ratio among reproducing humans led to a decreased birth rate and thus, presumably, a lowered population growth rate. The strength of these trends varied among parishes, suggesting that results from studies examining adaptiveness of sex ratio variation in only one or a few local populations should not be extrapolated beyond the populations under focus.

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REFERENCES

- Beiles, A. 1974 A buffered interaction between sex ratio, age difference at marriage, and population growth in humans, and their significance for sex ratio evolution. *Heredity* **33**, 265–278.
- Bereczkei, T. & Dunbar, R. I. M. 1997 Female-biased reproductive strategies in a Hungarian Gypsy population. *Proc. R. Soc. Lond. B* **264**, 17–22.
- Cassinello, J. & Gomendio, M. 1996 Adaptive variation in litter size and sex ratio at birth in a sexually dimorphic ungulate. *Proc. R. Soc. Lond. B* **263**, 1461–1466.
- Cavalli-Sforza, L. L. & Bodmer, W. F. 1971 *The genetics of human populations*. San Francisco: Freeman.
- Charnov, E. L. 1982 *The theory of sex allocation*. Princeton University Press.
- Clutton-Brock, T. H. 1982 Sons and daughters. *Nature* **298**, 11–13.
- Clutton-Brock, T. H. & Iason, G. R. 1986 Sex ratio variation in mammals. *Q. Rev. Biol.* **61**, 339–374.
- Clutton-Brock, T. H. & Vincent, A. C. J. 1991 Sexual selection and the potential reproductive rates of males and females. *Nature* **351**, 58–60.
- Ellegren, H., Gustafsson, L. & Sheldon, B. C. 1996 Sex ratio adjustment in relation to paternal attractiveness in a wild bird population. *Proc. Natn. Acad. Sci. USA* **93**, 11723–11728.
- Emlen, S. T. & Oring, L. W. 1977 Ecology, sexual selection, and the evolution of mating systems. *Science* **197**, 215–223.
- Fisher, R. A. 1930 *The genetical theory of natural selection*. Oxford University Press.
- Frank, S. A. 1990 Sex allocation theory for birds and mammals. *A. Rev. Ecol. Syst.* **21**, 13–55.
- Gille, H. 1949 The demographic history of the Northern European countries in the eighteenth century. *Popul. Stud.* **3**, 3–65.
- Hardy, I. C. W. & Krackow, S. 1995 Does sex appeal to zoos? *Trends Ecol. Evol.* **10**, 478–479.
- Hiraiwa-Hasegawa, M. 1993 Skewed sex ratios in primates: should high-ranking mothers have daughters or sons? *Trends Ecol. Evol.* **8**, 395–400.
- James, W. H. 1990 The hypothesized hormonal control of mammalian sex ratio at birth: an update. *J. Theor. Biol.* **143**, 555–564.
- James, W. H. 1992 The hypothesized hormonal control of mammalian sex ratio at birth: a second update. *J. Theor. Biol.* **155**, 121–128.
- James, W. H. 1996 Evidence that mammalian sex ratios at birth are partially controlled by parental hormone levels at the time of conception. *J. Theor. Biol.* **180**, 271–286.
- Komdeur, J., Daan, S., Tinbergen, J. & Mateman, C. 1997 Extreme adaptive modification in sex ratio of the Seychelles warbler's eggs. *Nature* **385**, 522–525.
- Krackow, S. 1995 Potential mechanism for sex ratio adjustment in mammals and birds. *Biol. Rev.* **70**, 225–241.
- Käär, P., Jokela, J., Helle, T. & Kojola, I. 1996 Direct and correlative phenotypic selection on life-history traits in three pre-industrial human populations. *Proc. R. Soc. Lond. B* **263**, 1475–1480.
- Lummaa, V., Lemmetyinen, R., Haukioja, E. & Pikkola, M. 1998 Seasonality of births in *Homo sapiens* in pre-industrial Finland: maximisation of offspring survivorship? *J. Evol. Biol.* (In the press.)
- MacMahon, B. & Pugh, T. F. 1954 Sex ratio of white births in the United States during the Second World War. *Am. J. Hum. Genet.* **6**, 284–292.
- McLain, D. K. & Marsh, N. B. 1990 Individual sex ratio adjustment in response to the operational sex ratio in the southern green stinkbug. *Evolution* **44**, 1018–1025.
- Nevanlinna, H. R. 1972 The Finnish population structure, a genetic and genealogical study. *Hereditas* **71**, 195–236.
- Parker, G. A. 1983 Mate quality and mating decisions. In *Mate choice* (ed. P. Bateson), pp. 141–166. Cambridge University Press.
- Rice, W. R. 1989 Analysing tables of statistical tests. *Evolution* **43**, 223–225.
- Russell, W. T. 1936 Statistical study of the sex ratio at birth. *J. Hygiene* **36**, 381–401.

- SAS Institute Inc. 1990 *SAS/STAT user's guide*, 6th edn. Cary, NC: SAS Institute Inc.
- Scheiner, S. M. 1994 MANOVA: multiple response variables and multispecies interactions. In *Design and analysis of ecological experiments* (ed. S. M. Scheiner & J. Gurevitch), pp. 94–112. New York: Chapman & Hall.
- Stinson, S. 1985 Sex differences in environmental sensitivity during growth and development. *Yb Phys. Anthropol.* **28**, 123–147.
- Svensson, E. & Nilsson, J.-Å. 1996 Mate quality affects offspring sex ratio in blue tits. *Proc. R. Soc. Lond. B* **263**, 357–361.
- Trivers, R. L. 1985 *Social evolution*. Menlo Park, CA: Benjamin Cummings Publishing Company, Inc.
- Trivers, R. L. & Willard, D. E. 1973 Natural selection of parental ability to vary the sex ratio of offspring. *Science* **191**, 249–263.
- Warner, R. R. 1975 The adaptive significance of sequential hermaphroditism in animals. *Am. Nat.* **109**, 61–82.
- Werren, J. H. & Charnov, E. L. 1978 Facultative sex ratios and population dynamics. *Nature* **272**, 349–350.
- Williams, G. C. 1979 The question of adaptive sex ratio in outcrossed vertebrates. *Proc. R. Soc. Lond. B* **205**, 567–580.
- Wrench, D. L. & Ebbert, M. A. (eds) 1993 *Evolution and diversity of sex ratio in insects and mites*. New York: Chapman & Hall.
- Yamaguchi, Y. 1985 Sex ratios of an aphid subject to local mate competition with variable maternal condition. *Nature* **318**, 460–462.