Spatial dynamics of adaptive sex ratios

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Abstract

According to Fisherian sex allocation theory, parents that can adjust their offspring sex ratio in response to skews in population sex ratio will maximize their fitness over parents lacking this ability. There is good evidence that adaptive sex ratio adjustment occurs in many natural populations, but deviations from theoretical predictions have also been observed. These anomalies may be more apparent than real. When the spatial dimension of sex ratio variation is ignored, then a mismatch between empirical data and theoretical predictions based on panmictic mating is to be expected. We illustrate this with data on human sex ratio variation in 21 preindustrial populations, and with a cellular automaton model built to obey Fisherian sex allocation rules. The results from the model generally match with the data. When information about the ambient sex ratio is limited, then the sex allocation decisions may appear locally maladaptive. In general, the results indicate that Fisher's sex-ratio theory may have greater explanatory power than previously thought.

Keywords

Adaptive, cellular automaton, human, operational sex ratio, sex allocation, spatial
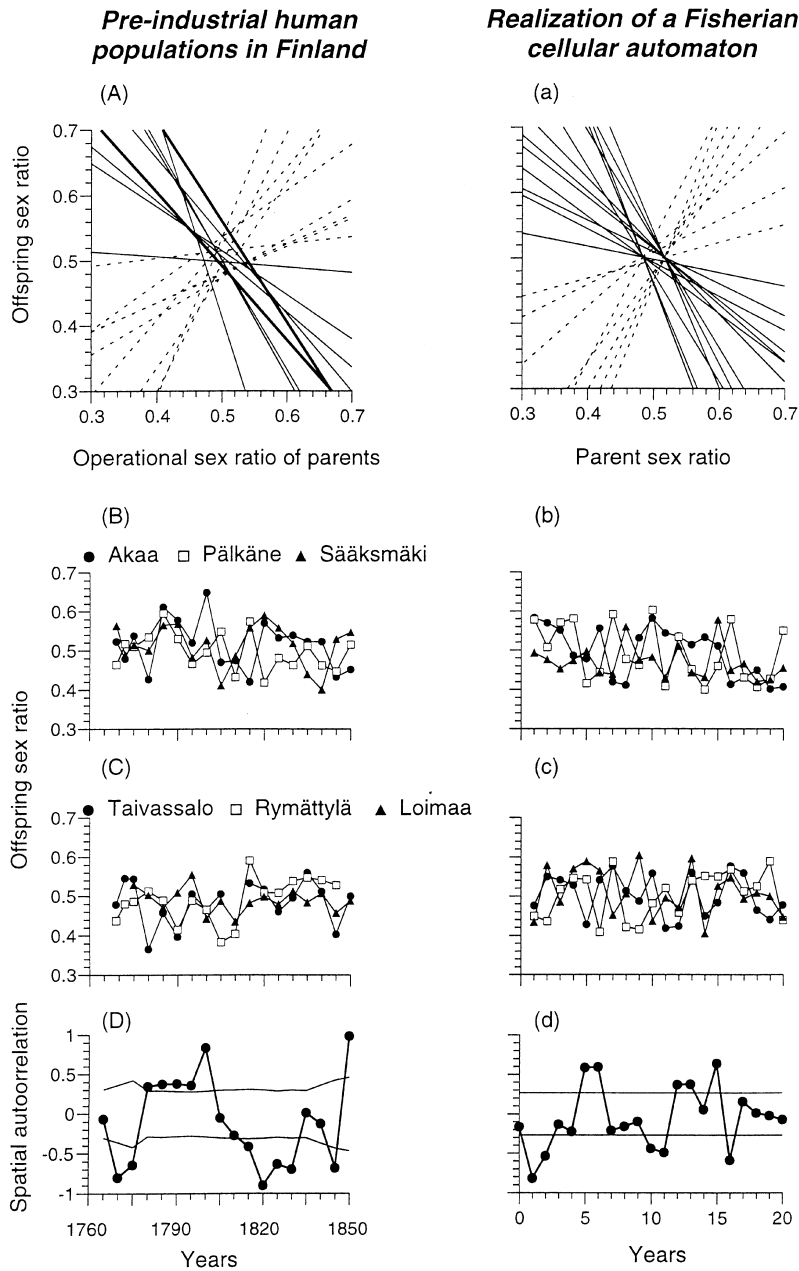
INTRODUCTION

Fisherian sex allocation theory predicts that in a population with one sex dominating, parents producing offspring of the opposite sex will experience a fitness advantage (Fisher 1930). After initial overproduction of the previously rarer sex, selection will turn to favour parents producing offspring with a bias towards the rarer sex. After repeated iterations – even with differential cost in production of either sex (Trivers & Willard 1973) – a balanced sex ratio should evolve (Fisher 1930; Hamilton 1967; Charnov 1982; Karlin & Lessard 1986; Frank 1990).

An increasing amount of evidence suggests that animals are capable of adjusting their progeny sex ratio in adaptive fashion at family level in relation to their own circumstances, such as attractiveness, condition or territory quality (Cassinello & Gomedio 1996; Ellegren *et al.* 1996; Bereczkei & Dunbar 1997; Komdeur *et al.* 1997; Bradbury & Blakey 1998; Kruuk *et al.* 1999). Moreover, one study has suggested that the adaptive sex allocation adjustment in response to the local operational sex ratio was apparently occurring in preindustrial human populations in Finland (Lummaa *et al.* 1998a). When the offspring sex ratio (females/[females + males]) was regressed against sex ratio of the parental population, 52% of the 21 human populations displayed a negative relationship as predicted by Fisher's theory (Fig. 1A). Hence, when the sex ratio in parental population was biased towards one sex, mothers produced excess of progeny with the opposite sex. However, an almost equal fraction of the populations displayed an opposite pattern – the more males (/females) there were in the parent population, the more sons (/daughters) were produced (Fig. 1A). Although this seems to be in a conflict with the prediction of Fisher's sex allocation theory, we show below that patterns of this kind are exactly what is to be expected from Fisher's model with spatial structure.

Consider that in its original form, Fisher's theory assumes a completely panmictic population without population subdivision. However, most populations are fragmented into partially isolated demes coupled via dispersing individuals. This can be expected to have important consequences for the optimal sex allocation strategy in a given population, since sex ratio dynamics can also be influenced by sex ratios of neighbouring populations. In order to investigate this, we modelled spatial sex ratio dynamics by making use of a cellular automaton (e.g. Sigmund 1993). The automaton was build to obey Fisherian adaptive sex allocation. In the model, we relaxed the assumption of global, all-with-all mate

Pre-industrial human populations in Finland

(A)

(B)

(C)

(D)

Realization of a Fisherian cellular automaton

(a)

(b)

(c)

(d)

Figure 1 (A) Regression lines describing offspring sex ratio as a function of adult sex ratio in 21 Finnish parishes between 1769 and 1850 (Lummaa *et al.* 1998a); thicker lines indicate overlapping lines. (a) Corresponding graph for offspring sex ratios as a function of adult sex ratio in a random sample of 21 cells in one realization of a Fisherian cellular automaton model. Parishes and cells with positive slope are shown with broken lines. (B, C) Examples of offspring sex ratio (at birth) through time in six parishes grouped by proximity. The average distance among the 21 parishes was 295 ± 30 km (±95% confidence limit), while in (B) they are 20 ± 15 km and in (C) 35 ± 18 km. (b, c) Sex ratio dynamics in two samples of three proximate cells in one realization of a Fisherian cellular automaton model. (D) Spatial autocorrelation with a radius of 50 km (radii up to 150 km yield matching pattern) in offspring sex ratio among the 21 preindustrial Finnish populations (with 95% confidence limits, values outside these bounds deviate from zero in statistical terms). (d) Spatial autocorrelations with one cell radius for one realization of the Fisherian cellular automaton (with increasing radii the proportion of statistically significant correlations declines).

competition (cf. Hamilton 1967) and assumed the focal cell to be the unit producing offspring. The focal unit allocated offspring to given sex on the basis of its own current sex ratio and the sex ratio in the neighbouring cells after the Fisherian rules. We then compared the results of these simulations with empirical data on human sex ratio variation from 21 preindustrial Finnish populations.

MATERIALS AND METHODS

The Finnish sex ratio data was obtained from local church books of 21 rural parishes covering the period 1769–1850,

well before industrialization and health care were likely to have had significant effects on the standard of living and survivorship (see Lummaa *et al.* 1998a). Sex ratios in the parental generation were obtained by counting the number of males and females of reproductive age (aged 15–50 years) recorded at 5-year intervals. Sex ratio of newborn babies was recorded in the same fashion. The records were not complete for all 21 parishes, but for most of them we had more than 15 parental and offspring sex ratio scores.

To examine the influence of sex ratios in neighbouring populations on sex ratio dynamics of a population, we

constructed a cellular automaton. The automaton used a 100×100 grid of cells, each representing a subpopulation. The extent of interaction among cells, i.e. the neighbourhood scanned, was varied from 0 to 10 cells, but the results are presented for neighbourhood size of one cell layer around the focal cell. Hence, sex ratio in the surrounding eight cells, plus the ratio in the focal cell itself, was used to determine offspring sex allocation for the focal cell (Fig. 2A). Here we employed the Fisherian fitness maximization rule, which – in a nonstructured population – would let the sex ratio to evolve towards the global 50:50 ratio (Fig. 2B, C). For example, in the neighbourhood of one cell layer we average the sex ratio in the focal cell and in the eight surrounding cells. The allocated sex ratio for the focal cell is one minus the average. We initiated the automaton by drawing random numbers from a distribution of sex ratios of the real data.

The automaton was updated for each generation on 12 occasions, and the proportion of units allocating sex was adopted to match the monthly frequency of births in preindustrial Finland (Lummaa *et al.* 1998b). The major outcome, however, is not sensitive as to whether the updating is asynchronous or synchronous. The automaton has two generations (younger and older), the generations overlap and make their own decisions of the offspring sex ratio. The final outcome is compromised by the relative weights between the generations. In our simulations we varied the number of overlapping generations, and the relative weight of the subsequent generations. The results presented here are based on a model with partially overlapping generations affecting the offspring sex (4:3 weights [youngest generation: older generation]). Experimentation with varying temporal weights and neighbourhood sizes showed that overlapping generations were required to obtain the results described below.

The automaton was left running for 200 generations, of which we used the final 100 to sample a consecutive section of 20 years. A total of 21 cells were selected at random from the middle of the grid to get comparable observations with the sex ratio data in the 21 Finnish populations. For these data, as also with the human data, we calculated spatial autocorrelation (Legendre & Fortin 1989) and regressed the offspring sex ratio against sex ratio of the parent generation. To generate an expectation for the frequency distribution of the slopes after the spatially limited information we proceeded as follows.

The cellular automaton simulation, as described above, was repeated 100 times, and the frequency distribution of the slopes was scored. We also generated a random expectation by generating 21 time series of data for 20 time steps by randomly drawing sex ratios from the human data. From these series we calculated the slopes between parent and offspring sex ratios, repeated the
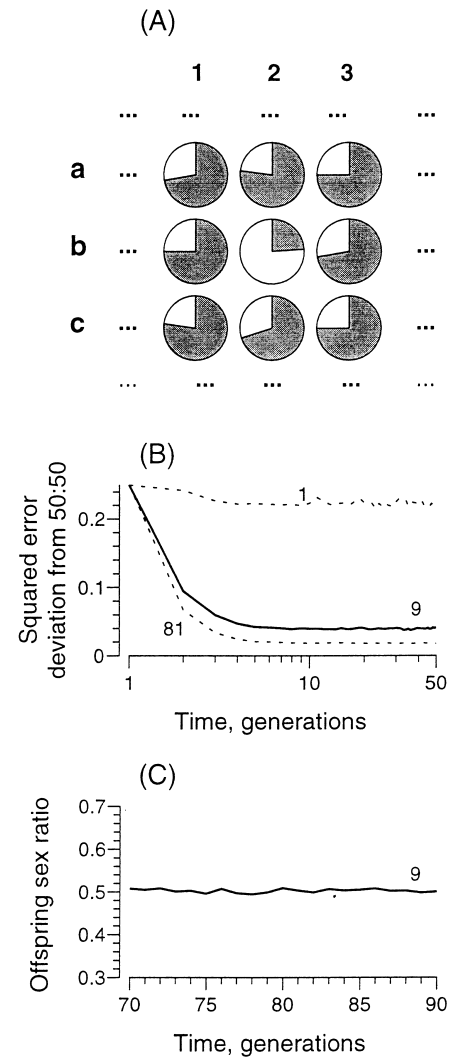
Figure 2 (left) (A) A schematic representation of sex ratio variation in spatial scale. Each of the circles represent a subpopulation with varying proportion of females (white) and males (dark). Under Fisher's theory, and without any migration between the subpopulations, the optimal offspring sex ratio in each of the subpopulations is determined by their current sex ratio. For example, in cell 2b, selection would favour parents producing more males (dark), thus yielding a negative slope for regression presented in Fig. 1(a). With subsequent iterations, the ratio will eventually evolve towards 50:50 (B, C). However, if information of sex ratio in the adjacent cells is allowed for, the optimal offspring sex ratio in cell 2b would be still in favour of females (white), thus yielding a positive slope for regression in Fig. 1(a). Parts (B) and (C) give performance scores of the Fisherian sex ratio allocation rule with the assumption that the size of the surrounding environment is constant between subsequent generations (this is not in the case of the cellular automaton as every cell in turn is the focal cell). The inserted numbers give the size of the neighbourhood (in the automaton we used 3×3 cells, the central one of which is the focal cell).

process 100 times, and scored the frequency distribution of the slopes. The match of the three cumulative frequency distributions was scored by using the Kolmogorov-Smirnov test (with 0.05 bins from −1 to 1).

RESULTS

The data on Finnish human populations show that sex ratio fluctuates in apparently cyclical manner around the 50:50 ratio (Fig. 1B, C). The Fisherian cellular automaton is capable of reproducing this result (Fig. 1b, c). It is noteworthy that for the two data sets there is no sign of stabilization towards a stable sex ratio, as predicted by Fisher's theory in a panmictic population (Fig. 2B, C). Spatial autocorrelation analyses of these real populations show that the correlation coefficients fluctuate from strongly negative to strongly positive, interspersed with periods of low spatial autocorrelation between different populations (Fig. 1D). This also features the results from the Fisherian automaton (Fig. 1d).

Both in the real data and in the data generated by the automaton, roughly one half of the observed slopes connecting parent generation and offspring generation sex ratios were negative whilst the remaining ones were positive (Fig. 1). To analyse whether the observed frequency distribution of the regression slopes deviates from a random outcome we generated two expectations. First, regression slopes were generated by random draws from the human sex ratio data. Second, the cellular automaton was used to generate a similar data from which the slopes were calculated. The match of the three cumulative frequency distributions (Fig. 3), analysed by the Kolmogorov-Smirnov test, indicates that the observed slopes in the human data differ from random draws from the human data ($D_{41} = 0.25$, $P < 0.02$), but not from the ones generated by the cellular automaton ($D_{41} = 0.11$, $P > 0.1$; also the random draw and cellular automaton distributions differed from each other, $D_{41} = 0.23$, $P < 0.05$).

Here we report results from runs with 4:3 weights between two subsequent generations. We have explored the weights ranging from 1:1 to 9:1, the results being qualitatively matching with the data presented here. Our experimentation showed that the conclusions between the observed data and the cellular automaton generated slopes are statistically valid (though the test statistics values vary) for weights 4:3–9:1 of the overlapping generations.

CONCLUSIONS

Sex ratios in neighbouring human populations in the preindustrial time in Finland fluctuated temporally. Sometimes the populations matched each other almost
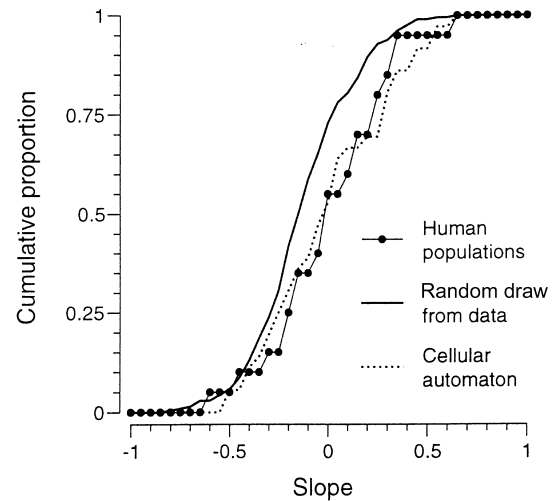
Figure 3 Cumulative frequency distribution of the regression slopes (in 0.05 bins) connecting parent and offspring sex ratios. The Finnish human population data are shown with solid line and dots, whereas the two expectations (random draw from the human sex ratio data and the one generated with the Fisherian cellular automaton) are shown with a solid and a broken line.

perfectly, while at other times sex ratios were in opposing phases. The results from cellular automaton yielded similar patterns. An interesting observation is that close to one half of the human populations displayed a negative relationship between parental and offspring sex ratios as predicted by Fisher's theory, whereas the other half showed positive relationships. Also this feature can be reproduced by the automaton. Mechanistically, this feature can be best understood with an aid of a simple example.

If we have a spatially structured population where each subpopulation has a limited knowledge of the prevailing sex ratio in neighbouring cells (Fig. 2A), and the focal cell (e.g. cell b2) is dominated by females and the surrounding cells by males, two outcomes for optimal sex allocation are possible depending on the spatial extent from which the information is gathered. First, if the cell b2 is alone in the universe, the Fisherian rule would drive its sex ratio towards males and ultimately to 50:50 ratio. Second, if the b2 can gather information also from the neighbouring cells, then the female dominating sex ratio would be produced. This occurs because the cell b2 would benefit from producing females that can be "exported" to neighbouring populations (cells) that have male biased sex ratios (Fig. 2A). Note also that these two possible outcomes in sex allocation can explain the negative and positive slopes for regressions of offspring sex ratio on sex ratio in parental generation (cf. Fig. 1).

Hence, the cellular automaton, built to obey Fisherian sex allocation rules faithfully, but gathering limited

information about the regional sex ratio while making the sex allocation (see also Hamilton 1967; Charnov 1982), is capable of mimicking qualitatively the spatial dynamics of human sex ratios as documented for the historical Finnish populations. We argue that the key for understanding sex ratio dynamics in the context of the population sex ratio is in limited regional linkage of local populations. The limited linkage disturbs the local sex ratio allocation but is not a substantial enough disturbance to bring the subdivided population system into a panmictic population. Since there is both genetic and demographic evidence for limited dispersal in preindustrial Finnish societies (Nevanlinna 1973), it looks that the observed sex ratio dynamics of these populations is adequately explained by the spatial extension of the Fisherian sex ratio theory. It remains to be seen whether there are other data on spatial sex ratio dynamics, and whether the simple model presented here is capable of mimicking them.

In conclusion, our results add a new dimension to the understanding of adaptive sex ratio manipulation, and indicate that Fisher's famous theory has greater explanatory power than previously anticipated. Moreover, these results, together with the findings of several other recent studies (Bascompte & Solé 1995, 1998, Hassell *et al.* 1994; Ranta & Kaitala 1997; Ranta *et al.* 1997), suggest that spatial complexity can be an important component greatly affecting various population biological processes. In particular, our analyses suggest that equilibrium situations, such as balanced sex ratios, may seldom exist in nature. Finally, we note that incorporation of spatial dimension into ecological and evolutionary research such as the study of sex ratio dynamics can unravel how simple processes can often create complex and unexpected patterns.

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BIOSKETCH

Esa Ranta is interested in various aspects of ecology.