Sex ratio variance and the maintenance of environmental sex determination

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Abstract

Although variation in population sex ratios is predicted to increase the extinction rate of clades with environmental sex determination (ESD), ESD is still seen in a wide array of natural systems. It is unclear how this common sex-determining system has persisted despite this inherent disadvantage associated with ESD. We use simulation modelling to examine the effect of the sex ratio variance caused by ESD on population colonization and establishment. We find that an accelerating function of establishment success on initial population sex ratio favours a system that produces variance in sex ratios over one that consistently produces even sex ratios. This sex ratio variance causes ESD to be favoured over genetic sex determination, even when the mean global sex ratio under both sex-determining systems is the same. Data from ESD populations suggest that the increase in population establishment can more than offset the increased risk of extinction associated with temporal fluctuations in the sex ratio. These findings demonstrate that selection in natural systems can favour increased variance in a trait, irrespective of the mean trait value. Our results indicate that sex ratio variation may provide an advantage to species with ESD, and may help explain the widespread existence of this sex-determining system.

Introduction

Environmental sex determination (ESD) is seen in a diverse array of animal and plant taxa (Bull, 1983; Korpelainen, 1990). Several theoretical analyses have demonstrated that the temporal sex ratio variation that is expected to occur in populations of ESD species will increase the risk of population extinction or favour the evolution of genetic sex determination (GSD) from ESD (Bulmer & Bull, 1982; Bull, 1983; Berec et al., 2001; Van Dooren & Leimar, 2003). Williams (1992) proposed that the continued occurrence of ESD indicates that ESD must provide a clade-level advantage that offsets its inherent evolutionary disadvantage. While clade-level selection is predicted to favour lineages that speciate more or are less susceptible to extinction than others, no such advantage has been shown for ESD (Williams, 1992).

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Fisher (1930) first demonstrated that sex ratios should be even when the cost of producing each sex is the same. When one sex is more abundant, selection favours producing offspring of the minority sex, driving the sex ratio back to 1 : 1. When sex is determined environmentally, selection may still favour an even sex ratio, but environmental variation in factors affecting sex determination can cause considerable variance in population sex ratios. A variety of environmental factors are known to affect sex ratios in species with ESD, ranging from pH to host density to temperature (Korpelainen, 1990). Variance in the physical characteristics of developmental environments can cause offspring sex ratios to vary among populations in different locations (Lance et al., 2000), and temporal climatic variation can also cause population sex ratios to vary among generations within each population (Bulmer & Bull, 1982). By contrast, in most dioecious systems, sex ratio variance is generally limited to the binomial variance generated by the meiotic segregation of sex chromosomes (Williams, 1979; Charnov, 1982). Although there are factors known to

cause deviations from 1 : 1 sex ratios in species with GSD (Taylor, 1990), ESD populations are subject to an additional source of sex ratio variance associated with climatic variation (Bulmer & Bull, 1982). For example, in turtles, population sex ratios in ESD species exhibit a much higher sex ratio variance than in GSD species (Ewert & Nelson, 1991).

Substantial among-population sex ratio variation has been documented for a wide range of ESD species. Although comparisons of population sex ratios within ESD species are often confounded by methodological differences between studies or among-year variation in the environment, there are studies that have demonstrated differences in brood sex ratios among multiple, spatially separated populations over a given time span. For example, Barker & Hebert (1986) found significantly different sex ratios in four allopatric *Daphnia magna* populations observed over the same reproductive season. Among 11 American alligator nesting sites distributed throughout the coastal area of south-western Louisiana (USA), the location of nesting environment had a significant effect on juvenile sex ratios, with mean sex ratios ranging from 31% to 62% female across sites (Lance *et al.*, 2000). The strong differences in sex ratios between nearby environments in these studies suggest that physical attributes of the environments, and not genetic differences, were responsible for the among-site variation in offspring sex ratios. Although biased population sex ratios are expected to eventually return to 1 : 1 due to Fisherian selection, these types of transitory population sex ratio biases should often be associated with ESD (Bulmer & Bull, 1982).

We used simulation modelling to investigate the effects of sex-determining system on the probability of success of colonizing species. Because the sex-determining system rarely varies within a species, yet often differs between related species, it is instructive to examine competition between ESD and GSD species. Specifically, we examined how the greater spatial and temporal variance in sex ratio that occurs under ESD affects the probability that colonizers will invade established populations. We introduced populations of ESD and GSD species into resident populations of GSD species, and recorded the probability of population establishment of the invading populations. We modelled the effects of both spatial (among-population) and temporal variation in sex ratios, utilizing relevant life history estimates from species with ESD. These results provide a potential mechanism for explaining the persistence and distribution of environmental sex-determining systems.

Methods

The model

We use a standard birth–death simulation model adapted from Wilson (2000). We consider a polygynous mating system where reproduction was not limited by the availability of males, except when the number of males was zero (Bateman, 1948). We consider a source population from which small numbers of individuals disperse and inoculate areas inhabited by resident populations. Each simulation began with an inoculum of 20 individuals entering a resident population of 1000 individuals. There was no migration among resident populations or colonizing populations and each resident population was colonized by only one inoculum. The resident population possessed GSD and therefore each resident female had a 50% chance of producing a daughter every time she reproduced. The resident population did not interbreed with the colonizing population. We considered two types of colonizing populations; those with GSD and those with ESD. For colonizing GSD populations, each female had a 50% chance of producing a daughter every time she reproduced. For colonizing ESD populations, the global sex ratio was 50%, but population sex ratios were allowed to vary among generations and/or among populations (see next section). Each generation, every female in both the colonizing and resident populations produced a brood of offspring composed of a proportion of females that was determined by the sex-determining system and the local breeding environment.

We incorporated interspecific competition and density-dependent regulation by setting a carrying capacity of 1000 individuals for the combined population size of the colonizing and resident populations. The carrying capacity affected the reproductive rate (Ψ) of each generation:

$$\Psi = \frac{2K}{\varphi + \mu},$$

where K is the carrying capacity, μ is the number of individuals in the resident population and φ is the number of individuals in the colonizing population. In each generation therefore, Ψ offspring from each mother survived to reproduce. Because the combined population was always near carrying capacity, the mean reproductive output of the combined population always approximated the replacement rate (i.e. $\Psi \approx 2.0$).

We monitored 10 000 colonizing populations for each level of among-population and among-generation sex ratio variation. We ran each simulation until either the resident or colonizing population was driven to extinction. We recorded population establishment as the proportion of colonizing populations that competitively excluded the resident populations.

We examined the long-term survival of established populations of ESD species by simulating their susceptibility to displacement by colonizing populations of GSD species. Each simulation started with an initial colonizing GSD population entering a resident ESD population exhibiting only among-generation variation in sex ratios. Because sex ratio biases will eventually be eliminated by Fisherian selection within populations, among-population variation in sex ratios should therefore be transient,

with the mean sex ratio of established ESD populations eventually approaching 1 : 1 due to natural selection within populations. We monitored colonizing populations exhibiting various levels of among-generation sex ratio variation and recorded the proportion of resident populations that were competitively excluded by the colonizing population.

Offspring sex ratios

Because the local environment is known to affect offspring sex ratios in species with ESD (Vogt & Bull, 1984), spatial environmental heterogeneity should result in substantial among-population sex ratio variation. We assumed a global sex ratio of 0.5 for both ESD and GSD, but allowed sex ratios to vary among populations in the ESD treatments. For each ESD population, the initial sex ratio (R) was randomly selected from a normal distribution with a mean of 0.5 and standard deviations ranging from 0 to 0.2 (Fig. 1). R is defined as the probability that any given offspring developed as a female. Because sex ratios vary between 0 and 1, the tails of the sex ratio distributions were truncated in the simulations with high levels of sex ratio variance. For all GSD populations, R was set at 0.5 and sex ratio variation only arose as a result of the binomial variance associated with the 50% chance that each offspring developed as a male or female.

In the next set of simulations, we examined the effects of short-term temporal sex ratio variation in ESD populations by varying sex ratios across generations within each population. The sex ratio of each generation in each population was randomly selected from a normal distribution with a mean of R, and standard deviations of 0.05, 0.10, or 0.20 (Fig. 2a). There was no autocorrelation among R of each generation. In natural populations, there will always be some combination of spatial and temporal environmental variation. Therefore, we simultaneously varied temporal and spatial sex ratio variance in a factorial design.

When temporal environmental changes occur less frequently, as might happen with periodic variation in population density or vegetational distribution, population sex ratios may shift over periods of several generations. We incorporated periodic sex ratio variation by varying sex ratios randomly every 10 or 25 generations. In these simulations, a perfect autocorrelation of R was achieved by fixing R for 10 or 25 generation intervals and then randomly varying R for another 10 or 25 generations. Thus, for instance, using the 10 generation period, the sex ratio for each 10 generation period was randomly selected from a normal distribution with a mean of 0.5, and standard deviations of 0.05, 0.10, or 0.20 (SD = 0.10, shown in Fig. 2b).

When sex ratios varied among populations, sex ratios within most populations deviated from 1 : 1, creating Fisherian selection favouring the rare sex. Because our model is phenotypic and not genotypic, we cannot
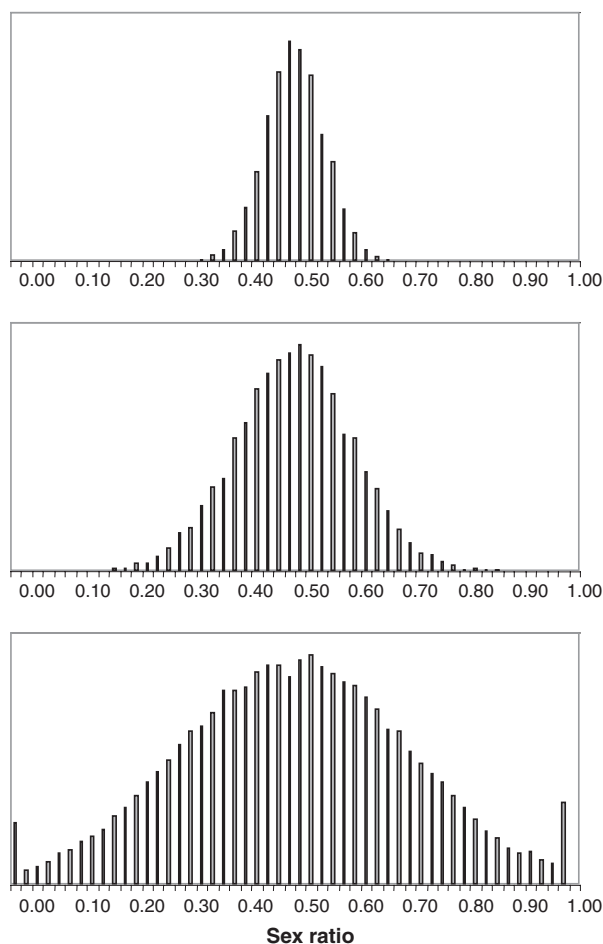

Fig. 1 Distribution of initial sex ratios among environmental sex determination populations. For each population, the initial sex ratio (proportion female) was randomly selected from a normal distribution with a mean of 0.5 and standard deviations of 0.05 (top), 0.10 (middle), or 0.20 (bottom).

directly calculate Fisherian selection on sex-determining genes. We can, however, incorporate Fisherian evolution by replicating the sex ratio trend shown to occur in genetic models of sex ratio evolution in ESD systems. Morjan (2003) modelled Fisherian sex ratio evolution under ESD using estimates of sex ratio heritability calculated for ESD species. We incorporated Fisherian evolution in each simulation through an equation that produced a sex ratio trend over time that mirrors the sex ratio trend produced by Morjan's model:

$$R' = 0.95(R + 0.02632),$$

where R is the mean population sex ratio prior to selection and R' is the sex ratio after selection. This equation resulted in a sex ratio function that closely approximated the pattern of sex ratio evolution in Morjan's simulations of Fisherian evolution under ESD,
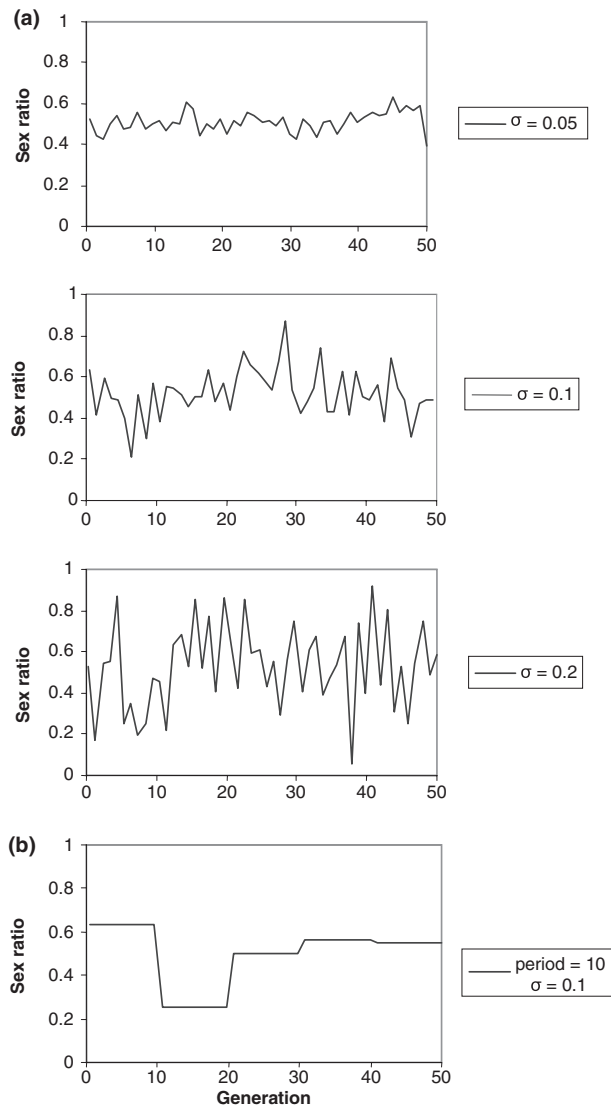
(a)

(b)

Fig. 2 Temporal sex ratio variation. (a) In the first three graphs, the sex ratio (proportion female) of each generation in each population was randomly selected from a normal distribution with a mean of 0.5 and standard deviations of 0.05 (top), 0.10 (middle), or 0.20 (bottom). (b) The sex ratio for each period (10 generation time interval) was randomly selected from a normal distribution with a mean of 0.5, and a standard deviation of 0.10.

both in the shape of the function and in the time required to evolve a 1 : 1 sex ratio.

Sex ratios in natural populations

In order to test if the level of sex ratio variance in natural colonizing populations is high enough affect population establishment, we parameterized our simulations with data collected from wild ESD populations. Most available ESD sex ratio data are not suitable for estimating the among-population sex ratio variation of colonizing pop-

ulations because they come from long-standing populations where Fisherian evolution has likely diminished any initial sex ratio bias. However, as American alligators (*Alligator mississippiensis*) were hunted to the brink of extinction in the first half of 20th century, most nesting sites have been colonized in the past 5–10 generations, and Fisherian selection has most likely not had time to eliminate the sex ratio variation. Lance *et al.* (2000) report juvenile sex ratio data collected over several years for 11 distinct nesting localities of *A. mississippiensis*. Using the mean sex ratio for each locality, we calculated a standard deviation for this data set of 0.0891.

Quantitative estimates of among-generation sex ratio variance are also difficult to obtain because they require monitoring of populations over several generations. The best long-term sex ratio data for an ESD species come from Janzen (1994), who calculated sex ratio estimates over 49 years for a population of *Chrysemys picta*, a turtle with ESD, based on climatological data. Because a generation is composed of individuals that were born over several years, the sex ratio for each generation can be calculated by averaging the yearly sex ratios over the entire generation. Generation times for this species have been estimated at 12 years, although the breeding pool for a single generation for *C. picta* can consist of individuals produced over a span of more than 30 years (Wilbur, 1975). Because preliminary simulations indicated that temporal sex ratio variance negatively affects population establishment, we assumed a 12-year generation time to produce a conservative estimate for the probability of establishment of an ESD population; including more years would reduce the temporal sex ratio variance and make ESD more likely to invade. Treating each consecutive 12-year period as a discrete generation is also conservative because it assumes that the sex ratio experienced by a parent and its offspring are independent, when in fact the breeding pools each generation contain many of the same individuals, lessening the variation in sex ratios among generations. By averaging the yearly sex ratios for the each of the first four 12-year periods in Janzen's 49-year data set, we estimated a standard deviation of 0.0406 for the among-generation sex ratio variation.

We ran simulations incorporating the values of among-population and among-generation sex ratio variances extrapolated from these data sets of ESD reptiles. Specifically, we simulated colonizing ESD populations with a mean sex ratio of 0.5 and an among-population standard deviation of 0.0891 and an among-generation standard deviation of 0.0406. We then examined the long-term survival of these populations by simulating their susceptibility to displacement by colonizing GSD populations after Fisherian selection has eliminated the among-population sex ratio variation. To do this, we monitored populations exhibiting 50 : 50 sex ratios with a standard deviation of 0.0406 for the among-generation sex ratio variation and recorded the proportion of resident

populations that were competitively excluded by colonizing GSD populations. The source code for all simulations is available from S.F. upon request.

Results

Spatial variation

Population establishment was strongly affected by among-population variance in the sex ratio. In the simulations incorporating only among-population sex ratio variation, the variable sex ratio treatments (ESD) produced a higher proportion of established populations than the treatment incorporating no among-population sex ratio variance (GSD). Successful population establishment increased with increasing levels of among-population sex ratio variance. This effect was significant even at low levels of variance [the $\sigma = 0.05$ treatment exhibited a higher fraction of established populations than the $\sigma = 0$ treatment (0.0404 vs. 0.0012; $\chi^2 = 988.5$, d.f. = 1, $P < 0.0001$, Fig. 3)].

The mean initial sex ratio was a good indicator of the probability of population establishment, with female-biased populations having substantially higher success than unbiased and male-biased populations (Fig. 4). This trend was strong despite the fact that Fisherian selection eventually eliminated the among-population sex ratio variation in ESD populations. While even the most strongly female-biased populations evolved to 1 : 1 within the first 90 generations, most had competitively excluded the resident populations before doing so. Although male-biased populations at one end of the distribution of population sex ratios tended to rapidly go extinct (no population that was initially <47% female successfully became established), this effect was more than compensated for by the higher establishment of female-biased populations at the other end of the sex ratio distribution.
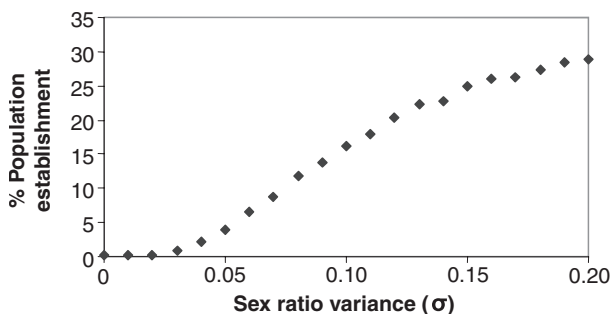
Fig. 4 Sex ratio (proportion female) vs. percentage population establishment. The probability of successful invasion initially increases with female frequency due to increased reproductive output of the populations. Establishment decreases at high female frequencies due to the increased occurrence of all-female cohorts.

Temporal variation

In the simulations incorporating only among-generation sex ratio variation, sex ratio variance negatively affected population establishment. For all levels of among-generation sex ratio variance, variable sex ratio treatments (ESD) produced lower establishment than the constant sex ratio treatment (GSD; Table 1, column 1). No populations out of 10 000 became established for the ($\sigma = 0.20$) treatment.

In the simulations incorporating both among-population and among-generation sex ratio variance, the increased population establishment due to among-population variance generally had a greater impact than the decreased establishment resulting from among-generation variance. In eight of the nine simulations incorporating both among-population sex ratio variance and among-generation sex ratio variance, population establishment was significantly higher than in the no variance treatment (Table 1; $\chi^2 > 12.79$, d.f. = 1, $P < 0.001$ for all treatments). Only the simulation with the lowest among-population variance ($\sigma = 0.05$) and highest among-generation variance ($\sigma = 0.20$) exhibited lower population establishment than the no variance treatment.

When sex ratios varied over longer temporal periods, sex ratio variation increased the fraction of established colonizing populations (Table 2; $\chi^2 = 497.8$, d.f. = 1,

Fig. 3 Among-population sex ratio variation vs. percentage population establishment. The proportion of invading populations that successfully established populations was negligible with no sex ratio variance (GSD), but increased with higher levels of among-population sex ratio variance (ESD).
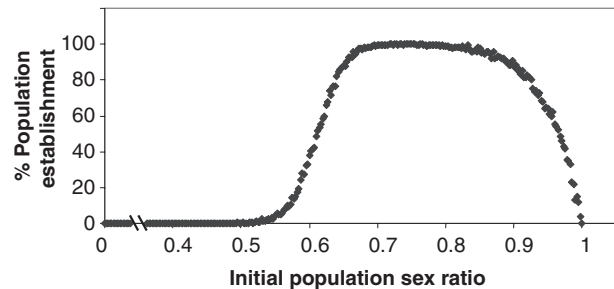
Table 1 Establishment (proportion of established populations) of colonizing populations characterized by varying levels of among-generation sex ratio variance ($\sigma 1$) and among-population sex ratio variance ($\sigma 2$).

$\sigma 1$	$\sigma 2$			
	0	0.05	0.10	0.20
0	0.0012	0.0404	0.1615	0.2886
0.05	0.0006	0.0137	0.0870	0.2130
0.10	0.0006	0.0037	0.0369	0.1410
0.20	0	0.0006	0.0065	0.0416

Table 2 Establishment (proportion of established populations) of colonizing populations characterized by varying levels of among-period sex ratio variance (σ) over periods of 10 or 25 generations.

Period (generations)	σ			
	0	0.05	0.10	0.20
10	0.0012	0.0510	0.1069	0.1579
25	0.0011	0.1158	0.2208	0.2952

$P < 0.0001$ for all treatments). Population establishment increased with increasing sex ratio variance for both period lengths, and was greatest in the 25 generation period treatment. Most established populations exhibited female-biased periods early, which produced rapid population growth, and frequently resulted in exclusion of the resident populations.

When we examined the susceptibility of established ESD populations to competitive exclusion by colonizing GSD populations, we found that among-generation sex ratio variance in the resident ESD populations allowed some colonizing GSD populations to competitively exclude the resident populations. In the simulations involving low among-generation sex ratio variance, $σ = 0$ or 0.05, population extinction was low (0.1–4.6 %). When sex ratio variance of resident ESD populations was higher, $σ = 0.10$, 25.3% of populations went extinct, while high sex ratio variance, $σ = 0.20$, resulted in extinction of 66.5% of resident ESD populations.

Natural sex ratios

The simulation incorporating among-population and among-generation sex ratio variances estimated from data sets of ESD reptiles resulted in significantly increased population establishment. The colonizing ESD populations competitively excluded the resident GSD populations in 7.9% of all populations, compared with colonizing GSD populations which excluded resident GSD populations in only 0.1% of populations ($χ^2 = 789.5$, d.f. = 1, $P < 0.0001$). Furthermore, once the ESD populations had become established, they were competitively excluded by colonizing GSD populations in only 2.8% of populations.

Discussion

Under ESD, spatial and temporal stochasticity in the environmental factors affecting sex determination can produce substantial variation in population sex ratios. We examined the implications of this sex ratio variation on the ability of ESD species to colonize and compete with GSD species. We found that variation in population sex ratios, as is likely to occur under ESD, can greatly increase the probability of population colonization, even if the mean sex ratio under both systems is predicted to be the same. Because population colonization and establishment can increase the opportunity for speciation and reduce the probability of extinction within a clade, sex ratio variation can provide an inherent advantage to taxa characterized by ESD relative to those with GSD. The increased opportunity for population colonization in ESD taxa may help explain the persistence and widespread distribution of this sex-determining system.

Regardless of the magnitude of sex ratio variation, spatial variance in the sex ratio increased the probability of establishment of ESD populations. The reason for this stems first from the fact that when two species with equal net reproductive rates are competing for the same resources, the initially more abundant species is likely to exclude the rarer species (Lotka, 1925; Hardin, 1960). Thus, the colonizing populations that produced the same unbiased sex ratio as the resident populations were excluded in nearly all of the simulations. Similarly, male-biased populations had both small initial population sizes and lower reproductive rates than the resident populations and therefore nearly always went extinct. Conversely, female-biased populations were substantially more likely than unbiased and male-biased populations to exclude resident populations. Because fecundity is directly linked to the production of female offspring, female-biased colonizing populations had a higher net reproductive rate of each generation than resident GSD populations, and thus were often able to outcompete the resident populations. Although equal numbers of female-biased and male-biased populations occurred under ESD, the overall mean population establishment under ESD was higher due to the colonization success of a minority of female-biased populations.

The observation that sex ratio variance increases mean population establishment is a unique example of Jensen's inequality (Jensen, 1906), which states that variance will either increase or decrease the mean value of the response variable depending on whether the function is accelerating or decelerating (Ruel & Ayres, 1999). To see this, notice that the relationship between sex ratio and population establishment is a complex nonlinear function (Fig. 4). In the vicinity of a mean sex ratio of 0.5, however, the relationship is a concave-upward function. The concave shape of this part of the function can be attributed to the negligible establishment success in male-biased and unbiased populations followed by a sharp increase in establishment resulting from the greater reproductive rate experienced by female-biased populations. Our simulations focused on sex ratio variance in the neighbourhood of a mean sex ratio of 0.5, where GSD populations will generally occur (Fig. 4). In this region of the parameter space, the average establishment among two populations with sex ratios of, say, 0.4 and 0.6 will be higher than the average establishment of two populations with even sex ratios. Because of the complexity of this function, however, this selection for increased variance will not hold up for all levels of sex ratio. In a hypothetical system where mean GSD sex

ratios were 0.7, the function would be decelerating at this point and sex ratio variance would be selected against, favouring GSD over ESD. Environmental stochasticity has been shown to lower the mean value of a variable when the function is decelerating in this way. For example, Wilson & Harder (2003) showed that increased variance in pollen import and seed production reduces mean recruitment as a result of Jensen's inequality, favouring hermaphroditism in gynodiocious systems.

At first glance, the estimates of sex ratio variance calculated from natural ESD populations seem small, but our simulations reveal that they, nevertheless, could have significant effects on the persistence of ESD. Specifically, we found a greater than 60-fold increase in population establishment when we parameterized our simulations with data from natural populations. Although the variance estimates for the among-generation and among-population sex ratios used in these simulations are approximations derived from a limited number of observed sex ratios, they nonetheless reveal that the sex ratio variation present in natural colonizing ESD populations could provide a selective advantage to ESD.

Our simulations show that population sex ratio variance provides a clade-level advantage to ESD populations, often allowing them to outcompete existing GSD populations and become established. In the absence of any interspecific competition, both GSD and ESD species should be able to readily colonize suitable habitats if their net reproductive rate exceeds the replacement rate. In a species where the net reproductive rate of an unbiased population is less than the replacement rate, a female-bias may confer enough of an increase in reproductive rate to temporarily avoid extinction, but the reproductive rate should fall below the rate necessary to sustain the population if the sex ratio returns to even. Woodward & Murray (1993) showed that when fecundity is sufficiently low, unbiased crocodile populations will go extinct, while female-biased populations may survive. However, when Fisherian evolution is taken into account and female biases are transitory, these populations rapidly succumb to extinction as well (Girondot & Pieau, 1996). Thus it appears that the sex ratio variation caused by ESD can provide an advantage only when there is competition between ESD and GSD populations.

One conceivable limitation to the ecological advantage we have demonstrated is the effect of sex ratio evolution on the sex-determining mechanism. For example, when a population colonizes a female-producing environment, the sex-determining system is expected to eventually evolve to produce a 50 : 50 sex ratio in the new environment. Therefore, if the environment in this population does not change over time, migrants from this population should be less likely to produce a female bias upon colonizing similar environments in future. However, because the environmental conditions affecting sex determination are expected to vary over time, populations can experience a sex-determining environ-

ment at the time of colonization that differs markedly from the environment characterizing the population when individuals are dispersing. In order for sex ratio variation to provide an ecological advantage, it is only necessary that the environment of the colonizing habitat is female-biasing at the time of colonization; any environmental change between the time of initial colonization and subsequent dispersal can allow the colonization advantage to be maintained over successive colonization events.

Effects of temporal sex ratio variance on population establishment

We found that among-generation sex ratio variation generally reduced the level of population establishment. This result is concordant with Bull (1983), who showed that sex ratio variance over time can favour the evolution of GSD from ESD. The effect can be attributed to the reduction in mean fitness of lineages that exhibit intergenerational variation in productivity (Yoshimura & Jansen, 1996). Because the fitness of a lineage is dependent on its geometric mean fitness, a population that alternatively produces sex ratios of 0.6 and 0.4 of every other generation will decrease in size relative to a population that consistently produces 50% females. However, the impact of the reduction in population establishment resulting from low to moderate among-generation sex ratio variation was generally smaller than impact of the increase in population establishment resulting from among-population variation, as populations exhibiting the same level of both sources of variance exhibited higher establishment than GSD populations. Thus, ESD is expected to be favourable unless the temporal sex ratio variation substantially exceeds the spatial variation. It is unlikely that high levels of among-generation sex ratio variation are found in ESD species, because such species would be commonly prone to extinction. Among-generation sex ratio variation will be particularly low in long-lived species, as yearly variation in the environment has been shown to have a negligible effect on sex ratios over entire multi-year generations (Bull & Bulmer, 1989).

In contrast to the effects of among-generation sex ratio variance, sex ratio variation over periods of several generations resulted in substantially higher population establishment than in populations with no sex ratio variance (Table 2). The occurrence of multiple periods of female-biased sex ratios following the initial colonization event created several consecutive female-biased generations and allowed fledgling populations to achieve a healthy population size in some populations. The long periods of biased sex ratios essentially create spatial variance in the sex ratio that lasts long enough to provide an advantage to many ESD populations. Conversely, when sex ratios varied every generation, there was a negligible opportunity for an extended period of

consecutive female-biased generations. Thus, when temporal environmental changes affect sex ratios over time in ESD species, the time span of the sex ratio shift affects the probability of population establishment; the direction of the effect changes with increasing time between sex ratio shifts.

Our results indicate that ESD can provide an advantage in the establishment of colonizing populations, but it is also important to consider the long-term implications on population persistence. In simulations examining a colonizing GSD species entering a resident population of an ESD species exhibiting only among-generation variation in sex ratios, the GSD population excluded the resident ESD population only when among-generation sex ratio variation was high. As noted above, there are characteristics of ESD populations that make high levels of among-generation sex ratio variation unlikely. Nonetheless, it is important to note that the advantage conferred by sex ratio variation on ESD species pertains to initial establishment, and in certain cases, some of these established populations may be susceptible to subsequent colonization attempts themselves.

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