

Evolution of the sex ratio and effective number under gynodioecy and androdioecy

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Abstract

We analyze dynamic models of the evolution of androdioecy and gynodioecy under autosomal
3 modifiers of weak effect. In our zygote control models, the sex expressed by a zygote depends
on its own genotype, while in our maternal control models, the sex expressed by a zygote
depends on the genotype of its maternal parent. Our study addresses the Li-Price equation,
6 which for all its heuristic appeal, describes evolutionary change over a single generation. Our
analysis unifies full multi-dimensional local stability analysis with the Li-Price equation by
identifying a point in the neighborhood of a fixation state from which a single-generation
9 step indicates the asymptotic behavior of a rare, introduced allele initiated at an arbitrary
location near the fixation state. We incorporate our theoretical analysis into our previously-
developed Bayesian inference framework to develop a new method for inferring the viability
12 of gonochores (males or females) relative to hermaphrodites. Applying this approach to
microsatellite data derived from natural populations of the gynodioecious plant *Schiedea*
salicaria and the androdioecious killifish *Kryptolebias marmoratus*, we find that while fe-
15 male and hermaphrodite *S. salicaria* appear to have similar viabilities, male *K. marmoratus*
appear to survive to reproductive age at less than half the rate of hermaphrodites.

Keywords:

18 sex ratio evolution, gynodioecy, androdioecy, effective population size, Li-Price equation

1 Introduction

21 Changes in the breeding system and effective number induce genome-wide transformations of
the context in which evolution operates. Here, we address the evolution of effective number
under androdioecy and gynodioecy. This analysis seeks to unify questions regarding evolu-
24 tionary stability (Maynard Smith and Price 1973) of the sex ratio, the nature of heritability
as defined within the Li-Price framework (Li 1967; Price 1970), and the evolution of effective
number.

1.1 Effective number

27 **Relative effective number:** Wright (1931) introduced the notion of effective number
in the context of generalizing fundamental aspects of evolutionary change to populations
structured by sex, fluctuations through time in numbers of individuals, or other factors. In
30 their analysis of the concept, Ewens (1982) and Crow and Denniston (1988) showed that
the various definitions give rise to different expressions for effective number in even simple
models.

33 Let N_H and N_G respectively denote the effective number of hermaphrodites and gono-
chore (males or females) among reproductives. We refer to the probability that a pair of
autosomal genes randomly sampled from distinct reproductives in the present (offspring)
36 generation derive from the same reproductive in the preceding (parental) generation as the
rate of parent-sharing ($1/N_P$):

$$\frac{1}{N_P} = \frac{C^2}{N_H} + \frac{(1-C)^2}{N_G}. \quad (1)$$

for C the probability that an autosomal gene randomly sampled from a reproductive in the
39 offspring generation derives from a hermaphroditic parent. Here, we treat as equivalent the
interpretation that C represents the collective contribution to the offspring generation from
hermaphrodites in the parental generation. Descent of the sampled genes from the same
42 hermaphrodite entails that both derive from hermaphrodites (with probability C^2) and from
the same individual (with probability $1/N_H$). Similarly, the second term on the right side
of (1) corresponds to the descent of the gene pair from the same gonochore. Crow and
45 Denniston (1988) designated the inverse of the rate of parent-sharing (N_P) as “inbreeding
effective size.”

Redelings *et al.* (2015) defined relative effective number (R) as the ratio of inbreeding
48 effective size and the total effective number of reproductives ($N = N_G + N_H$):

$$R = \frac{N_P}{N}. \quad (2)$$

From (1), we obtain

$$\begin{aligned} R &= \frac{N_P}{N_H + N_G} = \frac{1}{\frac{C^2}{h} + \frac{(1-C)^2}{1-h}} \\ &= \frac{h(1-h)}{h(1-h) + (h-C)^2}, \end{aligned} \quad (3)$$

for h the proportion of hermaphrodites among reproductives:

$$h = \frac{N_H}{N_G + N_H}. \quad (4)$$

Clearly, relative effective number cannot exceed unity ($R \leq 1$), attaining unity only for

$$h = C, \quad (5)$$

51 at which the proportion of hermaphrodites among reproductives (h) is identical to C , the
probability that a random gene sampled from reproductives derives from a hermaphrodite
in the parental generation. Both (1) and (2) differ conceptually and quantitatively from
54 indices proposed by Laporte *et al.* (2000), who explored effective number in gynodioecious
populations. That distinct concepts of effective number exist is not unexpected under even
the most basic forms of population structure, including sex (Ewens 1982; Crow and Denniston
57 1988).

Empirical observations: Redelings *et al.* (2015) developed a Bayesian method for
the estimation of the rate of self-fertilization in pure hermaphrodite, gynodioecious, and
60 androdioecious populations. It provides a means of inferring all model parameters, including
the determinants of relative effective number R (2).

Figure 1 presents posterior distributions of R (2) for the three data sets studied by
63 Redelings *et al.* (2015), including those derived from two populations of the androdioecious
killifish *Kryptolebias marmoratus* (Mackiewicz *et al.* 2006; Tatarenkov *et al.* 2012). An
intriguing empirical observation is the near-maximization of relative effective number R in
66 all three populations. A primary question motivating the present study is whether this
apparent skewing reflects adaptive evolution of the sex ratio.

1.2 Reproductive value

69 Fisher (1958) explored the evolutionary modification of the sex ratio under gonochorism,
with N_f females and N_m males participating in reproduction. Under the assumption that
reproduction is limited by the number of females, the total number of zygotes is proportional
72 to N_f and the *reproductive value* of a male relative to a female corresponds to N_f/N_m . Under
gonochorism, males and females make equal collective contributions at each autosomal locus,
which then implies that autosomal modifiers evolve toward equal investment in male and
75 female offspring (Fisher 1958). Edwards (2000) provides an account of the origins of this
insight.

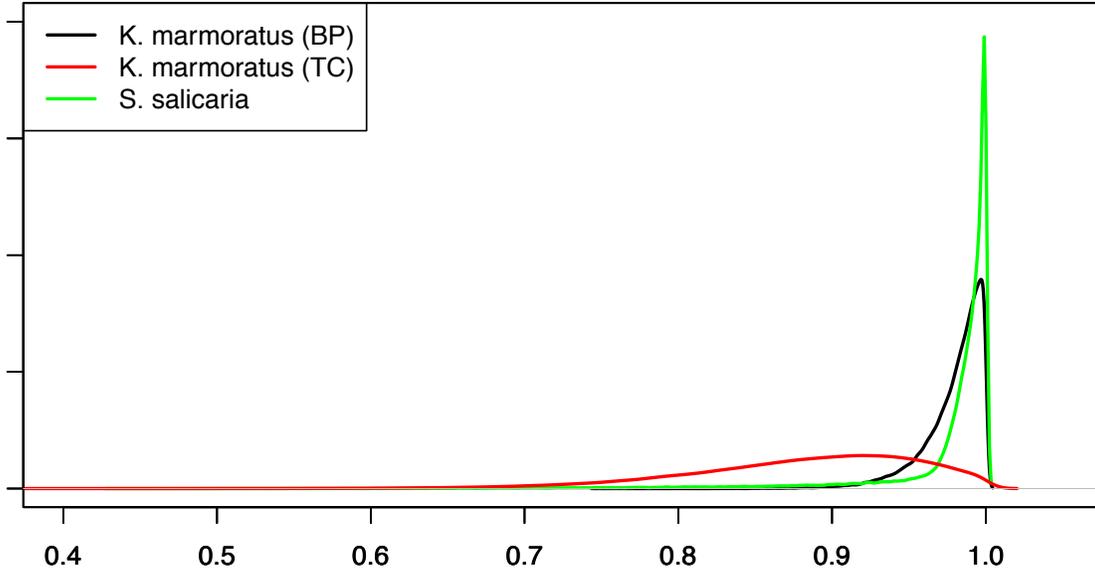


Figure 1: Posterior distributions of relative effective number R (2).

The evolution of the sex ratio has also been addressed in the context of the marginal
 78 value of parental investment in offspring of each sex (*e.g.*, Shaw and Mohler 1953; Lloyd
 1975; Charnov *et al.* 1976). Increased investment in the sex with the highest marginal value
 affords increased transmission to the grandoffspring generation. For sexual forms corre-
 81 sponding to hermaphrodites and gonochores, the per capita contribution of hermaphroditic
 offspring to the grandoffspring generation corresponds to C/N_H , reflecting the partitioning
 among N_H reproductive hermaphrodites of the collective contribution to the gene pool by
 84 hermaphrodites (1). The marginal value of investing in hermaphroditic offspring exceeds the
 marginal value of investing in gonochorous offspring only if

$$\frac{C}{N_H} > \frac{Z(1-C)}{N_G}, \quad (6)$$

for Z the expected number of gonochores of reproductive age that can be produced with the
 87 investment required to produce a single hermaphrodite of reproductive age. In this context,
 the reproductive value of a sex is proportional to a ratio of marginal values.

An evolutionarily stable strategy (ESS, Maynard Smith and Price 1973) corresponds to
 90 an investment allocation against which no other allocation can increase when rare. Equal
 marginal value among mating types implies that all investment strategies give equal returns.
 Candidate ESS hermaphrodite proportions (h^*) among offspring at reproductive age (Adults
 93 in Table 1) correspond to points of equality between the marginal values of hermaphrodites
 and gonochores:

$$\frac{h^*}{1-h^*} = \frac{C}{Z(1-C)} \quad (7a)$$

(a rearrangement of (6), using (4)). If the departure of the relative cost of a hermaphrodite
 96 (Z) from unity derives entirely from differential viability of gonochorous and hermaphroditic

offspring between their conception and attainment of reproductive age, this candidate ESS corresponds to a sex ratio among offspring at conception (Zygotes in Table 1) of

$$\frac{\hat{h}}{1 - \hat{h}} = \frac{C}{1 - C}. \quad (7b)$$

99 A candidate hermaphrodite proportion would in fact correspond to an ESS only if any
rare modifier of the sex ratio fails to increase at a geometric rate in a monomorphic popula-
102 tion exhibiting the candidate sex ratio. Further, \hat{h} would correspond to an ESS that is locally
attracting in parameter space if rare autosomal enhancers of hermaphrodite production in-
vade a population with hermaphrodite proportion h_c only if $h_c < \hat{h}$ and suppressors invade
only if $h_c > \hat{h}$. Such an investment allocation has been described as a continuously stable
105 strategy (Eshel and Motro 1981) or as showing m -stability (Taylor 1989) or convergence
stability (Christiansen 1991).

1.3 Analytical and empirical exploration

108 Here, we address evolutionarily stable strategies for the sex ratio in androdioecious and gyn-
odioecious populations and its implications for effective number. We then apply this theoret-
ical framework to empirical observations to infer Z (6), the relative viability of gonochores, in
111 natural populations of the androdioecious *Kryptolebias marmoratus* and the gynodioecious
Schiedea salicaria.

Evolution of the sex ratio: Among the central questions regarding the evolution of
114 breeding systems is the nature of Darwinian fitness in this context. Reproductive success of
an individual may depend not only on its own sex expression but on the sex expression of
other members of the present or descendant populations. Numerous authors have explored
117 definitions of Darwinian fitness under androdioecy and gynodioecy (Ross and Weir 1975;
Lloyd 1975; Charlesworth and Charlesworth 1978). An alternative approach, and the one
we have adopted here, entails modeling the genetic dynamics without appeal to an external
120 definition of fitness (Ross and Weir 1975, 1976; Wolf and Takebayashi 2004).

While previous work has explored short-term change in the frequencies of major genes,
our analysis addresses long-term change in parameter space (Eshel and Motro 1981; Tay-
123 lor 1989; Christiansen 1991) by means of mutations of minor effect arising at modifier loci
across the genome. Sex expression in the androdioecious killifish *Kryptolebias marmoratus*
in particular reflects epigenetic regulation of genes throughout the genome in response to
126 temperature and other variables. Ellison *et al.* (2016) studied methylation patterns in brain
tissue isolated from fish derived from eggs incubated at controlled temperatures, demonstrat-
ing significant genome-wide differences due to multiple factors, including sex, temperature,
129 and laboratory strain. In addition to candidates for major sex determination genes, loci
showing responses in methylation levels included amplified fragment length polymorphism
regions across the genome. These observations are consistent with the conceptual framework
132 of our models, which envisions many loci with the potential to influence sex expression in

response to temperature and other factors. Whether enhancement of gonochore development by a particular allele is advantageous depends on genome-wide expression patterns.

135 Our central theoretical result for the evolution of androdioecy and gynodioecy under both zygote and maternal control of sex expression is that the current population resists invasion of a mutation of weak effect at a modifier locus only if

$$(h - \hat{h})(\alpha_0 - \alpha_1) > 0, \quad (8)$$

138 for h the sex expression level of the population prior to the introduction of the mutation, \hat{h} the candidate ESS sex expression level (Section 2.1), and $(\alpha_0 - \alpha_1)$ the average effect of substitution of the new mutation inferred from the Li-Price approach extended to inbreeding
141 (Section 2.2). This expression signifies that the population resists the introduction of a new mutation if the current sex expression level exceeds the ESS ($(h - \hat{h}) > 0$) and the average effect of the mutation would raise the sex expression level even further ($(\alpha_0 - \alpha_1) > 0$), or if
144 both conditions are reversed.

Estimation of relative viability: Merging our theoretical analysis with a previously-developed Bayesian inference framework (Redelings *et al.* 2015), we develop a new method
147 for inferring the viability of gonochores (males or females) relative to hermaphrodites.

Central to both reproductive value (Fisher 1958) and effective number (Wright 1931) is the collective reproductive contribution of a sex. Figure 2 presents posterior distributions of
150 C (1), the collective contribution of hermaphrodites, inferred from the three microsatellite data sets analyzed by Redelings *et al.* (2015). In the androdioecious killifish *Kryptolebias marmoratus*, hermaphrodites collectively contribute a substantially greater proportion of the
153 population gene pool in the more highly inbred BP population than in the TC population. In *Schiedea salicaria*, the collective contribution of females (male-steriles) lies close to the population proportion of females of 12% reported by Campbell *et al.* (2010).

156 Attainment of the presumptive ESS sex ratio (7) implies maximization of relative effective number (2) only if gonochores and hermaphrodites have equal viability ($Z = 1$). The departure from unity of relative effective number provides a basis for inferring the relative
159 viability of gonochores (Z). Under the assumption that the natural populations under study have in fact evolved to the ESS sex ratio at conception, we use the Bayesian sampler of Redelings *et al.* (2015) to obtain posterior densities for the relative viability of gonochores (Z)
162 in *Kryptolebias marmoratus* and *Schiedea salicaria*. Our results suggest that *K. marmoratus* males have significantly lower viability than hermaphrodites in populations with both high (TC) and low (BP) frequencies of males.

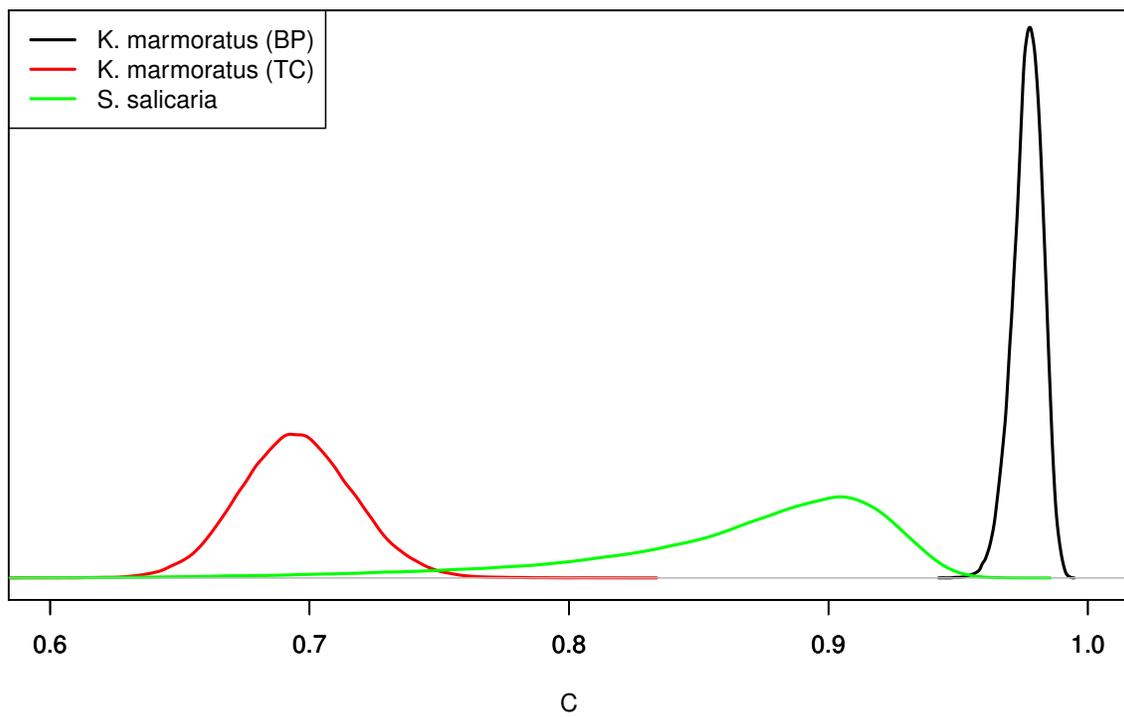


Figure 2: Posterior distributions of the collective contribution of hermaphrodites to the population gene pool (C) for two populations of androdioecious *Kryptolebias marmoratus* and for gynodioecious *Schiedea salicaria*.

165 2 Methods

2.1 Candidate ESS sex expression levels

We derive candidate ESS values under zygote and maternal control of sex expression in
 168 populations comprising N_H hermaphrodites and N_G gonochores (males or females). These
 candidate ESS levels extend those proposed by Lloyd (1975). Our full local stability analysis
 (Section 3) demonstrates that these candidates do in fact correspond to continuously stable
 171 strategies.

Life cycle: Table 1 summarizes offspring production by maternal parents through the
 major phases of the life cycle. In the androdioecy models, all maternal parents are her-
 174 maphroditic. In the gynodioecy models, females produce offspring at rate $\tilde{\sigma}$ relative to
 hermaphrodites ($\tilde{\sigma}$ corresponds to σ in Redelings *et al.* 2015). A proportion \tilde{s} of egg cells
 177 produced by hermaphrodites are self-fertilized (uniparental) and all egg cells produced by
 females are outcrossed (biparental). Inbreeding depression occurs between the zygote and
 juvenile stages, with uniparental offspring (“Uni”) surviving to the juvenile stage at rate
 τ relative to biparental offspring (“Bi”). Under a rescaling at the juvenile stage, a female

Table 1
 Offspring production

Maternal Parent	Life Stage		
	Zygotes	Juveniles	Adults
Hermaphrodite	Uni	\tilde{s}	$s = \frac{\tilde{s}\tau}{\tilde{s}\tau+1-\tilde{s}}$
	Bi	$1 - \tilde{s}$	$1 - s = \frac{1-\tilde{s}}{\tilde{s}\tau+1-\tilde{s}}$
Female	Bi	$\tilde{\sigma}$	$\sigma = \frac{\tilde{\sigma}}{\tilde{s}\tau+1-\tilde{s}}$

180 has an average of σ surviving offspring relative to a hermaphrodite and a proportion s of
 the surviving offspring of a hermaphrodite are uniparental. Sex-specific viability selection
 occurs between the juvenile and adult stages, with gonochores (males or females) surviving
 183 to reproductive age at rate Z relative to hermaphrodites, irrespective of whether they are
 uniparental or biparental.

Our full dynamical models depict evolving autosomal modifiers of sex expression. In
 186 contrast, derivation of the ESS values assumes the absence of heritable variation in sex
 expression: for example, upon the fixation of a modifier allele that induces the ESS sex
 ratio. Under this assumption, offspring sex (gonochore or hermaphrodite) is independent of
 189 parental sex and independent of the level of inbreeding. Accordingly, the relative proportions
 of uniparental and biparental offspring (s and σ in Table 1) are identical at the juvenile and
 adult stages and the sex ratio among zygotes is identical to the sex ratio among juveniles.

192 **Androdioecy:** Under androdioecy (N_G males and N_H hermaphrodites), outcrossing en-
tails fertilization of egg cells from the pollen cloud, to which female-sterile (male) individuals
contribute at rate ω relative to hermaphrodites. In accordance with the laboratory experi-
195 ments of Furness *et al.* (2015) on *Kryptolebias marmoratus*, our *Kryptolebias* model imposes
the additional assumption that all biparental individuals have a male parent ($\omega = \infty$).

Under androdioecy, all egg cells derive from hermaphrodites, with a proportion \tilde{s} of those
198 egg cells fertilized by self-pollen. The uniparental proportion among juveniles,

$$s_A = \frac{\tilde{s}\tau}{\tilde{s}\tau + 1 - \tilde{s}}, \quad (9)$$

is independent of the population sex ratio.

The probability that an autosomal gene randomly sampled from juvenile offspring (Table
1) derives from a hermaphrodite in the parental generation corresponds to

$$C_A = 1 - (1 - s_A)G_A/2,$$

in which G_A reflects the relative contribution of males of the parental generation to the
201 pollen pool:

$$G_A = \frac{\omega N_G}{\omega N_G + N_H} = \frac{\omega(1-h)}{\omega(1-h) + h}, \quad (10)$$

for $(1-h)$ the frequency of males among reproductives in the parental generation (4). In the
Kryptolebias model, in which all biparental offspring have a male parent ($G_A = 1, \omega = \infty$),
the collective contribution of hermaphrodites reduces to

$$C_A = 1 - (1 - s_A)/2 = (1 + s_A)/2.$$

As indicated in our exposition of the life cycle (Table 1), the absence of heritable genetic
variation for sex expression (*e.g.*, at a genetically monomorphic ESS state) implies that the
204 uniparental proportion s_A is identical at the juvenile and adult stages. At such an ESS
state, C_A corresponds to the probability that a random autosomal gene sampled at either
the juvenile or the adult stage derives from a hermaphrodite in the preceding generation.

Candidate ESS sex ratios at reproductive age (7) satisfy

$$\frac{h^*}{1-h^*} = \frac{1 - (1 - s_A)/2 \left[\frac{\omega(1-h^*)}{\omega(1-h^*) + h^*} \right]}{Z(1 - s_A)/2 \left[\frac{\omega(1-h^*)}{\omega(1-h^*) + h^*} \right]}.$$

207 Solving, we obtain candidates for the unbeatable sex ratio at reproduction under androdi-
oecy:

$$\frac{h_A^*}{1-h_A^*} = \begin{cases} \frac{\omega(1+s_A)/2}{Z\omega(1-s_A)/2-1} & \text{if (11b) holds} \\ \infty & \text{otherwise.} \end{cases} \quad (11a)$$

Maintenance of androdioecy ($0 < h_A^* < 1$) requires that the expected contribution of a
210 juvenile male to the subsequent generation exceed that of a juvenile hermaphrodite by at
least twofold:

$$Z\omega(1 - s_A) > 2. \quad (11b)$$

This condition becomes more stringent as the rate of outcrossing ($1 - s_A$) or the relative
 213 viability of males (Z) decline. If (11b) fails, the sole candidate ESS corresponds to pure
 hermaphroditism ($h_A = 1$).

At the juvenile (rather than adult) stage, the candidate ESS (11a) corresponds to a sex
 216 ratio of

$$\frac{\hat{h}_A}{1 - \hat{h}_A} = \begin{cases} \frac{Z\omega(1+s_A)/2}{Z\omega(1-s_A)/2-1} & \text{if (11b) holds} \\ \infty & \text{otherwise.} \end{cases} \quad (11c)$$

indicating that the composite parameter $Z\omega$ represents the net effects on the ESS of differen-
 tial viability and pollen success of males. Appendix A describes conditions under which the
 219 unbeatable sex ratio proposed by Lloyd (1975) corresponds to our non-zero ESS candidate
 (11).

Gynodioecy: Under gynodioecy (N_G females and N_H hermaphrodites), females set
 seeds at rate $\tilde{\sigma}$ relative to hermaphrodites (Table 1). An autosomal gene randomly sampled
 from a juvenile offspring derives from a hermaphrodite parent with probability

$$\begin{aligned} C_G &= \frac{N_G\tilde{\sigma}/2 + N_H(\tau\tilde{s} + 1 - \tilde{s})}{N_G\tilde{\sigma} + N_H(\tau\tilde{s} + 1 - \tilde{s})} \\ &= \frac{(1 - h)\sigma/2 + h}{(1 - h)\sigma + h} \end{aligned} \quad (12)$$

for h the proportion of hermaphrodites among parents in the preceding generation (4) and
 σ the scaled seed fertility of females (Table 1). This expression also corresponds to

$$C_G = 1 - (1 - s_G)G_G/2,$$

for the uniparental proportion among juveniles given by

$$s_G = \frac{N_H\tau\tilde{s}}{N_G\tilde{\sigma} + N_H(\tau\tilde{s} + 1 - \tilde{s})} = \frac{hs}{(1 - h)\sigma + h}, \quad (13)$$

222 and the proportion of biparental offspring that have a female parent by

$$G_G = \frac{N_G\tilde{\sigma}}{N_G\tilde{\sigma} + N_H(1 - \tilde{s})} = \frac{(1 - h)\sigma}{(1 - h)\sigma + h(1 - s)}. \quad (14)$$

In contrast with androdioecy (9), the uniparental fraction s_G (13) depends on the population
 sex ratio. Once again, at a monomorphic ESS (absence of heritable genetic variation for sex
 225 expression), the uniparental proportion among offspring of reproductive age is identical to
 s_G among juvenile offspring.

From (7) and (12), the candidate ESS at reproductive age corresponds to

$$h = \frac{(1 - h)\sigma/2 + h}{(Z + 1)(1 - h)\sigma/2 + h}.$$

Solving, we obtain candidates for the unbeatable sex ratio under gynodioecy:

$$\frac{h_G^*}{1 - h_G^*} = \begin{cases} \frac{\sigma}{Z\sigma - 2} & \text{if (15b) holds} \\ \infty & \text{otherwise.} \end{cases} \quad (15a)$$

228 Maintenance of gynodioecy ($0 < h_G^* < 1$) requires that the expected number of offspring produced by a juvenile female exceed that of a juvenile hermaphrodite by at least twofold:

$$Z\sigma > 2. \quad (15b)$$

231 More intense inbreeding depression (smaller τ) and higher female viability or fertility (larger Z or $\tilde{\sigma}$) tend to promote gynodioecy. For cases in which (15b) fails, the sole candidate ESS corresponds to pure hermaphroditism ($h_G^* = 1$).

At the juvenile stage (Table 1), the candidate ESS (15a) corresponds to

$$\frac{\hat{h}_G}{1 - \hat{h}_G} = \begin{cases} \frac{Z\sigma}{Z\sigma - 2} & \text{if (15b) holds} \\ \infty & \text{otherwise,} \end{cases} \quad (15c)$$

234 with composite parameter $Z\sigma$ comprising the net effects on the ESS of differential viability and seed set of females. As in the androdioecy case (11), our non-zero ESS candidate (15) corresponds to the unbeatable sex ratio proposed by Lloyd (1975) under the conditions
237 described in Appendix A.

2.2 Li-Price framework

240 Li (1967) and Price (1970) expressed the one-generation change in the frequency of an allele as a covariance between fitness and the frequency of the allele across genotypes. Here, we extend this framework to the evolution of effective number and sex ratio in inbred populations.

Table 2 presents measures associated with genotypes at a biallelic autosomal locus. In the population, genotypes AA , Aa , and aa occur in frequencies u_0 , u_1 , and u_2 ($\sum_i u_i = 1$). The locus may influence the expression of a trait, with genotype i associated with trait deviation ($P_i - \bar{P}$), in which the average value of the trait corresponds to

$$\bar{P} = \sum_i u_i P_i.$$

243 Price (1970) defined the fitness of genotype i as proportional to the number of gametes transmitted to the offspring generation. In panmictic populations, in which genotypic frequencies at the point of zygote formation conform to Hardy-Weinberg proportions, this definition of fitness corresponds to the expected rate of survival to reproduction, as assumed
246 by Li (1967). Because fitness in the present context may include various components, we

Table 2
Phenotypic and genetic values

	Genotypes		
	<i>AA</i>	<i>Aa</i>	<i>aa</i>
Frequency	u_0	u_1	u_2
Trait deviation	$P_0 - \bar{P}$	$P_1 - \bar{P}$	$P_2 - \bar{P}$
Additive genotypic value	$2\alpha_0$	$\alpha_0 + \alpha_1$	$2\alpha_1$
Fitness deviation	$T(u'_0 - u_0)/u_0$	$T(u'_1 - u_1)/u_1$	$T(u'_2 - u_2)/u_2$

here define the fitness of genotype i as the ratio of numbers of individuals of genotype i at the same point in the life cycle in consecutive generations:

$$W_i = \frac{Tu'_i}{u_i}, \quad (16)$$

249 for the prime representing the next generation forward in time. Here, T converts the ratio
of frequencies (u'/u) to the ratio of numbers of individuals; in fully-specified genetic models
(Section 2.3), T denotes the normalizer that ensures that gene and genotypic frequencies
252 sum to unity. Denniston (1978) observed that (16) departs from more conventional notions
of fitness: high genotypic fitness reflects high production *of* the genotype rather than *by* the
genotype. Under this definition, fitness is virtually always frequency-dependent: even for
255 the most basic model of constant viability selection, (16) ceases to change only at equilibria
($u'_i = u_i$).

To genotypes AA , Aa , and aa , we associate additive genotypic values $2\alpha_0$, $\alpha_0 + \alpha_1$,
258 and $2\alpha_1$. Much previous work, designed for panmictic populations, has defined additive
genotypic value as the frequency of allele A in a genotype (Li 1967; Price 1970). Here,
we use the definition of Fisher (1941), under which the additive effects α_i are obtained by
261 minimizing the mean squared deviation (MSD) of the phenotype from the additive genotypic
value across genotypes:

$$\text{MSD} = u_0[P_0 - \bar{P} - 2\alpha_0]^2 + u_1[P_1 - \bar{P} - (\alpha_0 + \alpha_1)]^2 + u_2[P_2 - \bar{P} - 2\alpha_1]^2. \quad (17)$$

For general systems of mating, the *average effect* of substitution (Fisher 1941), the expected
264 effect on the trait of substituting allele A for allele a , corresponds to

$$\begin{aligned} \alpha_0 - \alpha_1 &= \frac{2u_0(P_0 - \bar{P}) + u_1(P_1 - \bar{P})}{4p(1-p) - u_1} \\ &= \frac{F(P_0 - P_2) + (1-F)[p(P_0 - P_1) + (1-p)(P_1 - P_2)]}{1+F}, \end{aligned} \quad (18)$$

for p representing the frequency of allele A ($p = u_0 + u_1/2$) and F the fixation index (Wright 1933). In the additive case, in which

$$(P_0 - P_2) = 2(P_1 - P_2),$$

the average effect reduces to

$$\alpha_0 - \alpha_1 = (P_1 - P_2),$$

irrespective of the magnitude of F .

Using the definitions summarized in Table 2, we obtain the covariance across genotypes
267 between fitness W (16) and additive genotypic value G_α with respect to the trait:

$$\begin{aligned} \text{Cov}(WG_\alpha) &= u_0 \frac{T(u'_0 - u_0)}{u_0} 2\alpha_0 + u_1 \frac{T(u'_1 - u_1)}{u_1} (\alpha_0 + \alpha_1) + u_2 \frac{T(u'_2 - u_2)}{u_2} 2\alpha_2 \\ &= 2(\alpha_0 - \alpha_1)T\Delta p, \end{aligned} \quad (19)$$

in which Δp represents the change in frequency of allele A over a single generation. This
expression indicates that the frequency of the A allele increases ($\Delta p > 0$) if either (1)
270 its average effect of substitution on the trait is positive ($(\alpha_0 - \alpha_1) > 0$) and the trait is
positively correlated with fitness ($\text{Cov}(WG_\alpha) > 0$) or (2) its average effect of substitution
on the trait is negative ($(\alpha_0 - \alpha_1) < 0$) and the trait is negatively correlated with fitness
273 ($\text{Cov}(WG_\alpha) < 0$). To address Fisher's (1930) fundamental theorem of natural selection, Li
(1967) and Price (1970, 1971) assigned the trait of interest as fitness itself, in which case the
covariance $\text{Cov}(WG_\alpha)$ reduces to the additive variance in fitness.

For all its heuristic appeal, the Li-Price equation (19) provides a one-dimensional de-
276 scription of evolutionary change across a single generation. In the present context, the trait
of interest corresponds to the long-term evolution of sex expression in a multi-dimensional
279 state space. Unless sex expression is uncorrelated with fitness ($\text{Cov}(WG_\alpha) = 0$) or the focal
modifier locus has no additive variance with respect to this trait ($(\alpha_0 - \alpha_1) = 0$), natural
selection will induce genetic change. Because both the average effect of substitution (18)
282 and the covariance $\text{Cov}(WG_\alpha)$ depend on genotypic frequencies in the general case, the re-
lationship between the one-generation description provided by (19) and the outcome of the
evolutionary process needs clarification.

Key to the application of the Li-Price framework to the evolution of sex expression is the
285 elucidation of the component of the population to which the genotypic frequencies (u_i) in
Table 2 correspond. In the present context, populations may comprise both gonochores and
288 hermaphrodites, and sex expression in a zygote depends on either its own genotype or the
genotype of its maternal parent. This genotypic distribution (u_i) defines both the average
effect of substitution (18) and heritability for the evolutionary process under study.

291 2.3 Dynamic models of sex ratio evolution

We address two genetic mechanisms for the determination of sex expression. In the zygote
control models, zygotes of genotypes AA , Aa , and aa respectively develop into hermaphro-
294 dites at rates h_0 , h_1 , and h_2 ($0 \leq h_i \leq 1, i = 0, 1, 2$), with the remaining zygotes developing
into gonochores. In the maternal control models, it is the genotype of the maternal parent
of the zygotes that determines sex expression rates.

297 Hermaphrodites set a proportion \tilde{s} of seeds by self-fertilization. Uniparental offspring
survive to reproduction at rate τ relative to biparental offspring, with this differential survival
occurring immediately upon zygote formation, even before sex expression.

300 2.3.1 Zygotic control of sex expression

Following differential survival of uniparental and biparental offspring (but before sex expres-
sion and reproduction by the offspring), genotypes AA , Aa , and aa occur in proportions z_0 ,
303 z_1 , and z_2 ($z_0 + z_1 + z_2 = 1$).

Androdioecy: In the next generation forward in time, genotypic frequencies correspond
to

$$\begin{aligned} z'_0 &\propto \tilde{s}\tau(z_0h_0 + z_1h_1/4) + (1 - \tilde{s})(z_0h_0 + z_1h_1/2)q \\ z'_1 &\propto \tilde{s}\tau z_1h_1/2 + (1 - \tilde{s})[(z_0h_0 + z_1h_1/2)(1 - q) + (z_1h_1/2 + z_2h_2)q] \\ z'_2 &\propto \tilde{s}\tau(z_1h_1/4 + z_2h_2) + (1 - \tilde{s})(z_1h_1/2 + z_2h_2)(1 - q), \end{aligned}$$

for q denoting the frequency of the A allele in the pollen pool:

$$q = \frac{h_0z_0 + h_1z_1/2 + \omega Z[(1 - h_0)z_0 + (1 - h_1)z_1/2]}{h_0z_0 + h_1z_1 + h_2z_2 + \omega Z[(1 - h_0)z_0 + (1 - h_1)z_1 + (1 - h_2)z_2]}. \quad (20a)$$

These expressions imply

$$\begin{aligned} Tz'_0 &= s_A(z_0h_0 + z_1h_1/4) + (1 - s_A)(z_0h_0 + z_1h_1/2)q \\ Tz'_1 &= s_A z_1h_1/2 + (1 - s_A)[(z_0h_0 + z_1h_1/2)(1 - q) + (z_1h_1/2 + z_2h_2)q] \\ Tz'_2 &= s_A(z_1h_1/4 + z_2h_2) + (1 - s_A)(z_1h_1/2 + z_2h_2)(1 - q), \end{aligned} \quad (20b)$$

306 for s_A given in (9) and the normalizer by

$$T = h_0z_0 + h_1z_1 + h_2z_2. \quad (20c)$$

In the absence of selection on the modifier locus ($h_0 = h_1 = h_2$), recursion system (20) indicates that allele frequency in seeds and pollen ($z_0 + z_1/2 = q$) remains at its initial value, with asymptotic convergence at rate $s_A/2$ of the frequency of heterozygotes (z_1) to

$$2q(1 - q)(1 - F_{neut}),$$

for F_{neut} the fixation index (Wright 1933):

$$F_{neut} = \frac{s}{2 - s}, \quad (21)$$

with s_A substituted for s .

Gynodioecy: Genotypic frequencies in the next generation forward in time correspond to

$$\begin{aligned}
 z'_0 &\propto \tilde{s}\tau(z_0h_0 + z_1h_1/4) \\
 &\quad + \{(1 - \tilde{s})(z_0h_0 + z_1h_1/2) + \tilde{\sigma}Z[z_0(1 - h_0) + z_1(1 - h_1)/2]\}q \\
 z'_1 &\propto \tilde{s}\tau z_1h_1/2 \\
 &\quad + \{(1 - \tilde{s})(z_0h_0 + z_1h_1/2) + \tilde{\sigma}Z[z_0(1 - h_0) + z_1(1 - h_1)/2]\}(1 - q) \\
 &\quad + \{(1 - \tilde{s})(z_1h_1/2 + z_2h_2) + \tilde{\sigma}Z[z_1(1 - h_1)/2 + z_2(1 - h_2)]\}q \\
 z'_2 &\propto \tilde{s}\tau(z_1h_1/4 + z_2h_2) \\
 &\quad + \{(1 - \tilde{s})(z_1h_1/2 + z_2h_2) + \tilde{\sigma}Z[z_1(1 - h_1)/2 + z_2(1 - h_2)]\}(1 - q),
 \end{aligned}$$

309 in which q represents the frequency of the A allele in the pollen pool (which derives entirely from hermaphrodites),

$$q = \frac{h_0z_0 + h_1z_1/2}{h_0z_0 + h_1z_1 + h_2z_2}. \quad (22a)$$

After division by $(\tilde{s}\tau + 1 - \tilde{s})$, we obtain

$$\begin{aligned}
 Tz'_0 &= s(z_0h_0 + z_1h_1/4) \\
 &\quad + \{(1 - s)(z_0h_0 + z_1h_1/2) + \sigma Z[z_0(1 - h_0) + z_1(1 - h_1)/2]\}q \\
 Tz'_1 &= sz_1h_1/2 \\
 &\quad + \{(1 - s)(z_0h_0 + z_1h_1/2) + \sigma Z[z_0(1 - h_0) + z_1(1 - h_1)/2]\}(1 - q) \\
 &\quad + \{(1 - s)(z_1h_1/2 + z_2h_2) + \sigma Z[z_1(1 - h_1)/2 + z_2(1 - h_2)]\}q \\
 Tz'_2 &= s(z_1h_1/4 + z_2h_2) \\
 &\quad + \{(1 - s)(z_1h_1/2 + z_2h_2) + \sigma Z[z_1(1 - h_1)/2 + z_2(1 - h_2)]\}(1 - q),
 \end{aligned} \quad (22b)$$

312 for the normalizer corresponding to

$$T = \sum_{i=0}^2 z_i[h_i + \sigma Z(1 - h_i)]. \quad (22c)$$

In the absence of selection on the modifier locus ($h_0 = h_1 = h_2 = h$), allele frequency in seeds and pollen ($z_0 + z_1/2 = q$) remains at its initial value. Unlike the uniparental fraction s_A (9) under androdioecy, s_G (13) depends on the population sex ratio. The frequency of heterozygotes (z_1) converges asymptotically at rate $s_G/2$ (13) to

$$2q(1 - q)(1 - F_{neut}),$$

for F_{neut} given in (21) but with s_G (13) substituted for s . Selective neutrality at the modifier locus entails that the transformation (22) has an eigenvalue of unity (reflecting no changes in allele frequency) and an eigenvalue of $s_G/2$ (reflecting convergence of z_1 under inbreeding).
315

2.3.2 Maternal control of sex expression

Under the maternal control model, the genotype of the maternal parent determines sex expression in zygotes. We describe recursions in genotypic frequencies at the point of reproduction (rather than zygote formation), with genotypes AA , Aa , and aa occurring in proportions x_0 , x_1 , and x_2 in hermaphrodites and y_0 , y_1 , and y_2 in gonochores ($x_0 + x_1 + x_2 + y_0 + y_1 + y_2 = 1$).

Androdioecy: At the point of reproduction, genotypic frequencies among hermaphrodites correspond to

$$\begin{aligned} Tx'_0 &= s_A(x_0h_0 + x_1h_1/4) + (1 - s_A)(x_0h_0 + x_1h_1/2)q \\ Tx'_1 &= s_Ax_1h_1/2 + (1 - s_A)[(x_0h_0 + x_1h_1/2)(1 - q) + (x_1h_1/2 + x_2h_2)q] \\ Tx'_2 &= s_A(x_1h_1/4 + x_2h_2) + (1 - s_A)(x_1h_1/2 + x_2h_2)(1 - q), \end{aligned} \quad (23a)$$

for q the frequency of the A allele in the pollen cloud,

$$q = \frac{x_0 + x_1/2 + \omega(y_0 + y_1/2)}{x_0 + x_1 + x_2 + \omega(y_0 + y_1 + y_2)}, \quad (23b)$$

and s_A given in (9). Substitution of $Z(1 - h_i)$ for h_i in the hermaphrodite recursion Tx'_i produces the male recursion Ty'_i , which implies the normalizer

$$T = \sum_{i=0}^2 x_i[h_i + Z(1 - h_i)]. \quad (23c)$$

Because male genotypic frequencies (y_i) affect transmission only through the pollen cloud (23b), description of the transformation requires a smaller set of variables, including x_0 , x_1 , x_2 , $(y_0 + y_1/2)$, and $(y_1/2 + y_2)$.

In the absence of selection on the modifier locus ($h_0 = h_1 = h_2 = h$), the population ratio of hermaphrodites to males converges in a single generation to

$$\frac{\sum_i x'_i}{\sum_i y'_i} = \frac{h}{h + Z(1 - h)} \quad (24a)$$

and the genotypic frequencies in hermaphrodites and males are proportional:

$$\frac{x'_i}{y'_i} = \frac{h}{Z(1 - h)}. \quad (24b)$$

Accordingly, the frequencies of allele A among hermaphrodites ($x_0 + x_1/2$), males ($y_0 + y_1/2$), and pollen (q) converge to equality in a single generation,

$$q' = \frac{x'_0 + x'_1/2}{\sum_i x'_i} = \frac{y'_0 + y'_1/2}{\sum_i y'_i},$$

333 and attain their common equilibrium value in two generations,

$$p = \frac{x_0 + x_1/2}{\sum_i x_i} (1 + s_A)/2 + q(1 - s_A)/2, \quad (25)$$

in which the uniparental proportion s_A is given in (9) and x_i and q represent the initial values of those variables. The frequency of heterozygotes converges asymptotically, at rate $s_A/2$, to

$$x_1 + y_1 = 2p(1 - p)(1 - F_{neut}),$$

for p given in (25) and F_{neut} in (21), with s_A (9) substituted for s .

336 Near the state of fixation of the a allele, the neutral transformation has a single eigenvalue of unity (corresponding to allele frequency), a single eigenvalue of $s_A/2$ (governing convergence of the frequency of heterozygotes to the value dictated by F_{neut} and allele frequency), and two eigenvalues of zero (representing the near-instantaneous convergence to equality of allele frequencies in hermaphrodites, males, and pollen).
339

Gynodioecy: Genotypic frequencies in the next generation forward in time correspond to

$$\begin{aligned} Tx'_0 &= s(h_0x_0 + h_1x_1/4) + q[(1 - s)(h_0x_0 + h_1x_1/2) + \sigma(h_0y_0 + h_1y_1/2)] \\ Tx'_1 &= sh_1x_1/2 + (1 - s)[(1 - q)(h_0x_0 + h_1x_1/2) + q(h_1x_1/2 + h_2x_2)] \\ &\quad + \sigma[(1 - q)(h_0y_0 + h_1y_1/2) + q(h_1y_1/2 + h_2y_2)] \\ Tx'_2 &= s(h_1x_1/4 + h_2x_2) + (1 - q)[(1 - s)(h_1x_1/2 + h_2x_2) + \sigma(h_1y_1/2 + h_2y_2)] \end{aligned} \quad (26a)$$

342 for q the frequency of A in the pollen cloud (to which hermaphrodites alone contribute):

$$q = \frac{x_0 + x_1/2}{x_0 + x_1 + x_2}. \quad (26b)$$

Similar to the androdioecy model, the Ty'_i have the same form as Tx'_i , but with h_i replaced by $Z(1 - h_i)$, which implies

$$T = \sum_{i=0}^2 (x_i + \sigma y_i)[h_i + Z(1 - h_i)]. \quad (26c)$$

In the absence of selection on the modifier locus ($h_0 = h_1 = h_2 = h$), the population converges in a single generation to the state (24), with the y_i now representing genotypic frequencies in females. Frequencies of allele A among hermaphrodites, females, and pollen in the first generation correspond to

$$\begin{aligned} q' &= \frac{x'_0 + x'_1/2}{\sum_i x'_i} = \frac{y'_0 + y'_1/2}{\sum_i y'_i} \\ &= \frac{(x_0 + x_1/2) + (y_0 + y_1/2)\sigma + \sigma \sum_i y_i \left(\frac{x_0 + x_1/2}{\sum_i x_i} - \frac{y_0 + y_1/2}{\sum_i y_i} \right) / 2}{\sum_i (x_i + y_i\sigma)}, \end{aligned}$$

for the x_i and y_i representing genotypic frequencies at initialization, and attain their common equilibrium value in two generations. The frequency of heterozygotes converges asymptotically, at rate $s_G/2$ (13), to

$$x_1 + y_1 = 2q(1 - q)(1 - F_{neut}),$$

345 for F_{neut} given by (21), with s_G (13) substituted for s .

348 Near the state of fixation of the a allele, the neutral transformation has a single eigenvalue of unity (corresponding to allele frequency), a single eigenvalue of $s_G/2$ (governing convergence of the frequency of heterozygotes to the value dictated by F_{neut} and allele frequency), and two eigenvalues of zero (representing the convergence in two generations of allele frequencies in hermaphrodites and females to their common equilibrium value).

351 2.4 Weak selection

To explore the nature of selection on the sex ratio, we restrict most of the remaining analysis to weak selection on the modifier of the sex ratio, viewed as a perturbation from selective neutrality. Selective neutrality of the variation segregating at the focal locus entails that all 354 genotypes induce identical hermaphrodite fractions:

$$h_0 = h_1 = h_2. \quad (27)$$

Weak selection implies that differences among genotypes,

$$\begin{aligned} d_0 &= h_0 - h_2 \\ d_1 &= h_1 - h_2, \end{aligned} \quad (28)$$

357 are sufficiently small to justify treating as negligible quantities of the second or higher order in the d_i ($i = 0, 1$). This assumption of weak selection at the modifier locus implies no restriction on the magnitude of differences viability or fertility between inbred and outbred 360 offspring or between the sexes.

For each of the four models under study, we determine the conditions for local stability of the fixation of the a allele against the introduction of the A allele in small frequencies. 363 In the preceding section, we have shown that in the absence of selection on the modifier locus (27), all systems show rapid convergence to a state in which associations between genes within genotypes reflect inbreeding and associations between allele frequency and sex are absent. For each model, we enumerated the eigenvalues of the neutral transformation: a single 366 eigenvalue of unity (representing allele frequency) and a single eigenvalue of $s/2$ (reflecting asymptotic convergence of the frequency of heterozygotes), with any additional eigenvalues corresponding to zero. Because eigenvalues are continuous in complex space (*e.g.*, Serre 2010, 369 Chapter 5), the eigenvalues of the perturbed (weak-selection) transformation depart continuously in the d_i (28) from those of the neutral transformation. Accordingly, the dominant eigenvalue of the weak-selection transformation lies near unity, with the moduli of the other 372 eigenvalues remaining strictly less than unity. Because the maternal control models have

two eigenvalues of zero under neutrality, the perturbed transformation may have conjugate
375 pairs of imaginary eigenvalues. Even so, any imaginary eigenvalues do not determine asymptotic local stability because the dominant eigenvalue of a non-negative matrix corresponds to a simple, real root of the characteristic polynomial (Gantmacher 1959). Accordingly, the
378 dominant eigenvalue of the perturbed transformation lies near unity, with the moduli of the other eigenvalues remaining strictly less than unity. These properties of the weak-selection transformation imply that examination of the sign of the characteristic polynomial of the
381 local stability matrix evaluated at unity is sufficient to determine local stability.

While a full local stability analysis (including, if necessary, terms of second order in the perturbations in genotype frequencies) offers a definitive determination of the fate of
384 modifiers with weak effects on sex expression, we further undertake to elucidate the process of evolution by interpreting the results of our local stability analysis in terms of the Li-Price equation (Li 1967; Price 1970). Appendix B describes this method, which modifies an
387 approach developed previously (Uyenoyama 1988, 1991).

3 Analysis

We perform local stability analyses for each of the four multidimensional models of the evolutionary modification of sex expression in androdioecious and gynodioecious populations (Section 2.3). We demonstrate that under both zygote and maternal control of sex expression, the condition for local stability corresponds to (8):

$$(h - \hat{h})(\alpha_0 - \alpha_1) > 0.$$

390 for h the initial sex expression level, \hat{h} the candidate ESS (Section 2.1), and $(\alpha_0 - \alpha_1)$ the average effect of substitution (17) under the Li-Price approach extended to inbreeding.

3.1 Evolution of androdioecy

3.1.1 Zygote control of sex expression

393 Under zygote control of sex expression (20), genotype i occurs with frequency z_i , of which a proportion h_i develop into hermaphrodites and the complement into males.

Local stability condition: A necessary condition for the exclusion of allele A introduced in low frequency into a population monomorphic for the a allele, which induces
396 hermaphroditism at rate h_2 , is positivity of the characteristic polynomial of the local stability matrix evaluated at unity. Under zygote control (20), this condition corresponds to

$$(h_2 - \hat{h})[d_0 h_2 s / 2 + d_1 h_2 (1 - s) - d_0 d_1 s / 2] > 0, \quad (29)$$

399 in which the uniparental proportion s corresponds to s_A (9), \hat{h} to the ESS candidate (11c), h_2 the proportion of the common aa genotype that develop into hermaphrodites, and the d_i

(28) the phenotypic deviations of genotypes bearing the rare A allele. Under weak selection
 402 (small d_i), this condition reduces to

$$(h_2 - \hat{h})[d_0s/2 + d_1(1 - s)] > 0, \quad (30)$$

and is also sufficient for local stability. For the Kryptolebias model, in which males alone
 fertilize outcrossed eggs ($\omega = \infty$), we show in Appendix C that the sole condition for local
 405 stability corresponds to

$$(\hat{h} - h_2)(h_2 - r_L) > 0, \quad (31)$$

in which r_L denotes the larger root of the bracketed term in (29), viewed as a quadratic
 in h_2 , under arbitrary dominance levels and intensities of selection on the modifier of sex
 408 expression (d_i).

Average effect of substitution: A fundamental notion of heritability of sex expression
 is that hermaphrodites and gonochores differ in the frequencies of alleles that modify sex
 411 expression. In any generation, the difference in frequency of the A allele between herma-
 phrodites and gonochores corresponds to

$$\frac{z_0h_0 + z_1h_1/2}{\sum_i z_i h_i} - \frac{z_0(1 - h_0) + z_1(1 - h_1)/2}{\sum_i z_i(1 - h_i)} = \frac{z_0(h_0 - \bar{h}) + z_1(h_1 - \bar{h})/2}{\bar{h}(1 - \bar{h})}, \quad (32)$$

for

$$\bar{h} = \sum_i z_i h_i.$$

This expression corresponds to the average effect of substitution (18), with the genotypic
 414 frequencies at the point of sex expression (z_i) assuming the role of the u_i in Table 2.

New basis system: In accordance with (32), we designate as the new basis vectors near
 the fixation of the a allele (small z_0 and z_1)

$$\begin{aligned} t_0 &= z_0 + z_1/2 \\ t_1 &= z_0 - (z_0 + z_1/2)F_{neut}, \end{aligned} \quad (33a)$$

417 for F_{neut} corresponding to (21) with the uniparental fraction s_A (9) substituted for s . To the
 first order in the frequencies of rare genotypes, the genotypic frequencies correspond to

$$\begin{aligned} z_0 &= t_0 F_{sel} \\ z_1 &= 2t_0(1 - F_{sel}), \end{aligned} \quad (33b)$$

for F_{sel} the fixation index under weak selection. From (33) we obtain

$$F_{sel} = F_{neut} + \frac{t_1}{t_0}. \quad (34)$$

420 Near the fixation of the a allele, the average effect of substitution (18) corresponds to

$$\frac{z_0d_0 + z_1d_1/2}{4(z_0 + z_1/2) - z_1} = \frac{d_0F_{sel} + d_1(1 - F_{sel})}{1 + F_{sel}}. \quad (35)$$

For F_{sel} determined at the key vector (B.1) defined in Appendix B, this expression (35) for the average effect of substitution corresponds to the bracketed factor in (29).

Under weak selection (28), t_1 is $O(d_i)$ (Appendix B), implying that the departure between F_{sel} and F_{neut} is also $O(d_i)$. To the first order in the intensity of selection on the modifier locus ($O(d_i)$), the average effect of substitution (35) corresponds to

$$\frac{d_0 F_{neut} + d_1(1 - F_{neut})}{1 + F_{neut}} = d_0 s/2 + d_1(1 - s),$$

423 confirming that (30) corresponds to (8).

3.1.2 Maternal control of sex expression

426 Under maternal control of sex expression (23), genotype i occurs with frequency x_i among maternal parents, all of which are hermaphrodites, and with frequency y_i among reproductive males.

429 **Local stability condition:** The conditions for local stability under maternal control mirror those under zygote control. The characteristic polynomial evaluated at unity is positive (necessary for local stability) only if (29) holds. Under weak selection (28), (30) provides the necessary and sufficient condition for local stability.

Average effect of substitution: To address heritability, we again address differences between hermaphrodites and gonochores in the frequency of a modifier of sex expression. In the next generation forward in time, the difference in frequency of the A allele between hermaphrodites and gonochores corresponds to

$$\begin{aligned} & \frac{x'_0 + x'_1/2}{\sum_i x'_i} - \frac{y'_0 + y'_1/2}{\sum_i y'_i} \\ &= (1 + s_A)/2 \left[\frac{x_0 h_0 + x_1 h_1/2}{\sum_i x_i h_i} - \frac{x_0(1 - h_0) + x_1(1 - h_1)/2}{\sum_i x_i(1 - h_i)} \right] \\ &= (1 + s_A)/2 \left[\frac{x_0(h_0 - \bar{h}) + x_1(h_1 - \bar{h})/2}{\bar{h}(1 - \bar{h})} \right], \end{aligned} \quad (36)$$

for

$$\bar{h} = \sum_i x_i h_i.$$

432 This expression suggests that the average effect of substitution corresponds to (18) with the u_i replaced by

$$\frac{x_i(1 + s_A)/2}{\sum_i x_i(1 + s_A)/2} = \frac{x_i[\tilde{s}\tau + (1 - \tilde{s})/2]}{\sum_i x_i[\tilde{s}\tau + (1 - \tilde{s})/2]}. \quad (37)$$

Under maternal control model of androdioecy, the maternal genotypic frequencies (x_i) are weighted by the production of uniparental offspring, at rate

$$\frac{\tilde{s}\tau}{\tilde{s}\tau + (1 - \tilde{s})/2},$$

and of biparental offspring, at rate

$$\frac{(1 - \tilde{s})/2}{\tilde{s}\tau + (1 - \tilde{s})/2},$$

in which the $1/2$ appears to represent the relatedness of biparental offspring to their maternal parent relative to the relatedness of uniparental offspring.

New basis system: We use (37) to specify the change in basis. Under androdioecy, males contribute to future generations only through pollen or sperm. In populations fixed for the a allele, the ratio of hermaphrodites to males at reproductive age corresponds to

$$\frac{x_2}{y_2} = \frac{h_2}{Z(1 - h_2)}. \quad (38)$$

Near this fixation state, we designate as the new basis vectors

$$\begin{aligned} t_0 &= x_0 + x_1/2 \\ t_1 &= x_0 - (x_0 + x_1/2)F_{neut} \\ t_2 &= \frac{x_0 + x_1/2}{h_2} - \frac{y_0 + y_1/2}{Z(1 - h_2)}, \end{aligned} \quad (39)$$

for F_{neut} corresponding to (21) with the uniparental fraction s_A (9) substituted for s .

At the key vector (B.1) defined in Appendix B, t_2 (39), representing the difference in allele frequency between hermaphrodites and males, is proportional to the average effect of substitution (35). Also at this key vector, the fixation index under selection F_{sel} corresponds to (34) and the average effect of substitution (35) again corresponds to the bracketed factor in (29).

Maternal and zygote control of androdioecy entail distinct definitions of the average effect of substitution ($\alpha_0 - \alpha_1$) (17) and the new basis system. Even so, the condition for local stability (30) again corresponds to (8).

3.2 Evolution of gynodioecy

3.2.1 Zygote control of sex expression

For the zygote control model of gynodioecy (22), the condition for positivity of the characteristic polynomial of the local stability matrix evaluated at unity is identical to (29), with the uniparental proportion s now corresponding to s_G (13) and \hat{h} to the ESS candidate (15c). Under weak selection (28), (30) provides the necessary condition for local stability of the fixation state.

Also identical to the expressions under zygote control of androdioecy are the average effect of substitution (32) and the definition of the new basis system (33), but with s_G (13) substituted for s in F_{neut} (21).

459 3.2.2 Maternal control of sex expression

Local stability condition: For the maternal control model (26), the condition for local stability under weak selection corresponds to

$$(h_2 - \hat{h})\{B[h_2 + (1 - h_2)Z\sigma](1 + s_G) - (d_0 - d_1)[d_0s_G + d_1(1 - s_G)]s_GZ\sigma/2\} > 0, \quad (40)$$

462 in which s_G corresponds to the uniparental proportion (13), \hat{h} to the ESS candidate (15c), and B the bracketed factor in (29):

$$B = d_0h_2s_G/2 + d_1h_2(1 - s_G) - d_0d_1s_G/2. \quad (41)$$

465 Under weak selection (28), (40) reduces to (30), which provides the necessary and sufficient condition for local stability of the fixation state.

Average effect of substitution: To address heritability, we return to (36). From the full system of recursions for maternal control of sex expression (26), we obtain

$$\begin{aligned} & \frac{x'_0 + x'_1/2}{\sum_i x'_i} - \frac{y'_0 + y'_1/2}{\sum_i y'_i} \\ &= \Gamma_1 \left(\frac{x_0 + x_1/2}{\sum_i x_i} - \frac{y_0 + y_1/2}{\sum_i y_i} \right) \\ & \quad + \Gamma_2 \{ (1 - s)[x_0(h_0 - \bar{h}) + x_1(h_1 - \bar{h})/2] \\ & \quad \quad + \sigma[y_0(h_0 - \bar{h}) + y_1(h_1 - \bar{h})/2] \} \end{aligned}$$

in which

$$\begin{aligned} \Gamma_1 &= \frac{\sigma s \sum_i y_i \sum_i x_i (h_i - \bar{h})}{2 \sum_i (x_i + \sigma y_i) h_i \sum_i (x_i + y_i \sigma) (1 - h_i)} \\ \Gamma_2 &= \frac{\sum_i (x_i + y_i \sigma)}{2 \sum_i (x_i + \sigma y_i) h_i \sum_i (x_i + y_i \sigma) (1 - h_i)} \end{aligned}$$

and

$$\bar{h} = \frac{\sum_i \{x_i(1 + s) + y_i\sigma\} h_i}{\sum_i \{x_i(1 + s) + y_i\sigma\}}.$$

Under weak selection, for which terms of the form $(h_i - h_j)$ are small, the difference in allele frequency between the sexes are also small, with the difference converging rapidly to

$$\frac{x'_0 + x'_1/2}{\sum_i x'_i} - \frac{y'_0 + y'_1/2}{\sum_i y'_i} = \frac{E}{2h(1 - h) \sum_i (x_i + y_i \sigma)} + o(d) \quad (42a)$$

468 in which

$$E = (1 + s)[x_0(h_0 - \bar{h}) + x_1(h_1 - \bar{h})/2] + \sigma[y_0(h_0 - \bar{h}) + y_1(h_1 - \bar{h})/2], \quad (42b)$$

h represents any of the h_i , and $o(d)$ comprises quantities smaller than terms of the form $(h_i - h_j)$.

471 Expression (42b) suggests that the average effect of substitution corresponds to (18) with
the u_i replaced by

$$\frac{x_i[\tilde{s}\tau + (1 - \tilde{s})/2] + y_i\tilde{\sigma}/2}{\sum_i \{x_i[\tilde{s}\tau + (1 - \tilde{s})/2] + y_i\tilde{\sigma}/2\}}. \quad (43)$$

474 A major feature that distinguishes this gynodioecy model from the corresponding androdi-
oecy model (36) is that gonochores (females) as well as hermaphrodites may serve as maternal
parents, the individuals that control sex expression. Comparison of (37) and (43) indicates
477 that the weighting of the contributions to the offspring generation of hermaphroditic to
female maternal parents corresponds to

$$\frac{\tilde{s}\tau + (1 - \tilde{s})/2}{\tilde{\sigma}/2} = \frac{(1 + s)}{\sigma}, \quad (44)$$

implying a twofold weighting of uniparental offspring relative to biparental offspring.

New basis system: In defining the new basis system, we adopt the weighted average
480 of allele frequencies in hermaphrodites and females described in (44):

$$\begin{aligned} t_0 &= \frac{(x_0 + x_1/2)(1 + s) + (y_0 + y_1/2)\sigma}{h_2(1 + s) + Z(1 - h_2)\sigma} \\ t_1 &= \frac{[x_0 - (x_0 + x_1/2)F_{neut}](1 + s) + [y_0 - (y_0 + y_1/2)F_{neut}]\sigma}{h_2(1 + s) + Z(1 - h_2)\sigma} \\ t_2 &= \frac{x_0 + x_1/2}{h_2} - \frac{y_0 + y_1/2}{Z(1 - h_2)} \\ t_3 &= \frac{x_0}{h_2} - \frac{y_0}{Z(1 - h_2)} \end{aligned} \quad (45)$$

483 for F_{neut} corresponding to (21) with the uniparental fraction s_G (13) substituted for s . These
expressions reflect that near the fixation state, the ratio of hermaphrodites to gonochores in
the population (x/y) lies close to (38).

486 At the key vector (B.1) defined in Appendix B, both t_2 (45), representing the difference
in allele frequency between hermaphrodites and males, and the factor of $(h_2 - \hat{h})$ in local
stability condition (40) are proportional to the average effect of substitution (42b). As in
each of the other models explored, these results confirm key condition (8).

4 Data analysis

489 Redelings *et al.* (2015) developed a Bayesian method for the analysis of multilocus data
sampled from populations reproducing through pure hermaphroditism, androdioecy, or gyn-
odioecy. Using an explicitly coalescent-based framework, it generates posterior distributions
492 for the uniparental fraction (probability that a random individual is uniparental), the ana-
logue to estimates of selfing rates generated by earlier methods (*e.g.*, Ritland 2002; Enjalbert
and David 2000; David *et al.* 2007).

495 In any empirical investigation, modifiers of the sex ratio may have not yet evolved to the
ESS even if the model is appropriate. Subject to this caveat, we use our new theoretical
results to infer the viability of gonochores (males or females) relative to hermaphrodites in
498 the natural populations analyzed by Redelings *et al.* (2015).

Using microsatellite data derived from natural populations of the androdioecious killifish
Kryptolebias marmoratus (Tatarenkov *et al.* 2012) and the gynodioecious Hawaiian endemic
501 *Schiedea salicaria* (Wallace *et al.* 2011), Redelings *et al.* (2015) generated posterior distri-
butions of the basic parameters of the models, including the population sex ratio among
reproductives (7a). Those estimates imply posterior distributions of C , the collective contri-
504 bution of hermaphrodites to the next generation (Fig. 2), from which we infer the sex ratio
at the juvenile stage (7b). Under the assumption that the natural populations under study
have converged on the attracting ESS sex ratio, we use the departure between the sex ratios
507 at the two points in the life cycle ((7a) and (7b)) to obtain the posterior distribution of Z .

Figure 3 presents posterior distributions of Z in the *Schiedea* and *Kryptolebias* popula-
tions. We find little evidence of a difference in viability between females and hermaphro-
510 dites in the gynodioecious *S. salicaria* (median=1.08, 95% BCI=(0.34, 1.78)), in which the
Bayesian Credible Interval (BCI) denotes the interval comprising the highest posterior den-
sity. In contrast, male *K. marmoratus* appear to have substantially lower viability than
513 hermaphrodites in both the BP population (median=0.45, 95% BCI=(0.20, 0.81)) and the
TC population (median=0.48, 95% BCI=(0.25, 0.77)), even though the frequency of males
is several-fold higher in the TC population (0.17 versus 0.01; Turner *et al.* 1992; Tatarenkov
516 *et al.* 2012; Mackiewicz *et al.* 2006).

5 Discussion

We have explored the evolution of androdioecy and gynodioecy under the influence of autoso-
519 mal modifiers of weak effect. Our central theoretical finding (8) unifies full multi-dimensional
local stability analysis with the heuristically-appealing Li-Price framework (Li 1967; Price
1970) and evolutionary stability. In addition, we have used our theoretical results to infer the
522 viability of gonochores (males or females) relative to hermaphrodites in the gynodioecious
plant *Schiedea salicaria* and the androdioecious killifish *Kryptolebias marmoratus*.

5.1 Evolution by means of major and minor genes

525 A considerable body of work on the evolution of gynodioecy has addressed the joint control
of sex expression by major cytoplasmic and nuclear factors (reviewed by Bailey and Delph
2007; McCauley and Bailey 2009). Our analysis of autosomal modifiers does not exclude a
528 history of cytoplasmic sex determination. For example, exclusive nuclear control may arise
upon the fixation in a population of a cytoplasm that induces cytoplasmic male sterility
("cryptic CMS," Schultz 1994; Fishman and Willis 2006). Similarly, the genetic basis of sex

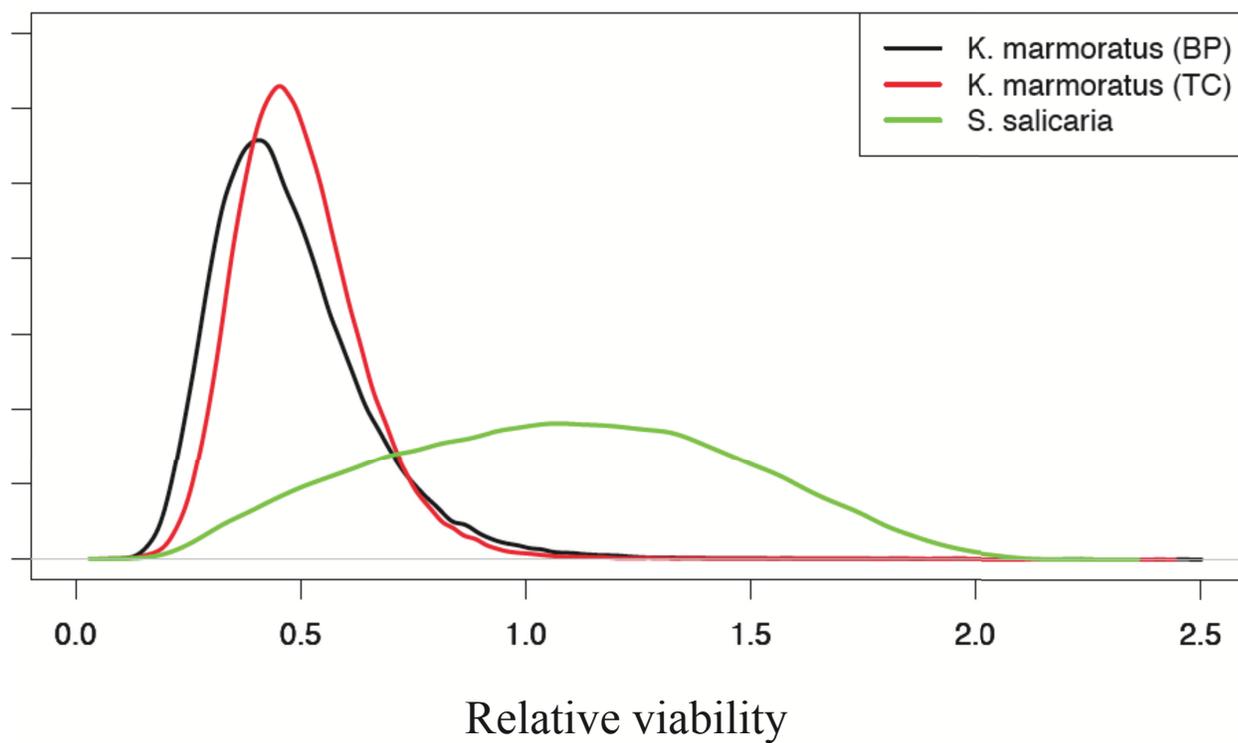


Figure 3: Posterior distributions of the viability of gonochores relative to hermaphrodites (Z).

531 expression may shift from a single major locus to many loci of minor effect upon fixation
at the major locus. Further, segregation of major nuclear or cytoplasmic factors does not
preclude simultaneous modification of the sex ratio by nuclear factors of small effect.

Lloyd (1977) acknowledged that changes in frequency of a major gene inducing complete
suppression of hermaphroditic expression induces direct convergence to the ESS (7a) only
under complete dominance of the major gene, under both androdioecy (Ross and Weir 1976;
Wolf and Takebayashi 2004) and gynodioecy (Ross and Weir 1975). Clearly, the failure of
major genes to evolve to the ESS under general dominance schemes remains true. To address
the special attributes of complete dominance, we here restrict consideration to complete
dominance of the gonochore allele ($h_0 = 0$) and determination of zygote sex by its own
genotype (zygote control model). All gonochorous individuals necessarily bear a single copy
of the dominant gonochore allele, transmitting it to half their offspring. As a consequence,
the sex ratio among offspring of reproductive age corresponds to

$$\frac{h'}{1 - h'} = \frac{C}{Z2(1 - C)/2},$$

534 for h' the proportion of hermaphrodites among offspring and $(1 - C)$ the probability that an
autosomal gene randomly sampled from offspring that survive inbreeding depression derives
from a gonochorous parent (1). Under complete dominance of male-sterility and zygote
537 control, the equilibrium population sex ratio among reproductives does indeed correspond
to the ESS (7a). However, this property holds neither under other dominance schemes (*e.g.*,
recessive gynodioecy, Ross and Weir 1975) nor under maternal determination of zygote sex,
540 even with complete dominance.

In their analysis of sex within broods generated by controlled crosses between females and
hermaphrodites of the gynodioecious *Schiedea salicaria*, Weller and Sakai (1991) recognized
543 two major groups of hermaphroditic pollen donors: those that generated hermaphroditic
offspring almost exclusively and those that generated the two sexes in approximately equal
proportions. Weller and Sakai (1991) proposed that male sterility derives from a recessive
546 allele at a single locus, and reported approximate agreement between the population sex ratio
and the predicted ESS (7b). However, Ross and Weir (1975) had already shown that short-
term evolution of a recessive major allele for male sterility implies an equilibrium population
549 sex ratio that departs from the ESS.

Departing from earlier work on short-term changes in gene frequency space, we have
addressed long-term changes in parameter space (Eshel and Motro 1981; Taylor 1989; Chris-
552 tiansen 1991). Our models accommodate general dominance among mutations of minor effect
arising at modifier loci across the genome. We have demonstrated long-term evolutionary
stability of candidate ESS values (Section 2.1) under maternal effects (maternal control) as
555 well as direct effects (zygote control) in sex expression.

Our analysis of microsatellite variation in *Schiedea salicaria* indicates near-maximal val-
ues of relative effective number (R near unity in Fig. 1), supporting the view of Weller and
558 Sakai (1991) of convergence to the ESS (7b). A possible reconciliation between their proposal
of a recessive major gene for male sterility in *S. salicaria* and the attainment of the ESS

(see Ross and Weir 1975) is that minor modifier loci distinct from the major gene may have
561 induced the convergence of the population sex ratio to the evolutionarily stable strategy.
For example, in the androdioecious killifish *Kryptolebias marmoratus*, the genome-wide epi-
564 genetic response to environmental factors documented by Ellison *et al.* (2016) is consistent
with the view that loci throughout the genome may influence sex expression.

5.2 Relative viability of gonochores

In generalizing the findings of Fisher (1958) to androdioecy and gynodioecy, we show that
the central determinant of the evolutionary modification of the sex ratio corresponds to
 C (1), the collective contribution of hermaphroditic parents to the offspring generation.
Natural selection on modifiers of weak effect promotes convergence in parameter space to
the evolutionarily stable sex ratio among juveniles (Table 1) of

$$\frac{\hat{h}}{1 - \hat{h}} = \frac{C}{1 - C}$$

(7b), for \hat{h} the ESS proportion of hermaphrodites among juveniles. At reproductive age, the
sex ratio corresponds to

$$\frac{h^*}{1 - h^*} = \frac{C}{Z(1 - C)}$$

(7a), for Z the relative rate of survival of juvenile gonochores to adulthood and h^* the
567 proportion of hermaphrodites after operation of sex-specific viability selection.

In the absence of sex-specific differences in rate of survival to reproductive age ($Z = 1$),
relative effective number (2) is maximized ($R = 1$) at the ESS sex ratio. Here, we use
570 the departure of relative effective number R from unity to infer the intensity of sex-specific
differences in viability. As the Bayesian MCMC method of Redelings *et al.* (2015) permits
inference of h^* and C , it also yields posterior distributions for Z , the relative viability of
573 gonochores (Fig. 3).

The near-maximal relative effective numbers (Fig. 1) inferred for a natural population of
the gynodioecious *Schiedea salicaria* (Wallace *et al.* 2011) suggests close convergence to the
576 ESS (7b), and indeed the posterior distribution of the relative viability of gonochores (Z , Fig.
3) provides little evidence of differential viability between the sexes. In contrast, males of the
androdioecious killifish *Kryptolebias marmoratus* (Tatarenkov *et al.* 2012) appear to have
579 about twofold lower viability than hermaphrodites (Fig. 3). Our analysis suggests similar
male viabilities in the highly inbred BP population, in which reproductively mature males
are very rare (posterior median = 1%), and the more outbred TC population, in which they
582 are more abundant (posterior median = 17%, Redelings *et al.* 2015).

Turner *et al.* (2006) suggested that the maintenance of males in highly inbred populations
of *K. marmoratus* may require “implausibly large” male fertility. Low viability of males
585 would further increase the stringency of the condition (11b). However, our analysis indicates

that if males alone fertilize eggs that are not self-fertilized ($\omega = \infty$, Furness *et al.* 2015), the existence of any viable biparental offspring ($s_A < 1$) is sufficient to favor the maintenance of males.

Turner *et al.* (2006) conducted common garden experiments to address male development in the killifish *K. marmoratus*, an emerging model system for environmental sex determination (Kelley *et al.* 2016). Lines derived from the progeny of individual hermaphrodites obtained from natural populations in Belize showed marked differences in the proportion of adult males, in spite of rearing under identical controlled conditions. While fewer males appeared in broods derived from the rare-male population, both sets of broods showed substantially higher frequencies of males than observed in the natural populations from which they descended. Our inference that the rate of survival to reproductive age of males is half the rate of hermaphrodites (Fig. 3) is consistent with the observed excess of males in laboratory compared to wild populations. Turner *et al.* (2006) described the orange-hued mature males as “highly conspicuous.” The considerable body of work on guppies indicates that predation can generate intense selection, with various indices of crypsis responding rapidly to predator abundance under both laboratory and field conditions (Endler 1980; Reznick *et al.* 1996).

Our estimates of the relative viability of gonochores (Z) entail that the proportions of individuals that are uniparental are identical before (juvenile stage) and after (adult stage) the manifestation of sex-specific differences in viability (Table 1). This assumption may be violated if sex expression is heritable. Because only hermaphrodites can generate uniparental offspring, heritability of sex may imply that hermaphroditic offspring have a higher chance both of having descended from hermaphroditic parents and of being uniparental. Consistent with this scenario is the observation that gonochorous adults are more outbred than hermaphroditic adults (Wolff *et al.* 1988; Collin and Shykoff 2003) in some gynodioecious species, including *Schiedea salicaria* (Weller and Sakai 2005). As a consequence, our estimates of Z are subject to the assumption that the population has attained the ESS level of sex expression as a genetically monomorphic state: the outcome of filtering of newly-arisen mutations of minor effect, for example.

The frequency of males in natural *K. marmoratus* populations appears to be positively correlated with level of heterozygosity (Mackiewicz *et al.* 2006). Possible mechanisms include that outcrossing or high heterozygosity may directly induce male development (Turner *et al.* 2006) or that the greater availability of males may favor the evolution of higher outcrossing rates (Ellison *et al.* 2016). Our analysis suggests that by reducing the collective contribution of hermaphrodites (C), higher outcrossing rates favor higher frequencies of males (7a). Factors that in turn determine the rate of outcrossing may include parasite loads, which appear to be greater in more inbred individuals (Ellison *et al.* 2011).

5.3 Local stability, evolutionary stability, and heritability

We have conducted local stability analyses for each of the four multidimensional models of the evolutionary modification of sex expression in androdioecious and gynodioecious populations (Section 2.3). Our central theoretical finding (8),

$$(h - \hat{h})(\alpha_0 - \alpha_1) > 0,$$

624 implies that a new mutation that induces small effects on sex expression fails to increase
when rare if the current sex expression level exceeds the ESS ($(h - \hat{h}) > 0$) and the mutation
would raise the sex expression level even further ($(\alpha_0 - \alpha_1) > 0$), or if both inequalities are
627 reversed. We have demonstrated that under the weak-effects assumption, the conditions for
local stability in multidimensional frequency space for arbitrary initial states and dominance
relationships reduce to this single inequality (Section 3). Our analysis shows that the sex
630 ratios corresponding to (7a) represent attracting evolutionarily stable strategies (ESSs) under
arbitrary schemes for dominance of rare alleles introduced at a monomorphic locus that
modifies sex expression.

633 For general systems of mating, Fisher (1941) defined the average effect of substitution
of the new mutation ($\alpha_0 - \alpha_1$) through the minimization of the mean squared deviation of
phenotype from additive genotypic value (17). Under random mating, the average effect of
636 substitution of a rare mutation depends only on the change in phenotype it induces. Under
inbreeding, determination of $(\alpha_0 - \alpha_1)$ requires the full array of genotypic frequencies (Sec-
tion 2.2). Accordingly, demonstration of (8) requires specification of a particular genotypic
639 array within the inherently multidimensional state space representing populations under-
going inbreeding. Further, elucidation of the appropriate measure of $(\alpha_0 - \alpha_1)$ is central
to the heuristically-appealing Li-Price framework (Li 1967; Price 1970), which provides a
642 one-dimensional, one-generational description of the evolutionary process (19).

Our unification of multidimensional local stability analysis with the Li-Price framework
entails specification of a key state in the full multi-dimensional space such that the change
645 in frequency of the rare allele over a single generation starting from this state indicates
its asymptotic fate (invasion or extinction) starting from arbitrary states in a sufficiently
small neighborhood of the fixation state (Appendix B). We have shown that the change in
648 frequency of the rare allele starting from the key initial state (B.1) is proportional to the value
of the characteristic polynomial, evaluated at unity, of the full transformation. Under our
weak-effects assumption (28), this criterion provides necessary and sufficient conditions for
651 local stability. However, under strong selection (introduction of genes with major effects on
sex expression), the sign of the characteristic polynomial evaluated at unity is not necessarily
sufficient as an indicator of local stability. In such cases, the key initial state (B.1) may
654 become invalid or undefined (Fig. B1).

The conceptual origins of the Li-Price equation (Li 1967; Price 1970) lie in Robertson's
(1966) exploration of the effects of culling, on the basis of informal criteria, on the genetic
657 variance of a desired trait (high milk yield in dairy cattle). With respect to the evolution
of mating systems, sex may influence various components of transmission of genes to future

generations, possibly including relatedness (Lloyd 1975). Here, the focal trait corresponds
660 to the propensity of a zygote to develop into a gonochore or a hermaphrodite under the
control of the genotype at a modifier locus of its maternal parent (maternal control models)
or its own genotype (zygote control models). In general, the genotypic distribution (u_i in
663 Table 2) with respect to which the average effect of substitution ($\alpha_0 - \alpha_1$) is determined
depends on the component of the population (zygotes versus maternal parents, in this case)
that influences sex expression. An additional question concerns the relevance of relatedness
666 of the controlling genotype to the two sex forms.

Our approach entails permitting the answers to these questions emerge naturally from
the models themselves. We adopt a notion of heritability that reflects associations between
669 sex and allele frequency. In populations in which modifiers of sex expression segregate, the
average effect of substitution (18) at a modifier locus is proportional to the difference in
allele frequency between gonochores and hermaphrodites. This property holds under both
672 zygote and maternal control of androdioecy and gynodioecy ((32), (36), (42)).

Under zygote control of both androdioecy (20) and gynodioecy (22), the average effect
is defined with respect to genotypic frequencies among zygotes at the point of sex expres-
675 sion (32). In this case, the controlling entities (zygotes) are equally related to themselves
regardless of sex.

In contrast, relatedness plays a role under maternal control of sex expression. For the
678 androdioecy model (23), hermaphrodites alone determine offspring number, with gonochores
(males) serving only as pollen or sperm donors. Under our notion of heritability, the average
effect is defined with respect to genotypic frequencies among maternal parents (hermaphro-
681 dites) at reproductive age (36). Uniparental offspring bear twofold higher relatedness to
their maternal parents than do biparental offspring, irrespective of the sex of the offspring
(36).

684 Among the unique features of maternal control of gynodioecy (26) is that gonochores
(females) as well as hermaphrodites contribute to offspring number. Accordingly, the average
effect of substitution depends on both sexes, with the offspring of females weighted by a factor
687 of $1/2$, reflecting their biparental derivation, and the biparental and uniparental offspring of
hermaphrodites weighted by $1/2$ and 1 , respectively (44).

Confirmation of our central theoretical finding (8) provides a reconciliation of ESS analy-
690 sis and the Li-Price framework with full multidimensional local stability analysis. In addition,
it has permitted insight into the meaning of heritability under zygote and maternal control
of phenotype under inbreeding.

693 Acknowledgments

We thank Bruce Turner for stimulating insights and Associate Editor Laurent Lehmann and
two anonymous reviewers for their helpful comments. Public Health Service grant GM 37841

696 (MKU) provided partial funding for this research.

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Appendix A Lloyd’s (1975) unbeatable sex ratios

- 819 Equation (2) of Lloyd (1975) provides the unbeatable sex ratio under gynodioecy:

$$\frac{p}{1-p} = \frac{b-2SX}{bS}, \quad (\text{A.1})$$

for p the proportion of females at reproductive age, b the seed set of females, S the viability of a hermaphrodite (described as “male”) relative to a female, and X the number of zygotes surviving to reproduction produced by a hermaphrodite relative to a female. In Lloyd’s notation,

$$X = i[a + be(1-a)(1-w) + (1-be)(1-a)r] + be(1-a)w,$$

in which i corresponds to the relative viability of uniparental offspring (our τ), the first bracket the proportion of seeds of hermaphrodites set by self-pollen (our \tilde{s}), and $be(1-a)w$ the proportion of seeds of hermaphrodites set by pollen from the pollen cloud (our $(1-\tilde{s})$). Substitution of

$$\begin{aligned}i &= \tau \\X &= (\tau\tilde{s} + 1 - \tilde{s}) \\b &= \tilde{\sigma} \\1/S &= Z.\end{aligned}$$

into (A.1) corresponds to our non-zero ESS candidate (15a).

In his treatment of androdioecy, Lloyd (1975, his equation (7)) proposed an unbeatable proportion of males of

$$q = \frac{t - 2lv[t + i(1 - t)]}{2iv(1 - t)(1 - l) + t(1 + v - 2lv)}, \quad (\text{A.2})$$

for q the proportion of males at reproductive age, t the proportion of seeds set by non-self pollen, l the pollen production of a hermaphrodite (described as “female”) relative to a male, v the rate of survival to reproduction of a hermaphrodite relative to a male, and i the viability of uniparental offspring relative to biparental offspring. Substitution of

$$\begin{aligned}t &= 1 - \tilde{s} \\1/l &= \omega \\1/v &= Z \\i &= \tau.\end{aligned}$$

into (A.2) corresponds to our non-zero ESS candidate (11).

Appendix B Change of basis

Here, we describe the relationship between the one-generational, one-dimensional description of evolution given by the Li-Price equation (19) and a full asymptotic, multi-dimensional local stability analysis. We describe a state of the population from which the change in allele frequency over a single generation does in fact correctly reflect the asymptotic condition for initial increase in the full multi-dimensional system under weak selection.

B.1 Weak selection

Under selective neutrality of variation at the modifier locus, the genotypic frequencies initiated at any state comprising both alleles rapidly converge to a configuration characterized by equality between sex forms of genotypic frequencies ($x_i = y_i$) and fixation index

834 (Wright 1933) given by (21). In the absence of differences among genotypes in sex expres-
sion (27), the multi-dimensional transformations we address (Section (2.3)) have a dominant
eigenvalue of unity, reflecting preservation of allele frequency, with all remaining eigenval-
837 ues, corresponding to classical measures of disequilibrium, having moduli strictly less than
unity. Weak-selection systems (28) represent perturbations in parameter space of such neu-
tral transformations. For cases, including the maternal control model of gynodioecy (26),
840 in which the neutral transformation has repeated eigenvalues, the perturbed transformation
may have conjugate pairs of imaginary eigenvalues. Even so, any imaginary eigenvalues do
not determine asymptotic local stability because the dominant eigenvalue of a non-negative
843 matrix corresponds to a simple, real root of the characteristic polynomial (Gantmacher 1959).
Because eigenvalues are continuous in complex space (*e.g.*, Serre 2010, Chapter 5), the eigen-
values of the weak-selection transformation depart continuously in the $d_i = (h_i - h_2)$ (28)
846 from those of the neutral transformation. In particular, the dominant eigenvalue of the local
stability matrix under weak selection lies near unity, with the moduli of the other eigenval-
ues remaining strictly less than unity. As a consequence, examination of the value of the
849 characteristic polynomial of the local stability matrix under weak selection is sufficient to
establish local stability.

B.2 Elucidating the Li-Price equation

852 To relate the Li-Price equation (19) to the full multi-dimensional local stability analysis, we
introduce a change of basis from the genotypic frequencies of the rare genotypes (AA and Aa)
in hermaphrodites and gonochores to allele frequency and disequilibrium measures. Here,
855 measures of disequilibrium reflect any departures of variables other than allele frequency
from their equilibrium values under the mating system in the absence of selection on the
modifier locus ($h_0 = h_1 = h_2$). In particular, disequilibrium corresponds to the departure of
858 the frequency of heterozygotes (Aa) from the frequency associated with F_{neut} (21) and not,
in particular, from Hardy-Weinberg proportions ($F = 0$).

Change of basis: We determine a key vector such that the direction of change in allele
frequency over a single generation starting from this vector reflects the asymptotic behavior
of the system starting from an arbitrary position in the neighborhood of the fixation state.
Let \mathbf{M} denote the local stability matrix under the original basis system. Because \mathbf{M} is a
non-negative matrix, its dominant eigenvalue is non-negative and corresponds to a simple
root of its characteristic polynomial (Gantmacher 1959). Under the new basis, the local
stability matrix corresponds to

$$\mathbf{N} = \mathbf{A}\mathbf{M}\mathbf{B},$$

for \mathbf{A} translating from the old basis to the new basis and \mathbf{B} translating from the new basis
to the old basis ($\mathbf{A}\mathbf{B} = \mathbf{I}$). For \mathbf{z} an arbitrary vector in the neighborhood of the fixation
state,

$$(\mathbf{I} - \mathbf{N})\mathbf{z}$$

861 describes change over a single generation. We define *key vector* $\tilde{\mathbf{z}}$ such that change may occur
only in the first dimension (allele frequency), irrespective of the magnitude of disequilibria

in other dimensions:

$$(\mathbf{I} - \mathbf{N})\tilde{\mathbf{z}} = \begin{pmatrix} -\Delta z \\ 0 \\ \vdots \\ 0 \end{pmatrix}, \quad (\text{B.1})$$

in which Δz denotes the change in allele frequency over a single generation. For \mathbf{M} and \mathbf{N} n -dimensional matrices, $\tilde{\mathbf{z}}$ is determined by the last $(n - 1)$ rows of $(\mathbf{I} - \mathbf{N})\tilde{\mathbf{z}}$.

Asymptotic behavior: Here, we show that under weak selection (28), a one-generation step from key vector $\tilde{\mathbf{z}}$ (B.1) indicates the asymptotic behavior of the system initiated from an arbitrary location in the neighborhood of the fixation state.

Let \mathbf{X} represent the matrix obtained by replacing the first column of an n -dimensional identity matrix by $\tilde{\mathbf{z}}$. Multiplication of $(\mathbf{I} - \mathbf{N})$ by \mathbf{X} on the right produces

$$(\mathbf{I} - \mathbf{N})\mathbf{X} = \begin{pmatrix} -\Delta z & \mathbf{R}_2 \\ \mathbf{R}_1 & (\mathbf{I} - \mathbf{N})_{n-1} \end{pmatrix}, \quad (\text{B.2})$$

in which \mathbf{R}_1 is an $(n - 1)$ -dimensional column vector of zeros, \mathbf{R}_2 is an $(n - 1)$ -dimensional row vector with elements equal to the corresponding elements of the first row of $(\mathbf{I} - \mathbf{N})$, and $(\mathbf{I} - \mathbf{N})_{n-1}$ is the matrix obtained by removing the first row and column from $(\mathbf{I} - \mathbf{N})$. Taking the determinant of both sides of (B.2) produces

$$\text{Det}[\mathbf{I} - \mathbf{N}]\text{Det}[\mathbf{X}] = -\Delta z \text{Det}[(\mathbf{I} - \mathbf{N})_{n-1}], \quad (\text{B.3a})$$

for $\text{Det}[(\mathbf{I} - \mathbf{N})_{n-1}]$ the principal minor obtained by deleting the first row and column of $(\mathbf{I} - \mathbf{N})$.

To achieve our objective of relating the Li-Price equation (19) to a full multi-dimensional local stability analysis, we demonstrate that

$$\text{Det}[\mathbf{I} - \mathbf{N}] \propto -\Delta z$$

under weak selection (d_i near zero). This expression implies that the direction of change over a single generation of the system initiated at $\tilde{\mathbf{z}}$ (B.1) corresponds to the sign of the characteristic polynomial of the multi-dimensional stability matrix evaluated at unity. Weak selection (28) entails small differences among genotypes in sex expression (small $d_i = h_i - h_2$). Because Δz is $O(d_i)$, (B.3a) implies

$$\text{Det}[\mathbf{I} - \mathbf{N}]\text{Det}[\mathbf{X}] = -\Delta z \text{Det}[(\mathbf{I} - \mathbf{N}^*)_{n-1}] + o(d_i), \quad (\text{B.3b})$$

for \mathbf{N}^* the linearized transition matrix under neutrality ($d_i = 0$). To show that

$$\text{Det}[(\mathbf{I} - \mathbf{N}^*)_{n-1}] > 0, \quad (\text{B.4})$$

we note that under neutrality, the absence of all disequilibria implies invariant gene frequency in all models studied here (Section 2.3). Accordingly,

$$(\mathbf{I} - \mathbf{N}^*)\mathbf{e} = \mathbf{0},$$

in which \mathbf{N}^* denotes the linearized transition matrix under neutrality and \mathbf{e} the unit vector with first element equal to 1 and zeros elsewhere. This expression implies that the element in the first column and row of \mathbf{N}^* corresponds to unity. Further, that the neutral system converges to the state in which all disequilibria are absent implies that all elements in the first column of \mathbf{N}^* other than the first are zero. As a result, \mathbf{N}^* has the form

$$\mathbf{N}^* = \begin{pmatrix} 1 & \cdots \\ \mathbf{R}_1 & (\mathbf{N}^*)_{n-1} \end{pmatrix},$$

in which $(\mathbf{N}^*)_{n-1}$ denotes the submatrix obtained by removing the first row and column from \mathbf{N}^* and \mathbf{R}_1 is again an $(n-1)$ -dimensional column vector of zeros. The characteristic polynomial of \mathbf{N}^* ,

$$\text{Det}[\lambda\mathbf{I} - \mathbf{N}^*] = (\lambda - 1)\text{Det}[(\lambda\mathbf{I} - \mathbf{N}^*)_{n-1}] = 0,$$

882 has a unit eigenvalue (corresponding to allele frequency), with the remaining eigenvalues (corresponding to disequilibria) given by the roots of $\text{Det}[(\lambda\mathbf{I} - \mathbf{N}^*)_{n-1}]$. That all eigenvalues associated with disequilibria are strictly less than unity in absolute value implies (B.4).

885 **Appendix C Local stability analysis of Kryptolebias model under zygote control of sex**

We address the local stability of recursion system (20) near the state of fixation of the a 888 allele at the modifier locus. Under Kryptolebias model, sex expression is determined by the genotype of the zygote itself and only males fertilize outcrossed eggs ($\omega = \infty$ and $Z > 0$). In the absence of males prior to the introduction of genetic variation at the modifier locus 891 ($h_2 = 1$), eggs that are not self-fertilized fail to become zygotes. As a consequence, any allele that induces the development of males ($h_0 > 0$ or $h_1 > 0$) derives an enormous selective advantage from the fertilization of the proportion $(1 - s_A)$ of all eggs produced. Accordingly, 894 we restrict further consideration to cases in which the common genotype produces some males ($h_2 < 1$).

We demonstrate that the sole condition for local stability corresponds to (31):

$$(\hat{h} - h_2)(h_2 - r_L) > 0, \tag{C.1}$$

897 for r_L the larger root of the bracketed term in (29), viewed as a quadratic in h_2 :

$$q_{AZ}(h_2) = h_2[d_0s_A/2 + d_1(1 - s_A)] - d_0d_1s_A/2, \tag{C.2}$$

in which

$$\begin{aligned} d_0 &= h_0 - h_2 \\ d_1 &= h_1 - h_2. \end{aligned}$$

These results imply that the proposed ESS (11c) corresponds to an attracting evolutionarily stable strategy under arbitrary dominance levels and intensities of selection on the modifier 900 of sex expression.

C.1 Linearized recursion system

At the fixation of the a allele, the population comprises only aa individuals ($z_2 = 1$), with normalizer

$$T = h_2.$$

Upon the introduction of the rare alternative allele A , genotypes AA and Aa arise in low frequencies (δ_0 and δ_1). Linearization of the full recursion system (20) by ignoring terms of the second order in the δ_i produces

$$\begin{aligned}\delta'_0 &= \frac{s_A(\delta_0 h_0 + \delta_1 h_1/4)}{h_2} \\ \delta'_1 &= \frac{[\delta_1 s_A h_1/2 + (1 - s_A)(\delta_0 h_0 + \delta_1 h_1/2)]}{h_2} \\ &\quad + \frac{(1 - s_A)[\delta_0(1 - h_0) + \delta_1(1 - h_1)/2]}{1 - h_2},\end{aligned}$$

with local stability determined by the dominant eigenvalue of

$$\mathbf{M} = \begin{pmatrix} \frac{s_A h_0}{h_2} & \frac{s_A h_1}{4h_2} \\ (1 - s_A) \left(\frac{h_0}{h_2} + \frac{1-h_0}{1-h_2} \right) & \left[s_A \frac{h_1}{h_2} + (1 - s_A) \left(\frac{h_1}{h_2} + \frac{1-h_1}{1-h_2} \right) \right] / 2 \end{pmatrix}. \quad (\text{C.3})$$

903 Because this matrix is non-negative, its dominant eigenvalue is real and non-negative (Gantmacher 1959, Chapter XIII). Its characteristic polynomial is proportional to

$$C_{AZ}(\lambda) = [(\lambda - 1)(1 - h_2) - (h_2 - \hat{h})] \left[\lambda - \frac{s_A(h_0 - h_1/2)}{h_2} \right] + (h_2 - \hat{h}) \frac{h_1}{h_2} \left[\lambda - \frac{s_A h_0}{2h_2} \right], \quad (\text{C.4})$$

906 in which the proposed ESS proportion of hermaphrodites at birth corresponds to (11c), with all biparental offspring derived from male parents ($\omega = \infty$):

$$\hat{h} = (1 + s_A)/2. \quad (\text{C.5})$$

Setting the resident hermaphrodite fraction to the proposed ESS ($h_2 = \hat{h}$), we find that $C_{AZ}(\lambda)$ (C.4) reduces to

$$(\lambda - 1)(1 - h_2) \left[\lambda - \frac{s_A(h_0 - h_1/2)}{h_2} \right] = 0,$$

909 confirming a dominant eigenvalue of unity near the fixation of an allele that induces the candidate ESS, as required for an ESS. Further, we show that ESS is evolutionarily attracting: in a population fixed for an allele that specifies a sex ratio different from the ESS ($h_2 \neq \hat{h}$), only alleles that locally bring the sex ratio closer to the ESS increase when rare (C.1).

912 A necessary condition for local stability is positivity of the characteristic polynomial $C_{AZ}(\lambda)$ (C.4) evaluated at unity. In addition, we determine the sign of $C_{AZ}(\lambda)$ at two

values:

$$\begin{aligned}\lambda_0 &= 1 + \frac{(\hat{h} - h_2)(h_0 - h_2)}{h_2(1 - h_2)} \geq 0 \\ \lambda_1 &= 1 + \frac{(\hat{h} - h_2)(h_1 - h_2)}{h_2(1 - h_2)} \geq 0.\end{aligned}\tag{C.6a}$$

We find that $C_{AZ}(\lambda)$ changes sign between these values:

$$\begin{aligned}C_{AZ}(\lambda_0) &\propto (\hat{h} - h_2)(h_0 - h_1) \\ C_{AZ}(\lambda_1) &\propto (\hat{h} - h_2)(h_1 - h_0).\end{aligned}\tag{C.6b}$$

915 C.2 Special cases

Under random mating ($s_A = 0$), the ESS \hat{h} (C.5) reduces to $1/2$ and the dominant eigenvalue of local stability matrix \mathbf{M} (C.3) corresponds to

$$\frac{1}{2} \left(\frac{h_1}{h_2} + \frac{1 - h_1}{1 - h_2} \right).$$

This condition implies that the fixation state is locally stable only if

$$(1/2 - h_2)(h_2 - h_1) > 0,$$

confirming both (C.1) and the classical results of Fisher (1958, Chapter VI): an equal sex ratio at birth corresponds to an attracting ESS under random mating.

Under complete selfing ($s_A = 1$), the ESS \hat{h} (C.5) is equal to unity. Matrix \mathbf{M} (C.3) is triangular, with the fixation state locally stable to the introduction of the A allele only if

$$(1 - h_2)[h_2 - \max(h_0, h_1/2)] > 0,$$

918 again confirming (C.1).

Under complete dominance of the rare allele ($h_0 = h_1$), characteristic polynomial (C.4) reduces to

$$[(\lambda - 1)(1 - h_2) - (h_2 - \hat{h})(h_2 - h_0)/h_2][\lambda - s_A h_0/(2h_2)],$$

and the larger (r_L) and smaller (r_S) roots of (C.2) correspond to

$$\begin{aligned}r_L &= h_0 \\ r_S &= h_0 s_A / 2.\end{aligned}$$

Local stability requires that both

$$\begin{aligned}(\hat{h} - h_2)(h_2 - r_L) &> 0 \\ h_2 &> r_S.\end{aligned}\tag{C.7}$$

Because

$$\hat{h} > r_S,$$

921 the necessary and sufficient condition for local stability under complete dominance corresponds to the first inequality in (C.7), in accordance with (C.1).

C.3 General dominance and selection intensity

In the remainder of this section, we assume partial inbreeding ($0 < s_A < 1$) and $h_0 \neq h_1$.
 924 We first demonstrate that (C.1) implies positivity of the characteristic polynomial (C.4)
 evaluated at unity for all h_0 and h_1 . We then show that this necessary condition for local
 stability is in fact sufficient: the (non-negative) dominant eigenvalue of \mathbf{M} (C.3) is less than
 927 unity under (C.1).

Substitution of $\lambda = 1$ into the characteristic polynomial (C.4) indicates

$$C_{AZ}(1) \propto -(\hat{h} - h_2)q_{AZ}(h_2), \quad (\text{C.8})$$

for $q_{AZ}(h_2)$ given in (C.2). In accordance with our earlier exposition of the full recursion
 930 system (20), neutrality ($d_0 = d_1 = 0$) implies that the eigenvalue associated with allele
 frequency corresponds to unity, with the frequency of Aa heterozygotes converging to the
 state corresponding to F_{neut} (21) at rate $s_A/2$.

We now assume that d_0 or d_1 is non-zero ($h_0 \neq h_2$ or $h_1 \neq h_2$). Because only hermaphro-
 dites produce egg cells, the existence of the population monomorphic for the a allele implies
 $h_2 > 0$. If the rare allele determines complete male development ($h_0 = 0$ or $h_1 = 0$), then
 936 smaller root $r_S = 0$ and

$$C_{AZ}(1) \propto \begin{cases} (\hat{h} - h_2)[h_2 - h_1(1 - s_A/2)] & \text{if } h_0 = 0 \\ (\hat{h} - h_2)(h_2 - h_0 s_A) & \text{if } h_1 = 0. \end{cases} \quad (\text{C.9})$$

If $h_0 = 0$ and $C_{AZ}(1) > 0$, then (C.6) indicates that

$$\begin{aligned} h_2 < \hat{h} &\Rightarrow \lambda_0 < 1 \text{ and } C_{AZ}(\lambda_0) < 0 \\ \hat{h} < h_2 &\Rightarrow \lambda_1 < 1 \text{ and } C_{AZ}(\lambda_1) < 0, \end{aligned}$$

Similarly, under $h_1 = 0$ and $C_{AZ}(1) > 0$,

$$\begin{aligned} h_2 < \hat{h} &\Rightarrow \lambda_1 < 1 \text{ and } C_{AZ}(\lambda_1) < 0 \\ \hat{h} < h_2 &\Rightarrow \lambda_0 < 1 \text{ and } C_{AZ}(\lambda_0) < 0. \end{aligned}$$

These relationships indicate the existence of a root of characteristic polynomial $C_{AZ}(\lambda)$ in
 (0, 1), which confirms (31) and (C.1): $C_{AZ}(1) > 0$ is both necessary and sufficient for local
 939 stability under $h_0 = 0$ or $h_1 = 0$.

Restricting consideration to the remaining case ($h_0, h_1, h_2 > 0$), we find that $q_{AZ}(h_2)$
 (C.2) corresponds to a quadratic in h_2 with a negative leading term with

$$q_{AZ}(0), q_{AZ}(\max(h_0, h_1)) < 0 < q_{AZ}(\min(h_0, h_1)),$$

which implies that the larger (r_L) and smaller (r_S) roots of this quadratic lie in

$$\begin{aligned} r_L &\in (\min(h_0, h_1), \max(h_0, h_1)) \\ r_S &\in (0, \min(h_0, h_1)). \end{aligned} \quad (\text{C.10})$$

We first establish that

$$r_S < 1/2 \leq \hat{h} \tag{C.11}$$

for all h_0 and h_1 in $(0, 1]$. In cases satisfying

$$\min(h_0, h_1) < 1/2,$$

the smaller root r_S (C.10) lies below $1/2$ and consequently \hat{h} . If

$$1/2 < \min(h_0, h_1),$$

both d_0 and d_1 are positive for $h_2 = 1/2$, which implies

$$q_{AZ}(1/2) = [d_1(1 - s_A) + d_0 s_A(1 - h_1)]/2 > 0$$

942 and confirms (C.11).

For small h_2 , satisfying

$$h_2 < r_S < \hat{h}, \min(h_0, h_1), \tag{C.12}$$

945 $C_{AZ}(1) > 0$ (C.8) and both λ_0 and λ_1 exceed unity (C.6). That the quadratic characteristic polynomial (C.4) is negative at one of these values ($C_{AZ}(\lambda_1) < 0$ or $C_{AZ}(\lambda_0) < 0$) implies that an eigenvalue in excess of unity exists. We conclude that under (C.12), alleles that increase the proportion of hermaphrodites beyond the level specified by the resident homozygote (h_2) 948 increase when rare, confirming (C.1).

We now consider higher hermaphroditic frequencies at the fixation,

$$r_S < h_2, \tag{C.13}$$

under which (C.8) indicates

$$C_{AZ}(1) \propto (\hat{h} - h_2)(h_2 - r_L),$$

the left side of (C.1). Accordingly, (C.1) ($C_{AZ}(1) > 0$) is a necessary condition for local stability. We now demonstrate that it is in fact sufficient for local stability under (C.13). For

$$r_S < h_2 < \hat{h},$$

$C_{AZ}(1) > 0$ implies

$$r_S < \min(h_0, h_1) < r_L < h_2 < \hat{h}.$$

Expressions (C.6) indicate that if $h_1 > h_0$, $\lambda_0 < 1$ and $C_{AZ}(\lambda_0) < 0$. If $h_0 > h_1$, $\lambda_1 < 1$ and $C_{AZ}(\lambda_1) < 0$. We conclude that quadratic characteristic polynomial (C.4) is negative at a value (λ_0 or λ_1) less than unity, which implies that that $C_{AZ}(1) > 0$ (C.1) is sufficient for local stability. We now restrict consideration to

$$\hat{h} < h_2,$$

which together with $C_{AZ}(1) > 0$ implies

$$\hat{h} < h_2 < r_L < \max(h_0, h_1).$$

951 Similar to the preceding case, $h_1 > h_0$ implies $\lambda_1 < 1$ and $C_{AZ}(\lambda_1) < 0$, while $h_0 > h_1$ implies $\lambda_0 < 1$ and $C_{AZ}(\lambda_0) < 0$ (C.6). We again conclude that the quadratic characteristic polynomial (C.4) has a root less than unity, which implies that (C.1) is indeed necessary and sufficient for local stability.

954 C.4 Limits of the Li-Price equation

Here, we illustrate that the weak-selection assumption is essential to the heuristically-appealing Li-Price equation (19) and the change of basis that relates it to a full local stability analysis. We provide an example showing that under strong selection on the modifier locus, the key vector \tilde{z} (B.1) can become invalid and the sign of the characteristic polynomial evaluated at unity insufficient to determine the asymptotic fate of a rare allele introduced into a population monomorphic at the modifier locus.

Local stability matrix \mathbf{M} (C.3) represents the linearized transformation with respect to a basis comprising the frequencies of rare genotypes AA (δ_0) and Aa (δ_1). We adopt the new basis described in Appendix B, which comprises the frequency of the rare allele (A) and the departure of the heterozygote frequency from the proportion expected under neutrality ($h_0 = h_1 = h_2$):

$$\begin{aligned} t_0 &= \delta_0 + \delta_1/2 \\ t_1 &= \delta_0 - (\delta_0 + \delta_1/2)F_{neut}, \end{aligned} \quad (\text{C.14})$$

for

$$F_{neut} = s_A/(2 - s_A),$$

966 the fixation index under uniparental fraction s_A (9). Matrix \mathbf{A} ,

$$\mathbf{A} = \begin{pmatrix} 1 & 1/2 \\ 1 - F_{neut} & -F_{neut}/2 \end{pmatrix}, \quad (\text{C.15})$$

translates points from the original to the new coordinate system. In the original coordinate system, the key vector (B.1) \tilde{z} corresponds to

$$\mathbf{B}\tilde{z} = \begin{pmatrix} \tilde{\delta}_0 \\ \tilde{\delta}_1 \end{pmatrix}, \quad (\text{C.16})$$

969 for $\mathbf{B} = \mathbf{A}^{-1}$.

For illustrative purposes, we assume additivity in sex expression,

$$h_1 = (h_0 + h_2)/2, \quad (\text{C.17a})$$

and set

$$\begin{aligned} h_2 &= 1/4 \\ s_A &= 3/4. \end{aligned} \quad (\text{C.17b})$$

Under these assignments, the ESS \hat{h} corresponds to 7/8 and the characteristic polynomial evaluated at unity (C.8) reduces to

$$C_{AZ}(1) \propto (\hat{h} - h_2)(h_2 - h_0)[h_2(2 + s_A) - h_0s_A].$$

The sole condition for local stability (C.1), which reduces to

$$(\hat{h} - h_2)(h_2 - h_0) > 0,$$

972 indicates that the fixation of the a allele resists the invasion of the rare A allele only for

$$h_0 < h_2 = 1/4. \tag{C.18}$$

Indeed, the characteristic polynomial evaluated at unity $C_{AZ}(1)$ is positive in this range and changes sign at $h_0 = 1/4$. However, under intense selection,

$$h_0 > h_2(2 + s_A)/s_A = 11/12, \tag{C.19}$$

975 $C_{AZ}(1)$ is positive in spite of the local instability of the fixation state.

Key vector (B.1), which connects the local stability criterion to the Li-Price equation (19), remains valid only in the range

$$h_0 < 1/2.$$

Figure B1 plots $\tilde{\delta}_0$ and $\tilde{\delta}_1$, elements of key vector (C.16), as a function of the value of h_0 . The relative frequency of heterozygotes ($\tilde{\delta}_1$) becomes non-positive for $h_0 \geq 1/2$. In addition, 978 at $h_0 = 3/4$, the principal minor $\text{Det}[(\mathbf{I} - \mathbf{N})_{n-1}]$ in (B.3) passes through zero, inducing a discontinuity in the key vector (vertical line in Fig. B1).

This simple example illustrates that the connection between the Li-Price equation (19) 981 and the full local stability analysis holds only for weak selection, which corresponds under (C.17) to the range $0 < h_0 < 1/2$ under additivity of sex expression.

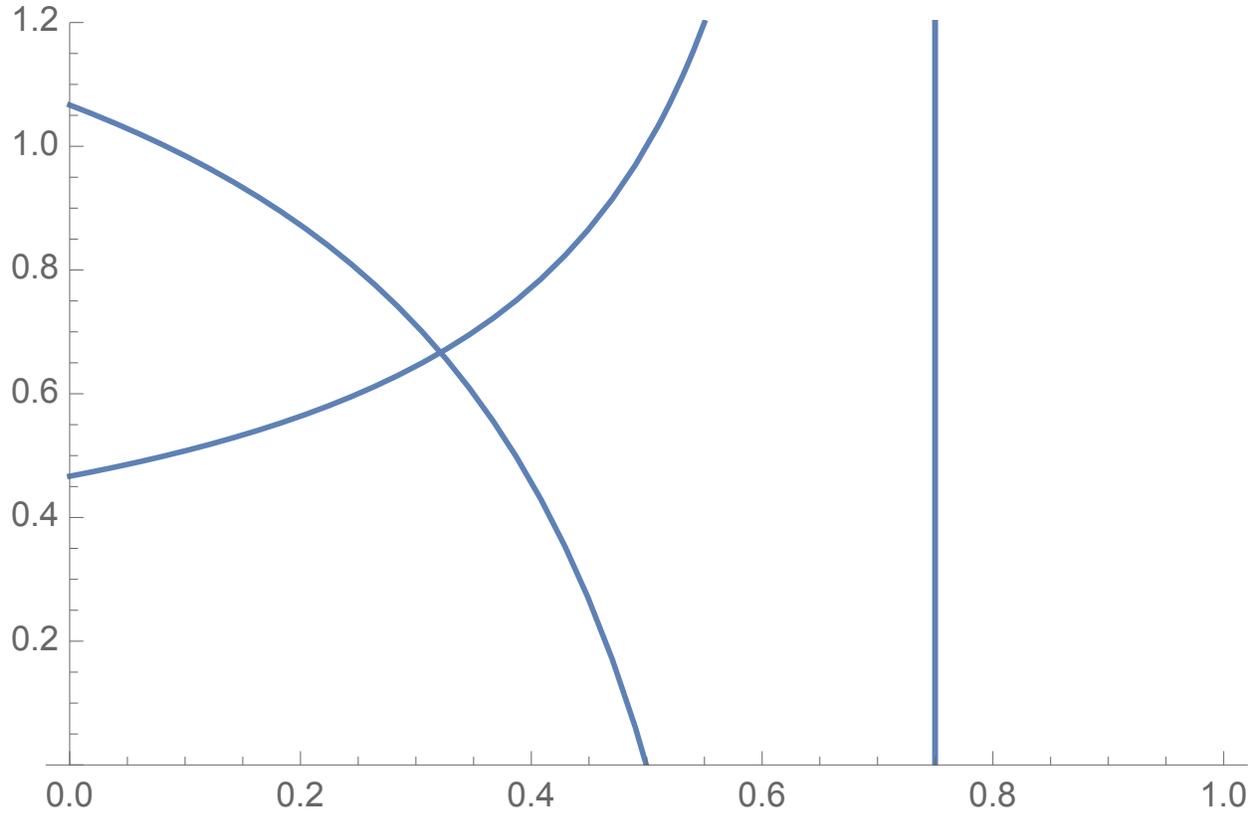


Figure B1: Relative magnitudes of the frequencies of rare homozygotes ($\tilde{\delta}_0$, increasing curve) and heterozygotes ($\tilde{\delta}_1$, declining curve) at the key vector (C.16) as a function of h_0 , the sex expression parameter associated with the rare homozygote. At the vertical bar ($h_0 = 3/4$), both elements have a discontinuity, which corresponds to the passage through zero of $\text{Det}[(\mathbf{I} - \mathbf{N})_{n-1}]$ in (B.3).

Tables

Table 1
Offspring production

Maternal Parent	Life Stage		
	Zygotes	Juveniles	Adults
Hermaphrodite	Uni	\tilde{s}	$s = \frac{\tilde{s}\tau}{\tilde{s}\tau+1-\tilde{s}}$
	Bi	$1 - \tilde{s}$	$1 - s = \frac{1-\tilde{s}}{\tilde{s}\tau+1-\tilde{s}}$
Female	Bi	$\tilde{\sigma}$	$\sigma = \frac{\tilde{\sigma}}{\tilde{s}\tau+1-\tilde{s}}$

Table 2
Phenotypic and genetic values

	Genotypes		
	<i>AA</i>	<i>Aa</i>	<i>aa</i>
Frequency	u_0	u_1	u_2
Trait deviation	$P_0 - \bar{P}$	$P_1 - \bar{P}$	$P_2 - \bar{P}$
Additive genotypic value	$2\alpha_0$	$\alpha_0 + \alpha_1$	$2\alpha_1$
Fitness deviation	$T(u'_0 - u_0)/u_0$	$T(u'_1 - u_1)/u_1$	$T(u'_2 - u_2)/u_2$

984 Figures

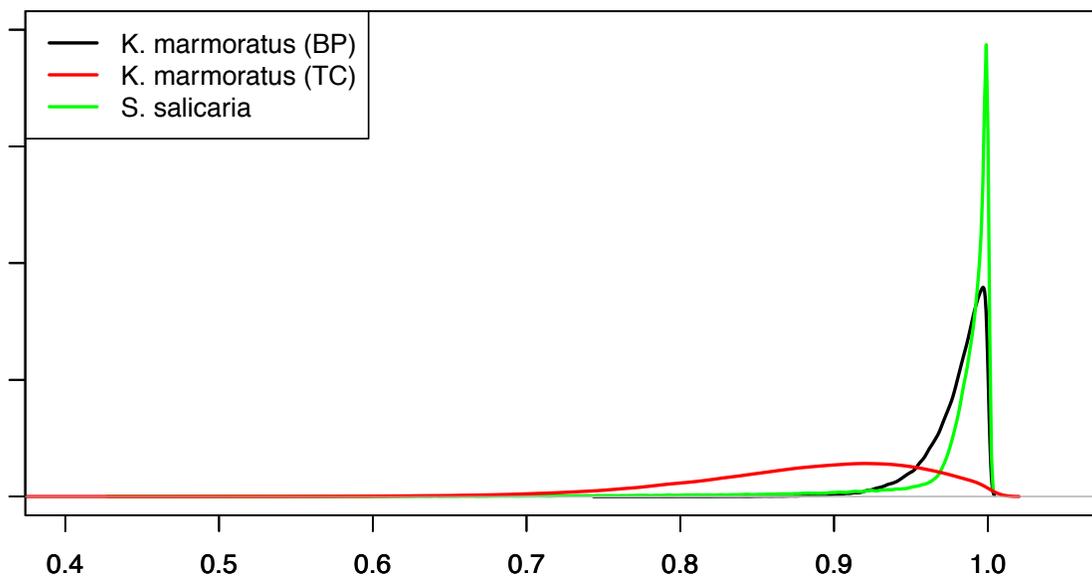


Figure 1: Posterior distributions of relative effective number $R(2)$.

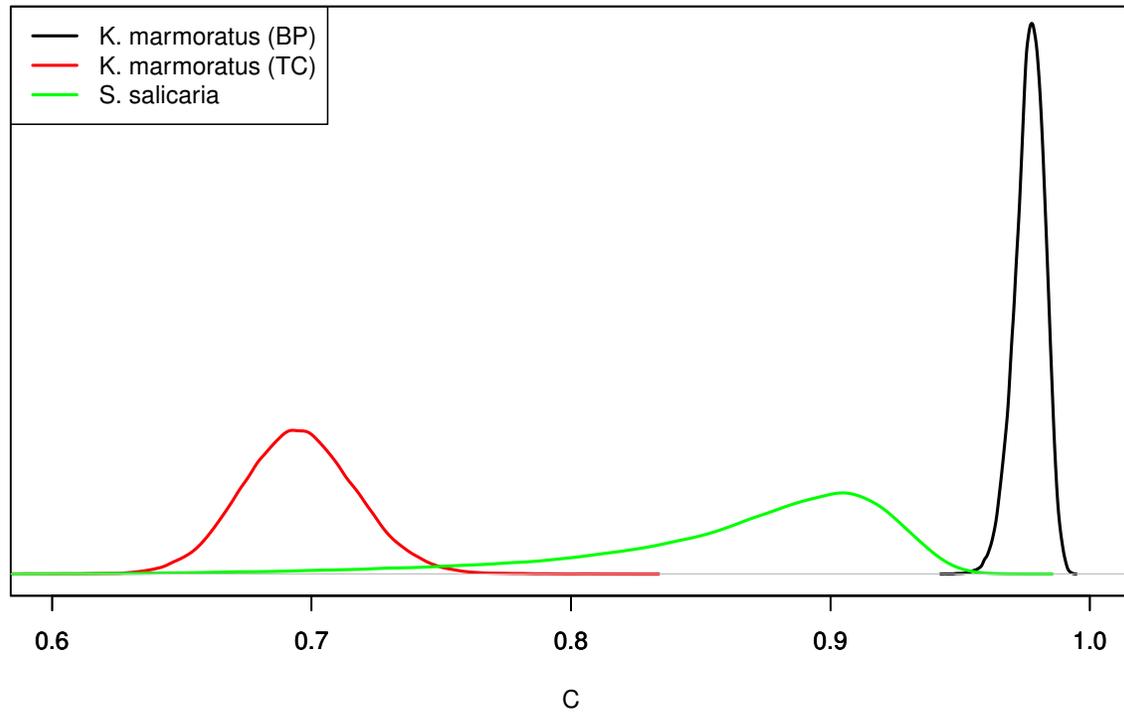


Figure 2: Posterior distributions of the collective contribution of hermaphrodites to the population gene pool (C) for two populations of androdioecious *Kryptolebias marmoratus* and for gynodioecious *Schiedea salicaria*.

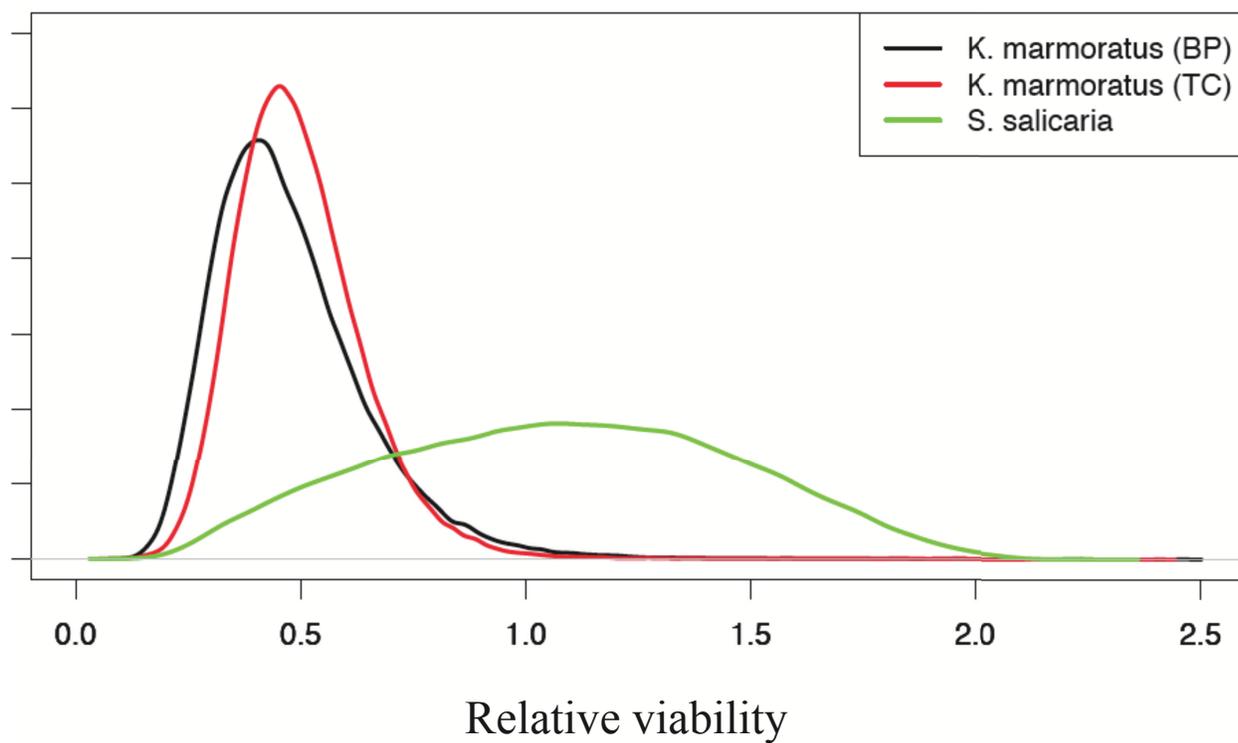


Figure 3: Posterior distributions of the viability of gonochores relative to hermaphrodites (Z).

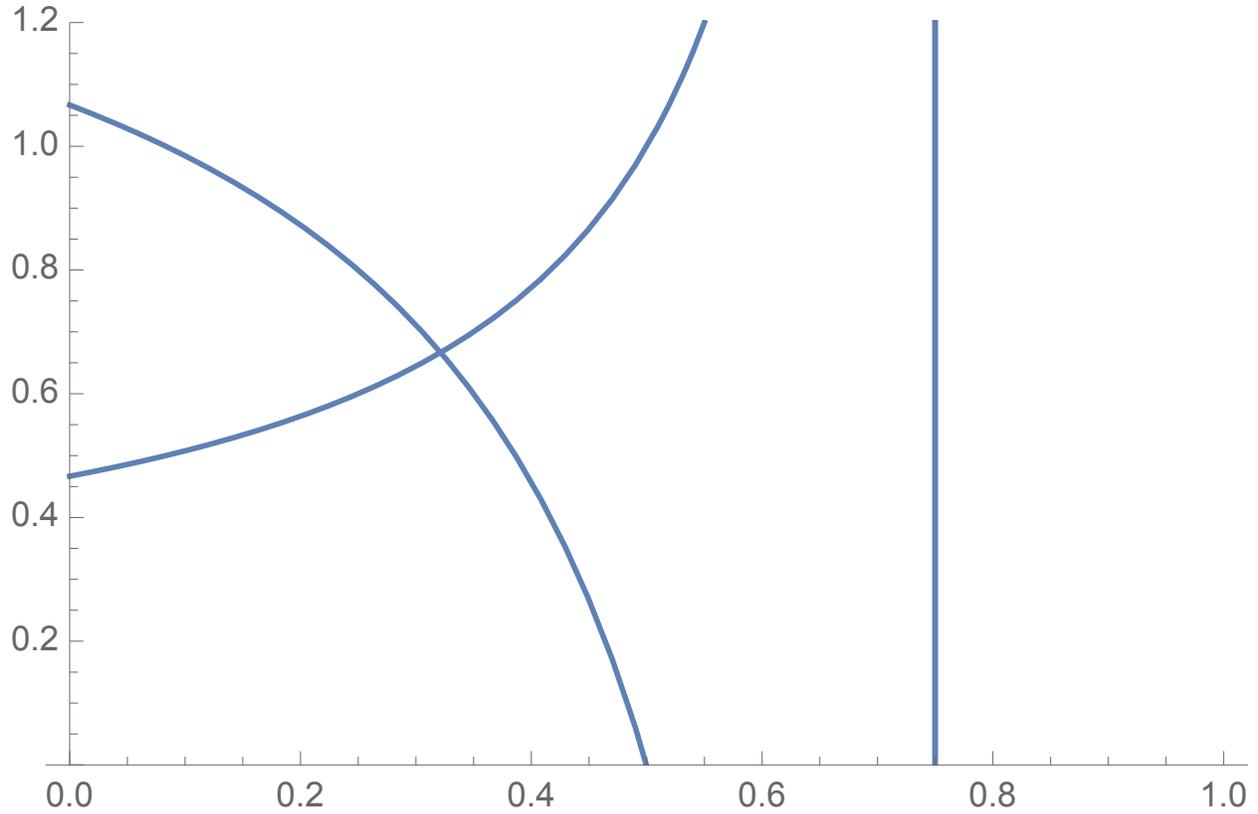


Figure B1: Relative magnitudes of the frequencies of rare homozygotes ($\tilde{\delta}_0$, increasing curve) and heterozygotes ($\tilde{\delta}_1$, declining curve) at the key vector (C.16) as a function of h_0 , the sex expression parameter associated with the rare homozygote. At the vertical bar ($h_0 = 3/4$), both elements have a discontinuity, which corresponds to the passage through zero of $\text{Det}[(\mathbf{I} - \mathbf{N})_{n-1}]$ in (B.3).