

Frequency-dependent population dynamics: Effect of sex ratio and mating system on the elasticity of population growth rate



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ABSTRACT

When vital rates depend on population structure (e.g., relative frequencies of males or females), an important question is how the long-term population growth rate λ responds to changes in rates. For instance, availability of mates may depend on the sex ratio of the population and hence reproductive rates could be frequency-dependent. In such cases change in any vital rate alters the structure, which in turn, affect frequency-dependent rates. We show that the elasticity of λ to a rate is the sum of (i) the effect of the linear change in the rate and (ii) the effect of nonlinear changes in frequency-dependent rates. The first component is always positive and is the classical elasticity in density-independent models obtained directly from the population projection matrix. The second component can be positive or negative and is absent in density-independent models. We explicitly express each component of the elasticity as a function of vital rates, eigenvalues and eigenvectors of the population projection matrix. We apply this result to a two-sex model, where male and female fertilities depend on adult sex ratio α (ratio of females to males) and the mating system (e.g., polygyny) through a harmonic mating function. We show that the nonlinear component of elasticity to a survival rate is negligible only when the average number of mates (per male) is close to α . In a strictly monogamous species, elasticity to female survival is larger than elasticity to male survival when $\alpha < 1$ (less females). In a polygynous species, elasticity to female survival can be larger than that of male survival even when sex ratio is female biased. Our results show how demography and mating system together determine the response to selection on sex-specific vital rates.

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1. Introduction

Demographic rates are *frequency-dependent* when they depend only on the relative frequencies of different types of individuals (“males” and “females”) and not on their absolute densities. For instance, demographic differences between males and females are common in several species (Caswell and Weeks, 1988) and availability of mates may depend on the sex ratio (ratio of females to males) of the population (Bessa-Gomes et al., 2004). Single-sex models may not be appropriate in such contexts (Rankin and Kokko, 2007) and population dynamics is better described by two-sex models where births depend on the sex ratio through a non-linear mating function (McFarland, 1972). Recently, there is a

growing interest in the use of frequency-dependent models, especially two-sex models, to understand population and evolutionary dynamics of a range of different species including, the bean beetles (*Callosobruchus maculatus*, Miller and Inouye, 2011), emperor penguins (*Aptenodytes forsteri*, Jenouvier et al., 2010), green-rumped parrotlets (*Forpus passerinus*, Veran and Beissinger, 2009), marine angiosperms (*Phyllospadix scouleri*, Shelton, 2010), common lizards (*Lacerta vivipara*, Le Galliard et al., 2005) and ungulates (Myerud et al., 2002). A salient feature of a frequency-dependent model is that, though non-linear in the vital rates, it can have a long-term growth rate λ , analogous to stage-structured density-independent models (Nussbaum, 1988). However, in contrast to density-independent models (Caswell, 2001), less is known about the properties of the response of λ to change in a vital rate (e.g., survival), known as sensitivity or elasticity, in the case of a proportional change. Elasticity analysis is an important tool in ranking management decisions (e.g. improving survival vs fertility, Morris and Doak, 2002) and in quantifying the response to selection on

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vital rates (selection gradient) and hence is used in evolutionary predictions (Charlesworth, 1994).

Predicting the effect of changing a vital rate on λ is challenging in frequency dependent models because change in a vital rate changes the stage-structure which produces secondary changes in parameters that depend on stage frequencies. For instance, in a two-sex model where fertility depends on adult sex ratio, increasing female adult survival would increase sex ratio (ratio of females to males) and change fertility. Hence, the elasticity of population growth rate depends on two effects: one due to direct linear changes in a parameter and the other due to nonlinear changes in stage structure acting through frequency-dependent parameters. For frequency-dependent models Caswell (2008) expressed the elasticity in terms of derivatives of vital rates and the stage-structure. However, for a qualitative understanding and making predictions about how frequency-dependence in a parameter affects the sign and magnitude of elasticity and how elasticity in a frequency-dependent model differs from its linear counterpart, one needs to express elasticity in terms of the vital rates and eigenvalues and eigenvectors of equilibrium projection matrix, as is readily done in density-independent models.

In this work we first present an explicit analytical formula for the elasticity of the population growth rate in a frequency-dependent model. We show that the frequency-dependent elasticity is the sum of the classical linear elasticity (obtained from the equilibrium projection matrix) and a non-linear component that depends on the relationship between vital rates and stage frequencies. Our formula, expressed in terms of the vital rates and eigenvalues and eigenvectors, is easy to calculate and provides clear insights into how the nature of frequency-dependence affects the elasticity of λ . We then apply this formula to explicitly derive elasticities in a two-sex model where male and female fertilities depend on the adult sex ratio and the average number of female mates per male (or harem size as in a polygynous species). We show how sex ratio and mating behavior (e.g., monogamy, polygyny) together determine the response of population growth rate to changes in sex-specific vital rates.

2. Frequency-dependent models

A general form of a frequency-dependent population model is given by

$$\mathbf{P}_t = \mathbf{A}(\mathbf{u}_{t-1})\mathbf{P}_{t-1} \quad (1)$$

where \mathbf{P}_t is the population vector in year t denoting the number of individuals in different stages. These stages could be a combination of different attributes, like age and sex or sex and size of an individual. The projection matrix $\mathbf{A}(\mathbf{u}_{t-1})$ consists of vital rates $A_{ij}(\boldsymbol{\theta}, \mathbf{u}_{t-1})$ where $\boldsymbol{\theta}$ is a vector of parameters and \mathbf{u}_{t-1} is the vector of stage frequencies. In general all vital rates could depend on the stage-structure \mathbf{u}_{t-1} . We assume that the rates are homogeneous functions of the stage structure of degree 0 (a non-negative function f is homogeneous of degree 0 if $f(\lambda x) = f(x)$, for every x and $\lambda > 0$), which assures that the rates depend only on the relative frequencies of the stages and not on absolute abundances. It is known for such models that the stage structure eventually approach an equilibrium (stable stage distribution, SSD) \mathbf{u} and correspondingly the long-term dynamics can be described by the projection matrix $\mathbf{A}(\mathbf{u})$ whose elements depend on \mathbf{u} (Nussbaum, 1988; Caswell and Weeks, 1988). At this demographic equilibrium, the population growth is given by the dominant eigenvalue λ of $\mathbf{A}(\mathbf{u})$.

A well-known example where frequency-dependence arises is a two-sex model (e.g., Lindström and Kokko, 1998). A form of

this model (at equilibrium) is given by the equation (Caswell and Weeks, 1988)

$$\begin{pmatrix} N_{new} \\ N_{1f} \\ N_{2f} \\ N_{1m} \\ N_{2m} \end{pmatrix}_t = \begin{pmatrix} 0 & 0 & F_f & 0 & F_m \\ \rho S_1 & 0 & 0 & 0 & 0 \\ 0 & S_{1f} & S_{2f} & 0 & 0 \\ (1-\rho)S_1 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & S_{1m} & S_{2m} \end{pmatrix} \times \begin{pmatrix} N_{new} \\ N_{1f} \\ N_{2f} \\ N_{1m} \\ N_{2m} \end{pmatrix}_{t-1}, \quad (2)$$

where N_{new} denotes number of newborns (including males and females), N_{1f} and N_{1m} denote, respectively, numbers of immature females and males and N_{2f} and N_{2m} denote numbers of reproducing adult females and males, respectively. F_f and F_m are female and male fertility rates, ρ is the fraction of females at birth, S_1 is survival rate of newborns, S_{1f} and S_{1m} are survival rates of immature females and males, and S_{2f} and S_{2m} are survival rates of adult females and males, respectively. Further, assume that both fertilities are determined by the fraction of females and males and is captured by a harmonic fertility function (Caswell and Weeks, 1988), given by

$$F_f = N_{2m}/(N_{2m} + (N_{2f}/h)) \quad (3)$$

and

$$F_m = N_{2f}/(N_{2m} + (N_{2f}/h)). \quad (4)$$

The parameter h represents the average number of females that a male mates with and can also be interpreted as the harem size as in a polygynous species ($h > 1$) though it applies to all mating systems including monogamy ($h = 1$) and polyandry ($h < 1$; Rosen, 1983). Fertility functions are usually derived from the male and female contributions to the total number of births, which could depend upon the relative fractions of males and females in the population. The harmonic fertility function makes the model in Eq. (2) frequency dependent (Nussbaum, 1988; Caswell and Weeks, 1988). In terms of adult sex ratio $\alpha = N_{2f}/N_{2m}$, we have $F_f = 1/(1 + (\alpha/h))$ and $F_m = \alpha/(1 + (\alpha/h))$, so that fertilities depend only on the fraction of females to males and not on their densities. Other forms of fertility functions have been discussed in the literature (e.g. McFarland, 1972), but the harmonic function has more empirical support, and has been shown to better capture the effect of both sexes on reproduction (e.g. Miller and Inouye, 2011).

3. Elasticity of λ in frequency-dependent models

For the frequency-dependent model given by Eq. (1), the elasticity of λ with respect to a parameter θ is the proportional change in λ when θ is increased by a small percentage. When a vital rate does not depend on the stage-structure we denote it simply by $A_{ij}(\boldsymbol{\theta})$. For the sake of brevity, we assume that parameters appearing in a given vital rate (i.e., a matrix element) do not appear in other vital rates. Elasticity to a parameter that appears in more than one vital rate (like the ρ or h in the two-sex model above) can be calculated from contributions from all vital rates using a chain rule (e.g., Eq. (9.101) of Caswell, 2001). Below we outline the general dynamics of the effect of perturbation of a parameter on λ , a detailed derivation is given in the online Appendix A.

The one-step growth rate, between years $t - 1$ and t , is given by $\lambda_t = N_t/N_{t-1}$ where N_t is the total size in year t . This can be written as,

$$\lambda_t = |\mathbf{A}(\mathbf{u}_{t-1}) \mathbf{u}_{t-1}|, \quad (5)$$

where $|\mathbf{A}(\mathbf{u}_{t-1}) \mathbf{u}_{t-1}|$ denotes the sum of elements of the vector $\mathbf{A}(\mathbf{u}_{t-1}) \mathbf{u}_{t-1}$. In the long-run, λ_t converges to the long-term

growth rate λ , which is equal to the dominant eigenvalue of the matrix $\mathbf{A}(\mathbf{u})$, where \mathbf{u} is the SSD. Hence elasticities e_t of λ_t converge to the elasticity e of λ (Haridas and Tuljapurkar, 2007).

The growth of the unperturbed population, starting from an initial stage-structure \mathbf{u}_0 , can be represented as: $\mathbf{u}_0 \xrightarrow[\lambda_1]{\mathbf{A}(\mathbf{u}_0)} \mathbf{u}_1 \xrightarrow[\lambda_2]{\mathbf{A}(\mathbf{u}_1)}$

$\mathbf{u}_2 \cdots \rightarrow \mathbf{u}_{t-1} \xrightarrow[\lambda_t]{\mathbf{A}(\mathbf{u}_{t-1})} \mathbf{u}_t \rightarrow \cdots$. First consider the perturbation of a parameter θ in a vital rate $A_{ij}(\theta)$ that *does not depend* on the stage-structure (e.g., S_1 , the survival of newborns in Eq. (2)): let θ be increased by the *same* proportion ϵ every year, $\theta \rightarrow \theta + \epsilon\theta$, where ϵ is small. This changes the vital rate $A_{ij}(\theta) \rightarrow A_{ij}(\theta + \epsilon\theta)$, which, up to first order, is equal to $A_{ij}(\theta) + \epsilon\theta \partial A_{ij}(\theta)$. Hence stage structure \mathbf{u}_1 will change to $\hat{\mathbf{u}}_1$ and in general \mathbf{u}_t will change to $\hat{\mathbf{u}}_t$. The new stage distribution in year t can be written, up to first order, as $\hat{\mathbf{u}}_t = \mathbf{u}_t + \epsilon \mathbf{w}_t$, where \mathbf{w}_t is the change in stage structure which satisfies a recurrence relationship (see Appendix A). Vital rates that depend upon \mathbf{u}_t will also change correspondingly: let $A_{kl}(\mathbf{u}_t) \rightarrow A_{kl}(\mathbf{u}_t + \epsilon \mathbf{w}_t)$ which, up to first order, is equal to $A_{kl}(\mathbf{u}_t) + \epsilon \mathbf{w}_t' \partial A_{kl}(\mathbf{u}_t)$, where \mathbf{w}_t' is the row vector and $\partial A_{kl}(\mathbf{u}_t)$ is the column vector of derivatives of the vital rate with respect to components of the stage-structure. For instance, in the two-sex model (Eq. (2)) increasing adult female survival (S_{2f}) increases female density and the resulting increase in sex ratio α , affects fertilities of both sexes (F_f and F_m). The term $\mathbf{w}_t' \partial A_{kl}(\mathbf{u}_t)$ captures the effect of frequency-dependence and shows the fundamental difference in the response of λ from a stage-structured density-independent model.

From Eq. (5) we infer that the change in λ_t when the parameter θ is perturbed, is determined by the change in the matrix $\mathbf{A}(\mathbf{u}_{t-1})$ and the change in stage structure \mathbf{w}_t , which approaches \mathbf{w} as the population approaches the SSD, \mathbf{u} . Then, the elasticity $e_{ij}(\theta)$ of λ with respect to the parameter θ is given by (see Appendix A for the complete derivation)

$$e_{ij}(\theta) = E_{lin} + E_{nonlin}, \quad (6)$$

where the first component $E_{lin} = \theta \partial A_{ij}(\theta) v(i) u(j) / \lambda$, where $v(\cdot)$ are the components of \mathbf{v} , the left eigenvector of $\mathbf{A}(\mathbf{u})$. Note that E_{lin} is precisely the classical linear elasticity of λ with respect to the parameter θ (Caswell, 2001: Eqs. (9)–(101); see also Appendix A), evaluated directly from the projection matrix $\mathbf{A}(\mathbf{u})$. The second component $E_{nonlin} = \sum_{kl} C_{kl} v(k) u(l) / \lambda$ is the non-linear part of elasticity that arises entirely due to frequency-dependence, where the coefficient $C_{kl} = \mathbf{w}' \partial A_{kl}(\mathbf{u})$, $(k, l) \neq (i, j)$. Caswell (2008: Eq. (97)) used matrix calculus to derive sensitivity of λ in terms of derivatives of vital rates and the stage-structure.

Finally, consider the perturbation of a parameter θ in a vital rate $A_{ij}(\theta, \mathbf{u}_{t-1})$ that *does depend* on the stage structure (e.g., the harem size h in the two-sex model, appearing in the vital rates F_f and F_m which depend on the stage-structure through sex ratio). Perturbation of θ will change $A_{ij}(\theta, \mathbf{u}_{t-1})$ to $A_{ij}(\theta + \epsilon\theta, \mathbf{u}_{t-1} + \epsilon \mathbf{w}_{t-1})$, which, up to first order, can be written as $A_{ij}(\theta, \mathbf{u}_{t-1}) + \epsilon(\theta \partial A_{ij}(\theta) + \mathbf{w}_{t-1}' \partial A_{ij}(\mathbf{u}_{t-1}))$. Any other vital rate $A_{kl}(\mathbf{u}_{t-1})$, $(k, l) \neq (i, j)$, that depends on the stage structure, will also change. Hence the elasticity of λ to θ in this case is the same as given in Eq. (6) except that $E_{nonlin} = (1/\lambda) \{ C_{ij} v(i) u(j) + \sum_{kl \neq ij} C_{kl} v(k) u(l) \}$.

4. Implications

(1) Eq. (6) shows that, in the presence of frequency dependence, the response of λ to a change in a parameter is different from the linear response (given by E_{lin}) by an amount equal to E_{nonlin} . The sign and magnitude of E_{nonlin} depend upon the nature of the relationship between the (frequency-dependent) vital rate and the frequencies of different stages. For instance, in the two-sex model

the female fertility decreases with adult sex ratio, while the male fertility increases (see Caswell and Weeks, 1988, Fig. 3a, c) so that contributions from male and female fertility to λ will have opposite signs. In the two-sex model we can explicitly determine the sign of E_{nonlin} in terms of the adult sex ratio and the harem size, as we show below (see Eq. (7)).

(2) Since our analysis can be used to describe the change in λ_t , above formulas can be applied to analyzing transient elasticities in frequency-dependent models (see Appendix A).

5. Explicit forms of elasticities in a two-sex model

We now use our general analytical results to first calculate elasticities of λ to male and female survival rates and then to the harem size h in the two-sex model in Eq. (2). We illustrate how sex ratio and the mating system (ie., monogamy, polygyny and polyandry), as described by different harem sizes h , affect elasticities.

5.1. Elasticity of λ to survival rates

Here we focus on the elasticity to immature female survival S_{1f} ; elasticities to other survival rates are derived similarly (see Appendix B). Suppose S_{1f} is increased by a small proportion, $S_{1f} \rightarrow S_{1f} + \epsilon S_{1f}$, so that the stable-stage distribution $\mathbf{u} = (u_1, u_2, u_3, u_4, u_5)'$ changes to $\mathbf{u} + \epsilon \mathbf{w}$, where $\sum_i u_i = 1$. The linear component of the elasticity (E_{lin} , Eq. (6)) is given by $(S_{1f}/\lambda) v_3 u_2$, as derived from linear matrix models (Caswell, 2001), where u_2 is the proportion of immature females and v_3 is the reproductive value of adult females. Note that the linear component of the elasticity of S_{1f} is the same as that of the linear component of the survival rate S_{1m} of immature males because of the matrix model structure (Figs. 1b, 2b, 3b, 4b; see Appendix B). The nonlinear component (E_{nonlin}) is given by

$$E_{nonlin} = (1/\lambda) C_{1,3} u_3 v_1 \left(1 - \frac{h}{\alpha} \right), \quad (7)$$

where $C_{1,3}$ is the change in female fecundity F_f due to the changes in S_{1f} , u_3 is the proportion of adult females in the (unperturbed) population and v_1 is the reproductive value of the newborns (see Appendix B). Here $C_{1,3}$ is negative (female fertility decreases with α , see Appendix B) and note that h/α is the average number of matings per male weighted by the reciprocal of adult sex ratio. When $h = \alpha$, every male has a harem where all females gather leaving no female or male unmated, and hence the nonlinear component $E_{nonlin} = 0$. When $h > \alpha$, all females gather in harems and get access to males and hence E_{nonlin} is positive. Hence the effect of improving female survival is larger than expected from a model that ignores the effect of changing sex ratios. When $h < \alpha$, not every female has access to males and increasing female survival only increases the competition for males and hence E_{nonlin} is negative (see below). Below we show the elasticities of female and male survival for species with different mating systems. In all cases, we assume that the proportion of females at birth, $\rho = 0.5$.

5.2. Harem size $h = 1$ (Monogamy)

Under monogamy, ($h = 1$), elasticities of λ to female and male survival rates coincide with the linear elasticities only when adult sex ratio $\alpha = 1$, since in this case the non-linear component is zero (Fig. 1b, c). The non-linear components of elasticities (E_{nonlin}) to female survival rates (S_{1f} and S_{2f}) are negative when $\alpha > 1$, positive when $\alpha < 1$ and equal to 0 when $\alpha = 1$ (Fig. 1a). Corresponding components for male survival rates (S_{1m} and S_{2m}) are positive when $\alpha > 1$, negative when $\alpha < 1$ and equal to 0 when $\alpha = 1$ (Fig. 1a).

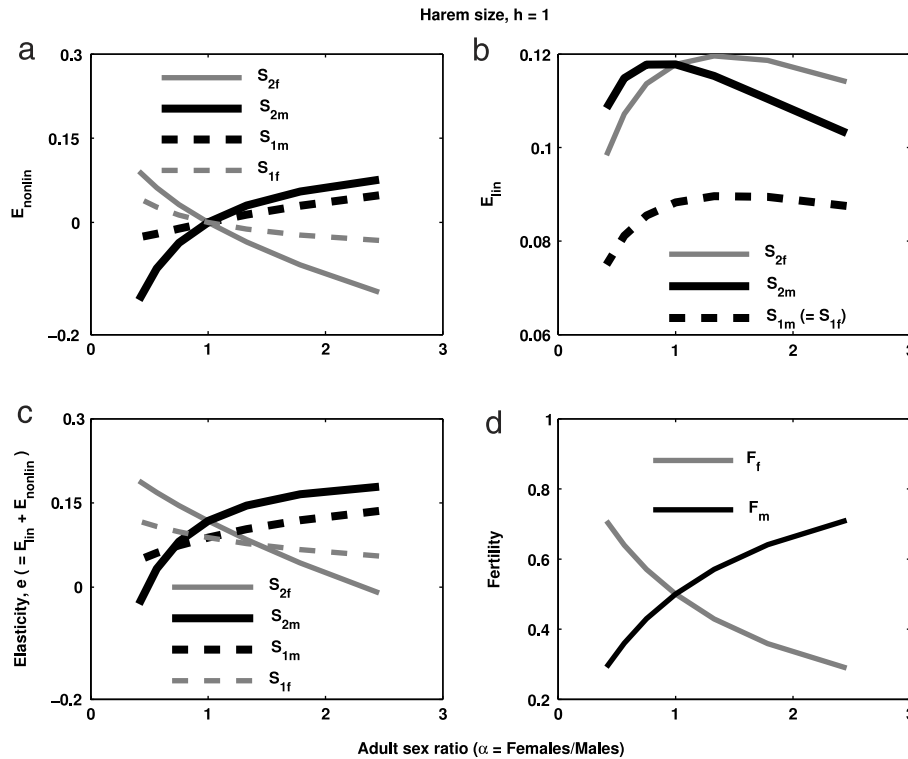


Fig. 1. Elasticities in a monogamous ($h = 1$) species: (a) Non-linear components (E_{nonlin}) of elasticities to female (S_{1f} , S_{2f}) and male (S_{1m} , S_{2m}) survival rates as a function of the adult sex ratio α . (b) Linear components (E_{lin}) of elasticities to female and male survival rates. (c) Elasticities ($e = E_{nonlin} + E_{lin}$) to female and male survival rates. (d) Female (F_f) and male (F_m) fertilities. Primary sex ratio $\rho = 0.5$, juvenile survival $S_1 = 0.6$ and harem size $h = 1$ in all cases. Sex ratio α on the x-axis is varied by fixing $S_{1f} = 0.65$ and varying all other survival rates from 0.5 to 0.8 in steps of 0.05.

Note that female fertility (F_f) decreases, while male fertility (F_m) increases with α (Fig. 1d) producing the opposite effects in the non-linear component of elasticity. Further, elasticity to adult female survival (S_{2f}) can be negative (i.e., λ decreases when adult female survival increases) as the sex ratio becomes more female skewed because the negative non-linear effect due to reduced fertility exceeds the positive linear effect that is entirely due to increased survival (Fig. 1a, b, c). Similarly, elasticity to adult male survival (S_{2m}) is negative (Fig. 1c) when sex ratio becomes more male skewed reducing male fertility (Fig. 1d). The rankings of vital rates in terms of their elasticities (e , Fig. 1d) differ from those predicted by the linear effects (E_{lin}) only (Fig. 1b): for instance, for female biased populations ($\alpha > 1$), male adult survival (S_{2m}) has the highest elasticity, while E_{lin} is highest for female adult survival. Furthermore, there are age-specific effects within each sex: female adult survival has larger elasticity than survival of immature (S_{1f}) when $\alpha < 1.5$, but as the population becomes more female skewed, survival of immature individuals becomes more elastic (Fig. 1c). Note that in many long-lived species, single-sex (female) models predict adult survival to be the most elastic vital rate (Gaillard et al., 2005). There is a similar switch in the age-specific ranking of elasticities of male survival rates (Fig. 1c).

5.3. Harem size $h > 1$ (Polygyny)

A polygynous species, where a single male mates with more than one female, can be described by $h > 1$. First note that even when males and females are equally abundant (i.e., $\alpha = 1$), elasticities of immature and adult survival rates are different for males and females and they are different from their respective linear components (Fig. 2b, c), unlike in the monogamous case. However, elasticities do coincide with their linear components (Fig. 2b) when $h/\alpha = 1$, when the nonlinear components vanish (Fig. 2a; see Eq. (7)). Secondly, elasticities of female survival rates can be

larger than that of male survival rates even when sex ratio is female biased ($\alpha > 1$) but this reverses as α becomes more female skewed ($\alpha \gg 2.2$, Fig. 2c). As the harem size increases, female survival rates always have higher elasticities than male survival rates ($h = 15$, Fig. 3c). Note that as harem size increases, female fertility becomes less dependent on the sex ratio (Fig. 3d) (since most females mate) and hence selection for increased female survival will result in larger population growth rate.

5.4. Harem size $h < 1$ (Polyandry)

In a polyandrous species a single female mates with several males, which in our model is equivalent to $h < 1$ (Rosen, 1983). As in the polygynous case, elasticities of survival rates of immature and adult individuals differ between the sexes and they are different from their respective linear components, even when sex ratio $\alpha = 1$ (Fig. 4c). In exact opposite to the polygynous case, elasticities of male survival rates can be larger than that of female survival rates even when sex ratio is male biased ($\alpha < 1$) but decreases when $\alpha < 0.5$ (Fig. 4c). When male abundance is large so that not all of them can be mated by females, increasing male survival reduces λ and hence one would expect selection against higher male survival rates.

5.5. Elasticity of λ to harem size h

Average harem size h affects both fertility rates (F_f and F_m) so that elasticity of λ to h will have contributions from changes in male and female fertilities (see Appendix B). When harem size $h < 1$ (polyandry, where a female has many male partners) and sex ratio is female skewed ($\alpha > 1$), increase in harem size increases elasticity of λ with respect to h (Fig. 5a). Note that increase in h would provide more females with males. At higher harem sizes ($h \geq 1$, representing monogamy and polygyny), elasticity

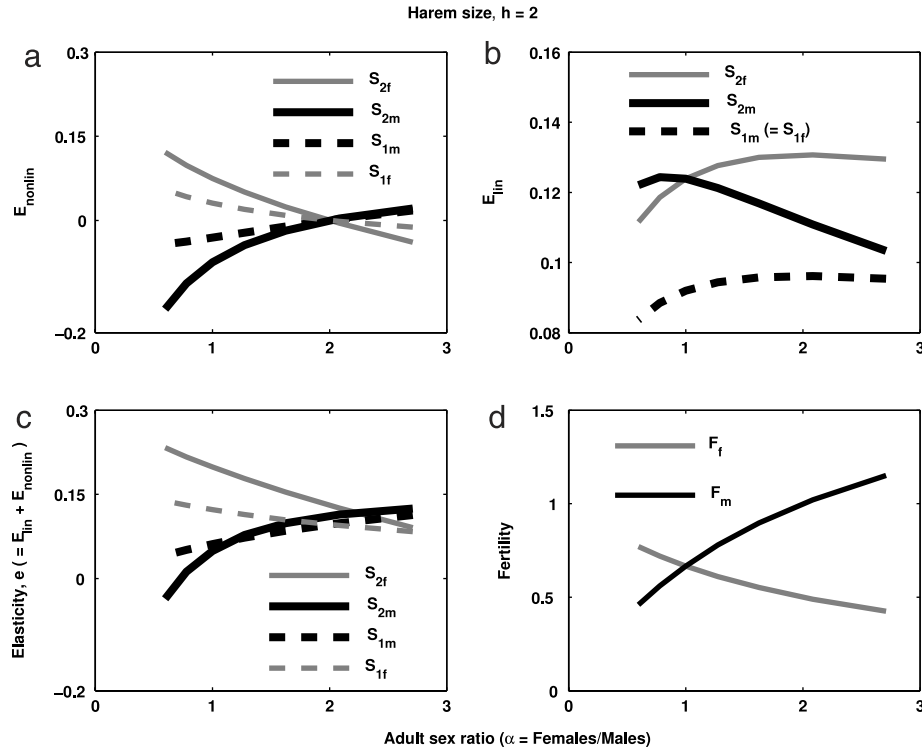


Fig. 2. Elasticities in a polygynous ($h = 2$) species: (a) Non-linear components (E_{nonlin}) of elasticities to female (S_{1f} , S_{2f}) and male (S_{1m} , S_{2m}) survival rates as a function of the adult sex ratio α . (b) Linear components (E_{lin}) of elasticities to female and male survival rates. (c) Elasticities ($e = E_{nonlin} + E_{lin}$) to female and male survival rates. (d) Female (F_f) and male (F_m) fertilities. Primary sex ratio $\rho = 0.5$, juvenile survival $S_1 = 0.6$ and harem size $h = 2$ in all cases. Sex ratio α on the x-axis is varied by fixing $S_{1f} = 0.7$ and varying all other survival rates from 0.5 to 0.8 in steps of 0.05.

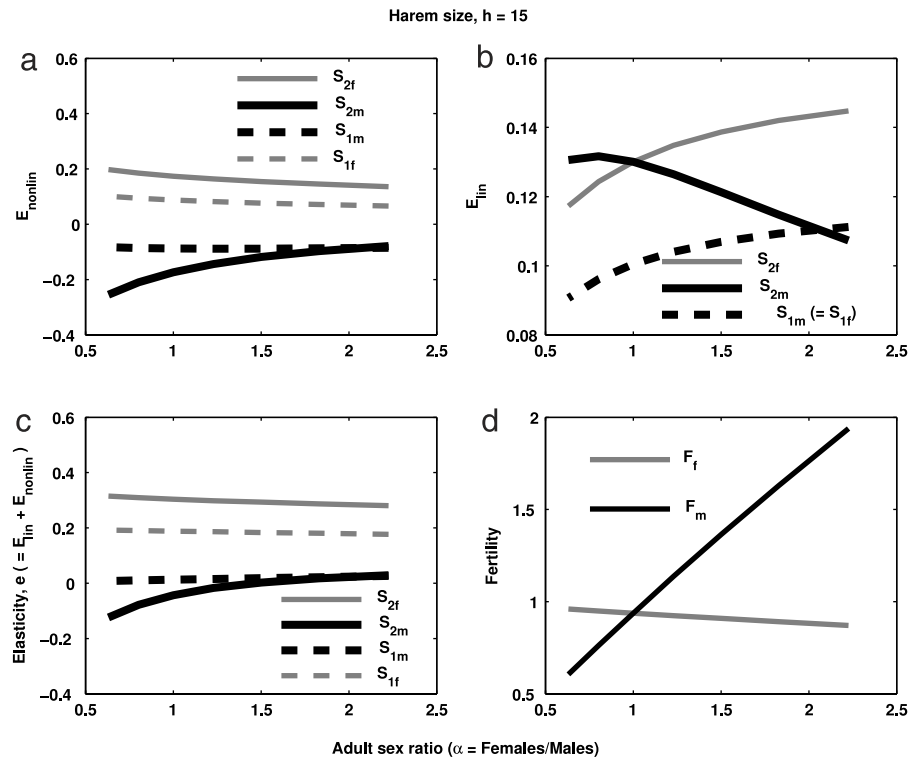


Fig. 3. Elasticities in a polygynous ($h = 15$) species: (a) Non-linear components (E_{nonlin}) of elasticities to female (S_{1f} , S_{2f}) and male (S_{1m} , S_{2m}) survival rates as a function of the adult sex ratio α . (b) Linear components (E_{lin}) of elasticities to female and male survival rates. (c) Elasticities ($e = E_{nonlin} + E_{lin}$) to female and male survival rates. (d) Female (F_f) and male (F_m) fertilities. Primary sex ratio $\rho = 0.5$, juvenile survival $S_1 = 0.6$ and harem size $h = 15$ in all cases. Sex ratio α on the x-axis is varied by fixing $S_{1f} = 0.7$ and varying all other survival rates from 0.5 to 0.8 in steps of 0.05.

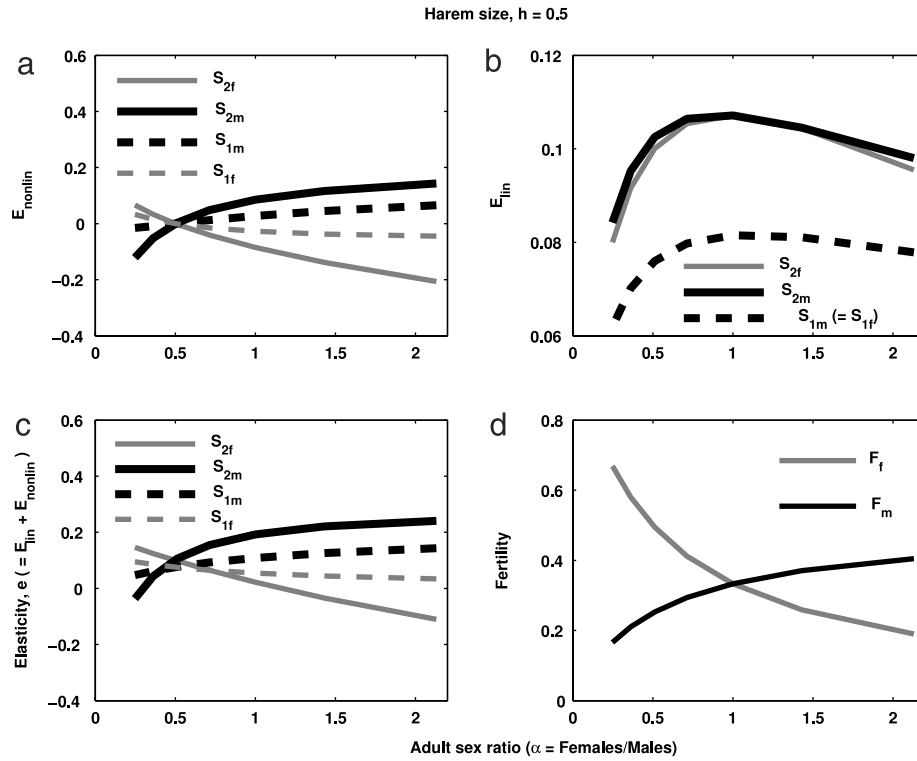


Fig. 4. Elasticities in a polyandrous ($h = 0.5$) species: (a) Non-linear components (E_{nonlin}) of elasticities to female (S_{1f} , S_{2f}) and male (S_{1m} , S_{2m}) survival rates as a function of the adult sex ratio α . (b) Linear components (E_{lin}) of elasticities to female and male survival rates. (c) Elasticities ($e = E_{nonlin} + E_{lin}$) to female and male survival rates. (d) Female (F_f) and male (F_m) fertilities. Primary sex ratio $\rho = 0.5$, juvenile survival $S_1 = 0.6$ and harem size $h = 0.5$ in all cases. Sex ratio α on the x-axis is varied by fixing $S_{1f} = 0.6$ and varying all other survival rates from 0.5 to 0.8 in steps of 0.05.

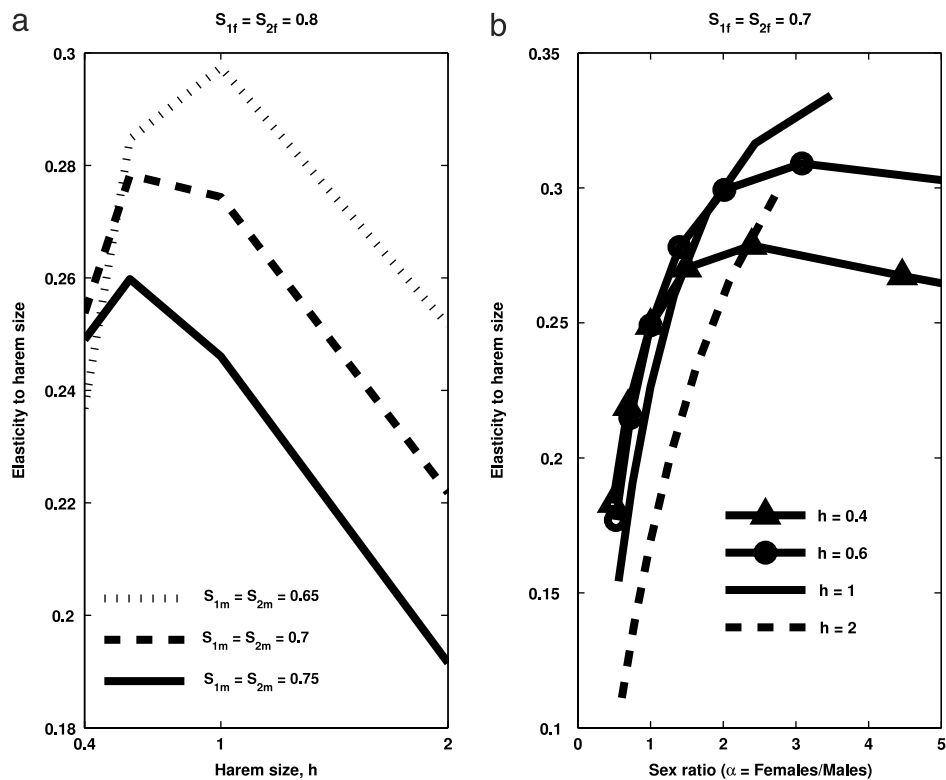


Fig. 5. (a) Elasticity to harem size as a function of the harem size. Shown are three scenarios: $S_{1f} = S_{2f} = 0.8$ and $S_{1m} = S_{2m} = 0.65$; $S_{1f} = S_{2f} = 0.8$ and $S_{1m} = S_{2m} = 0.7$; $S_{1f} = S_{2f} = 0.8$ and $S_{1m} = S_{2m} = 0.75$. (b) Elasticity to harem size as a function of the sex ratio α for four values of the harem size h . Primary sex ratio $\rho = 0.5$ and juvenile survival $S_1 = 0.6$ in all cases. Sex ratio α on the x-axis is varied by fixing $S_{1f} = S_{2f} = 0.7$ and varying all other survival rates from 0.5 to 0.8 in steps of 0.05.

decreases with harem sizes for all sex ratios (Fig. 5a) because female fertility is independent of sex ratio (Fig. 3d) and hence is not affected by increase in harem size. When $h > 1$, as in a polygynous species, elasticity to h always increases with sex ratio (Fig. 5b). At smaller harem sizes, elasticity to h first increases with α when females are relatively rare, but then decreases as the proportion of females in the population increases (Fig. 5b). This is because increasing h would initially increase opportunities for more females to find mates but as the sex ratio becomes more female-skewed resulting in competition for males, fertility decreases and eventually asymptotes (Eq. (3)).

6. Discussion

We derived an explicit analytical formula for the calculation of the elasticity of the population growth rate in a stage-structured frequency-dependent model. Elasticity in density-independent models (Caswell, 2001) can be explicitly expressed in terms of the population age-structure and reproductive value vector. Our formula extends this result to frequency-dependent models providing insights into the dynamics of elasticities in such models. We showed that frequency-dependent elasticity to a vital rate is the sum of the linear elasticity and a non-linear component that reflects the (frequency-dependent) relationship between vital rates and stage frequencies. Our work complements that of Caswell (2008) who used matrix calculus to express elasticities in terms of matrix derivatives. Elasticities represent selection pressure on vital rates (Stearns, 1992) and they are used in management of populations (Morris and Doak, 2002). Hence our results provide the basis for understanding population and evolutionary dynamics in the presence of frequency-dependence.

We applied our general results to a two-sex population model (Caswell and Weeks, 1988; Lindström and Kokko, 1998), where adult sex ratio α and the average number of mates per male h (harem size) affected male and female fertilities. We showed that the response of the population growth rate λ to changes in vital rates is determined by both the demography and the mating system of the species. McDonald (1993) suggested that the elasticity of λ to sex-specific vital rates could be used to quantify consequences of sexual selection and separately analyzed male and female life-histories in the long-lived, neotropical bird, the long-tailed manakin (*Chiroxiphia linearis*, Pipridae). However, this approach (using separate linear matrix models for each sex) ignores the potential non-linear effects of mating behavior and skewed-sex ratios on elasticities. We showed that the non-linear component of the elasticity to (female or male) survival, which quantifies the change in λ due to change in female and male fertilities in response to change in the sex ratio, can be ignored only when adult sex ratio is equal to the harem size of the species. In particular, this implied that in a strictly monogamous ($h = 1$) species, the population growth rate would respond similarly to changes in male and female survival rates only when sex ratio is even (Fig. 1c). In many monogamous bird species, adult sex ratio is not even; in many cases it is male biased ($\alpha < 1$), probably resulting from differential mortality between the sexes (Donald, 2007). Jenouvrier et al. (2010) showed that in emperor penguins (*Aptenodytes forsteri*), a strictly monogamous species, sex ratio was female skewed (due to excess male mortality) and the elasticity to female adult survival was negative. This is consistent with our analytic predictions: we showed that (Fig. 1c) in monogamous ($h = 1$) populations elasticity to survival of the more frequent sex is smaller and becomes negative as the sex ratio increases towards the more frequent sex. In polygynous and polyandrous species, however, we showed that selection for increased adult survival of the more frequent sex is possible unless sex ratio is extremely skewed towards this sex (Figs. 2c, 3c, 4c). This is because excess females (males) will find mates if harem

size is large, unlike in strict monogamy where skewed sex ratio ($\alpha \neq 1$) will result in unmated individuals of the more frequent sex. In polygynous mammals (e.g., red deer, *Cervus elaphus*; Indian fruit bat, *Cynopterus sphinx*; northern elephant seal, *Mirounga angustirostris*), adult sex ratio is often female skewed ($\alpha > 1$; Bessa-Gomes et al., 2004; Donald, 2007) and our results suggest that this could be due to selection for increased female survival. In general, we showed (Eq. (7)) that the response to selection that arises due to the sexual dimorphism in mortality rates, would be weak when adult sex ratio is close to the average harem size.

Our results have important implications for conservation and management of species. Though elasticities have been used to quantify response of λ to management and conservation strategies (Morris and Doak, 2002; Kareiva et al., 2000), no previous studies have addressed how skewness in sex ratio and mating behavior affect this response. Some studies (e.g., Bengal tigers (*Panthera tigris*) in India, Horev et al., 2012; red deer (*Cervus elaphus*) in Norway, Langvatn and Loison, 1999) used two-sex models in population viability analysis (PVA) but did not calculate the frequency-dependent elasticities to vital rates. This paper shows that this can be problematic. For instance, in a monogamous species with a female biased sex ratio, we would recommend management strategies that increase the survival of adult females based on the linear elasticity, but considering the nonlinear elasticity reveals that it would be more effective to enhance the survival of subadult females (Fig. 1b and c). Our approach allows management decisions to vary depending on the sex ratio, which can be an important determinant for population viability. For instance, extinction risk in monogamous and polygynous species is generally believed to increase with male-skewed sex ratios ($\alpha < 1$), as has been demonstrated in the PVA of Little Bustard *Tetrax tetrax* populations in Spain (Morales et al., 2005). Analyzing the effect of sex ratio may become increasingly important for species where sex determination is temperature dependent, like reptiles (e.g., Tuatara *Sphenodon guntheri* in New Zealand, Nelson et al., 2002) because sex ratio may change due to global warming.

To summarize, our study provides analytical tools for studying population response to changing vital rates in general frequency-dependent models. One particularly important application are two-sex models which are increasingly being used by population ecologists. Future work will focus on two important extensions: firstly we will extend our results to study the response of the stochastic growth rate λ_S as has been done in density-independent models (Tuljapurkar et al., 2003). Secondly, we will apply our approach to two-sex models with more general mating functions (Bessa-Gomes et al., 2010).

Appendix A. Supplementary data

Supplementary material related to this article can be found online at <http://dx.doi.org/10.1016/j.tpb.2014.08.003>.

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