



# A predictive relationship between population and genetic sex ratios in clonal species



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## ABSTRACT

Sexual reproduction depends on mate availability that is reflected by local sex ratios. In species where both sexes can clonally expand, the population sex ratio describes the proportion of males, including clonally derived individuals (ramets) in addition to sexually produced individuals (genets). In contrast to population sex ratio that accounts for the overall abundance of the sexes, the genetic sex ratio reflects the relative abundance of genetically unique mates, which is critical in predicting effective population size but is difficult to estimate in the field. While an intuitive positive relationship between population (ramet) sex ratio and genetic (genet) sex ratio is expected, an explicit relationship is unknown. In this study, we determined a mathematical expression in the form of a hyperbola that encompasses a linear to a nonlinear positive relationship between ramet and genet sex ratios. As expected when both sexes clonally have equal number of ramets per genet both sex ratios are identical, and thus ramet sex ratio becomes a linear function of genet sex ratio. Conversely, if sex differences in ramet number occur, this mathematical relationship becomes nonlinear and a discrepancy between the sex ratios amplifies from extreme sex ratios values towards intermediate values. We evaluated our predictions with empirical data that simultaneously quantified ramet and genet sex ratios in populations of several species. We found that the data support the predicted positive nonlinear relationship, indicating sex differences in ramet number across populations. However, some data may also fit the null model, which suggests that sex differences in ramet number were not extensive, or the number of populations was too small to capture the curvature of the nonlinear relationship. Data with lack of fit suggest the presence of factors capable of weakening the positive relationship between the sex ratios. Advantages of this model include predicting genet sex ratio using population sex ratios given known sex differences in ramet number, and detecting sex differences in ramet number among populations.

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## 1. Introduction

Population sex ratio reflects the availability of mates, but for clonally reproducing species this sex ratio might not indicate the number of genetically different mates (Hedrick, 2000; Bengtsson and Cronberg, 2009). Sex ratio indicates the proportion of males which can be based either on the relative abundance of the sexes (called population or ramet sex ratio), or estimated as the relative abundance of sexes of genetically unique individuals (called genetic or genet sex ratio, Allen and Antos, 1993). In clonally reproducing species, these ratios may substantially differ. For example, a

population containing 20 males and 20 females, each genetically unique, will have a population sex ratio as well as a genetic sex ratio of 0.5. In contrast, if the 20 females are the product of asexual reproduction by one genotype, the population sex ratio will be again 0.5 (i.e. proportion of males  $20/(20 + 20)$ ), but the genetic sex ratio will be 0.95 (i.e.  $20/(20 + 1)$ ). Notice that for equal population size, a population with the latter genetic sex ratio (i.e. 0.95) will have a smaller effective population size (Bengtsson and Cronberg, 2009). Because asexual reproduction will impact sex ratios, the establishment of a relationship between population and genetic sex ratios can facilitate the understanding of the eco-evolutionary dynamics and the patterns of sex ratio variation in populations of clonal organisms. In species with unisexual individuals and where asexual reproduction occurs in both sexes (e.g., animals (Bell, 1982), fungi (Alexopoulos et al., 1996), plants (Eckert, 2002; Field et al., 2013a), and protists (Wreede and Klinger, 1988)), the population

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sex ratios can be determined by visual observation of the phenotypic sex at sexual reproduction. In contrast, data on genetic (genet) sex ratios usually require the use of genetic markers to genotype individuals, which can be relatively expensive to develop and use, but are becoming more accessible (e.g. Kalia et al., 2011). Thus, developing an explicit relationship between these sex ratios may be useful in predicting genet sex ratios when data on population sex ratio and sex differences in ramets per genet are known.

Ramets refer to the set of individuals produced from asexual reproduction belonging to the same genotype (Harper, 1977), thus, ramet sex ratio takes into consideration sex differences in asexual recruitment success, as well as the number of genotypes existing in the population. However, theoretical predictions of the ramet-genet sex ratio relationship have not been explored explicitly. Nevertheless, there is an implicit and logical assumption that sex differences in asexual reproduction will lead to bias population sex ratios (ramet sex ratios) in favor of the sex with higher levels of asexual reproduction (Bierzychudek and Eckhart, 1988; Popp and Reinartz, 1988, Williams, 1995; Leslie and Klein, 1996; McGovern, 2002; Rydgren et al., 2010), but the specific relationship is unknown. Population sex ratio studies on plants that include data on ramet and genet sex ratios are scarce and most have assumed this relationship but did not explicitly test the relationship (Eppley et al., 1998; Obeso et al., 1998; Cronberg et al., 2003, 2006; Vandepitte et al., 2009; Petzold et al., 2013). However, for an exception of a study finding a strong correlation between these sex ratios, see Yakimowski and Barrett (2014).

There are many species where sex ratios vary among populations, including clonal dioecious seed plants, mosses and liverworts (Longton and Schuster, 1983; Bisang and Hedenäs, 2005; Field et al., 2013b). Several drivers of this variation, including sex function and the resulting reproductive cost in association with an ecological context, and historical processes occurring in populations (e.g. transient sex ratios from disturbances and colonization), have been implicated, tested, and debated (Bierzychudek and Eckhart, 1988; García-Ramos et al., 2007; Barrett et al., 2010; Rydgren et al., 2010; Shelton, 2010; Sinclair et al., 2012; Field et al., 2013ab, Barrett, 2015; Stieha et al., 2016). However the fundamental relationship between genet sex ratio and population sex ratio remains unknown. In this paper, we developed a mathematical equation that provides a theoretical framework linking ramet sex ratios to genet sex ratios, thus determining how these sex ratios can differ, and we applied this framework to field data of species with heterogeneous population sex ratios to assess the model predictions. We show that the relationship between these sex ratios is positive, as expected, but this relationship is nonlinear when the sexes differ in the average number of ramets per genet. Our model can help to detect patterns of deviations in relative number of ramets per genet between the sexes across populations.

## 2. Methods

*The model and analysis:* Our focal systems are species where individuals are unisexual (dioecious or gonochorous) and where both sexes are capable of clonal expansion. Sex determination is genetically fixed, that is, individuals and their asexual offspring cannot change sex. In this model, we focus on individuals in populations. We define sex ratio as proportion of males, and for any population, each ramet (individual) has assigned a genet (genotype) and sex. We represent the average number of ramets per male genet and female genet as  $r_m$  and  $r_f$  respectively. We represent the number of male and female genets as  $g_m$  and  $g_f$  respectively. Thus, population sex ratios are defined by using these four parameters, where the ramet sex ratio ( $R_{SR}$ ) is defined as:

$$R_{SR} = r_m g_m / (r_m g_m + r_f g_f), \quad (1)$$

and the genet sex ratio ( $G_{SR}$ ) as:

$$G_{SR} = g_m / (g_m + g_f). \quad (2)$$

From Eq. (2) the number of male genets can be expressed as:

$$g_m = G_{SR} g_f / (1 - G_{SR}). \quad (3)$$

Now we divide the numerator and denominator of (1) by  $r_m$

$$R_{SR} = g_m / \left[ g_m + \left( r_f / r_m \right) g_f \right], \quad (4)$$

then we replace  $g_m$  in Eq. (4) with Eq. (3); and with further rearranging, where  $a = r_f / r_m$  results in

$$R_{SR} = G_{SR} / [a + (1 - a)G_{SR}] \quad (5)$$

This equation describes ramet sex ratio ( $R_{SR}$ ) as a hyperbola function that depends on genet sex ratio ( $G_{SR}$ ) and the relative number of ramets among sexes ( $a = r_f / r_m$ ). In this equation (Eq. (5)), when  $a = 1$  both ramet and genet sex ratios are equal ( $R_{SR} = G_{SR}$ ). Because ramet sex ratios are dependent on genet sex ratios and genet production of ramets, we made  $R_{SR}$  the subject of the formula. Conversely, genet sex ratio can be expressed as a function of ramet sex ratio by using Eq. (5):

$$G_{SR} = a R_{SR} / [1 - (1 - a)R_{SR}]. \quad (6)$$

Equations (5) and (6) can describe the relationship between the sex ratios in any given population. However, we further extend our study to analyze the effect of having populations of the same species with different relative number of genets (genotypes) per sex, but the same relative number of ramets per sex. This analysis allows testing whether a hyperbolic pattern between ramet and genet sex ratios can be observed across same-species populations, as expected by the equation. We plotted the relationship between  $R_{SR}$  and  $G_{SR}$  given by Eq. (5) in Fig. 1. We evaluated the function for a fixed relative number of ramets per genet ( $r_f / r_m$ ) with values ranging from 0.2 to 5.0, including no sex difference ( $r_f / r_m = 1$ ). We then varied the genet sex ratio between 0 and 1 (only females genets to only males genets). In one additional evaluation on the figure,  $g_f / g_m$  was kept constant at 1 and  $r_f / r_m$  was allowed to vary.

*Application of the model to field data:* We found seven published studies on plants that presented data on both sex ratios  $R_{SR}$  and  $G_{SR}$ , as well as one unpublished data set (Brzyski et al., unpublished results). Except for Yakimowski and Barrett (2014), none of these explicitly examined the  $R_{SR} - G_{SR}$  relationship. All eight studies are represented in Fig. 2 and four were excluded from further analysis (Obeso et al., 1998; Cronberg et al., 2003, 2006; Petzold et al., 2013) because of small number of populations (e.g., two or three) or small number of genets per population (e.g. six or less).

We then use Eq. (5) to examine variation in sex ratios across populations as was described in Fig. 1. If a species has a fixed sex difference in ramet number per genet, then their populations or subpopulations are expected to fit along a single curve (Fig. 1), where the relative number of genets in that population determines the position along the curve. We tested the goodness of fit of data to the predicted relationship described by Eq. (5), which has the form of a modified hyperbola ( $f = x/[a+(1-a)x]$ , where  $f = R_{SR}$ ,  $x = G_{SR}$ , and  $a = r_f / r_m$ ). We used the Regression Wizard from SigmaPlot 12.3. In each of the studies, we tested, if averaged  $r_f / r_m$  and observed sex ratios ( $R_{SR}$  and  $G_{SR}$ ) across populations fit Eq. (5).

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