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Detecting non-binomial sex allocation when developmental mortality operates

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HIGHLIGHTS

- Existing statistical tests lack power for detecting under-dispersion in sex ratios.
- We introduce two statistical models of under/over-dispersion.
- A Bayesian inference scheme is derived for model selection and parameter estimation.
- This significantly improves our ability to detect under-dispersion in small samples.

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ABSTRACT

Optimal sex allocation theory is one of the most intricately developed areas of evolutionary ecology. Under a range of conditions, particularly under population sub-division, selection favours sex being allocated to offspring non-randomly, generating non-binomial variances of offspring group sex ratios. Detecting non-binomial sex allocation is complicated by stochastic developmental mortality, as offspring sex can often only be identified on maturity with the sex of non-maturing offspring remaining unknown. We show that current approaches for detecting non-binomiality have limited ability to detect non-binomial sex allocation when developmental mortality has occurred. We present a new procedure using an explicit model of sex allocation and mortality and develop a Bayesian model selection approach (available as an R package). We use the double and multiplicative binomial distributions to model over- and under-dispersed sex allocation and show how to calculate Bayes factors for comparing these alternative models to the null hypothesis of binomial sex allocation. The ability to detect non-binomial sex allocation is greatly increased, particularly in cases where mortality is common. The use of Bayesian methods allows for the quantification of the evidence in favour of each hypothesis, and our modelling approach provides an improved descriptive capability over existing approaches. We use a simulation study to demonstrate substantial improvements in power for detecting non-binomial sex allocation in situations where current methods fail, and we illustrate the approach in real scenarios using empirically obtained datasets on the sexual composition of groups of gregarious parasitoid wasps.

1. Introduction

The null model of sex allocation theory is the Düshing–Fisher theory of equal investment (West, 2009). When populations are both large and have unbiased sex ratios, selection for variance in the sexual composition of offspring groups is predicted to be absent (Kolman, 1960). Under these conditions mothers will not be selectively penalized if they randomly allocate sex to offspring, with fixed probability of $p=0.5$ that the offspring is male, independently of the sex of previous offspring. Thus, the number of males in each offspring group would have binomial variance, i.e., $np(1-p)$, where n is the number of offspring. In smaller populations and under sex ratio bias ($p \neq 0.5$), stabilizing selection for low sex ratio variance is predicted, i.e., variance less than $np(1-p)$ (Verner, 1965; West, 2009). Selection on sex ratio variance is likely to be strong when populations are structured into small reproductive subgroups within which offspring mate with each other on maturity and prior to the dispersal of the daughters (local mate competition; Hamilton, 1967); here, selection favours the evolution of low sex ratio variance, especially when one or a very

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few mothers contribute offspring to the locally mating group (Green et al., 1982; Hardy, 1992; Nagelkerke and Hardy, 1994; Nagelkerke, 1996; West and Herre, 1998). This is because low variance maximizes the production of mated daughters, a close correlate of maternal fitness. If one male is sufficient to mate successfully with all females within a group and all offspring in the group are progeny of one mother, then the optimal sexual composition is one male and the remainder of the group being females (Green et al., 1982). Similar arguments predict low variance under local resource competition (a generalization of local mate competition) and its converse, local resource enhancement (Lambin, 1994). Variance in the number of males among groups lower than expected under binomial sex allocation is known as under-dispersion, and sex allocation is then termed *precise* (Green et al., 1982; Lambin, 1994; Nagelkerke, 1996).

Control of sex allocation can be detected in some organisms by direct observation of sexually differential aspects of individual offspring production, such as maternal movements during egg laying, or the placement of offspring, or by non-random production sequences (Cole, 1981; Hardy, 1992; Heinsohn et al., 1997; Krackow et al., 2002; Khidr et al., 2013; Ambrosini et al., 2014) but such evidence is not often available. Empiricists must more frequently rely on the statistical analysis of offspring group sex ratios to detect whether sex allocation is being controlled or whether it is, for instance, binomial, as might be the null-expectation under several chromosomal mechanisms of sex-determination (Avilés et al., 2000; Krackow et al., 2002; Ewen et al., 2003; Macdonald and Johnson, 2008; Postma et al., 2011). Furthermore, empirical evaluations of sex ratio variance can provide tests of explicit predictions of sex ratio theory (e.g., Lambin, 1994; Morgan and Cook, 1994; Hardy and Cook, 1995; Hardy et al., 1998; Nagelkerke and Sabelis, 1998; West and Herre, 1998; Kapranas et al., 2011; Khidr et al., 2013; Bowers et al., 2013).

One practical problem often faced by investigations of sex ratios and sex ratio variance is that information on the sexual compositions of offspring is available at maturity but not at the time of sex allocation, and it is not uncommon for some offspring to die before maturity (e.g., Hardy et al., 1998; Dyrcz et al., 2004; Ewen et al., 2004; Forsyth et al., 2004; Dietrich-Bischoff et al., 2006; Øigarden and Lifjeld, 2013). Provided it has a stochastic component, developmental mortality will act to increase the variance of observed sex ratios, making initially under-dispersed data appear closer to binomial. This effect is expected on logical grounds (Section 3) and has been shown empirically both within and across several species of organisms with group structured mating (Hardy et al., 1998; Kapranas et al., 2011; Khidr et al., 2013; see also Dyrcz et al. (2004) and Dietrich-Bischoff et al. (2006)). Current statistical approaches to assessing sex ratio variance (Krackow et al., 2002) are, however, based on the implicit assumption that developmental mortality does not operate, and they consequently lack power to detect non-binomiality, unless mortality rates are low.

Our aim is to show that by introducing a model that represents the biological processes that generated the data (sex allocation followed by mortality) we can substantially improve our ability to detect underlying biological behaviours. We also demonstrate the advantage of using more descriptive statistical approaches such as estimating effect sizes (with measures of confidence), rather than relying on null-hypothesis significance testing, where the small dataset sizes mean we often fail to clear an arbitrary significance hurdle (usually $\alpha = 0.05$) even when the data indicate phenomena of interest. We begin by evaluating the performance, under developmental mortality, of the statistical methods commonly used to detect non-binomial sex ratio variance. We find that the power of these methods is adversely affected by developmental mortality. We then develop an alternative approach that explicitly models the mortality process. This has much improved power for detecting non-binomial sex allocation, particularly when there is high mortality or datasets are small.

2. Terms and notation

We define some terms and notation before describing current approaches and their limitations, and then introduce our new approach for detecting non-binomial sex allocation. A summary of the notation is provided in Table 1. The methods developed are general, but are likely to most readily be applied to egg-laying organisms such as birds, parasitoid wasps, fig wasps and phytoseiid mites (Hardy, 1992; Nagelkerke and Sabelis, 1998; West and Herre, 1998; West, 2009; Bowers et al., 2013), and this is reflected in the terminology we adopt (for a mammalian example see Macdonald and Johnson, 2008). Assume that we have a dataset containing data on C different clutches of eggs, all of which were laid in comparable environmental conditions. Offspring group size is called *clutch size* at the time of production (egg-laying) and *brood size* at the time of offspring maturity: brood size is less than clutch size when developmental mortality occurs.

A *primary* dataset consists of counts of the number of eggs and their sex for each clutch. Let N_i denote the number of eggs laid in the ith clutch, and M_i be the number of those N_i eggs that are male. A primary dataset is the collection $\{(N_i, M_i)\}_{i=1}^{C}$. However, for most empirical investigations M_i is not observed, as the sex of an offspring cannot be easily determined from the eggs: it is usual to wait until the eggs hatch and develop to the point at which offspring sex can be discriminated (e.g., Dietrich-Bischoff et al., 2006; Khidr et al., 2013). It is also usual that a proportion of the eggs fail to mature, due to some form of developmental mortality, and consequently their sex cannot be recorded.

A *secondary* dataset consists of counts of n_i, the number of offspring that reach maturity (brood size) and m_i, the number of those offspring that are male, with the complete secondary dataset denoted $\{(n_i, m_i)\}_{i=1}^{C}$. Although a small number of experiments have been conducted where primary datasets are obtained, either

Table 1
Summary of notation used in this paper. Letters in *bold* font indicate vector quantities, indices (e.g., n_i) indicate an instance of that variable, and hats (e.g., $\hat{p}$) indicate estimates.

Symbol	Definition
C	Number of clutches in the dataset
N	Number of eggs laid (primary)
M	Number of eggs laid that are male (primary)
n	Number of offspring that reach maturity (secondary)
m	Number of males that reach maturity (secondary)
D	The complete observed dataset, i.e., $D = \{(n_i, m_i)\}_{i=1}^{C}$
p	Sex ratio[a] (proportion of eggs that are male)
ψ	Dispersion parameter
λ	Average clutch size
d	Mortality rate
H_0, H_1	Null and alternative hypotheses
U	Test statistic for the Meelis' test
R	Descriptive ratio contrasting observed and expected variance
s^2	McCullagh's dispersion estimator
$\mathcal{S}$	Clutch sizes observed in the data, i.e., $\{k: n_j = k \text{ for some } j\}$
ν_k	Number of clutches of size k, i.e., $\sum_{i=1}^{C} \mathbb{1}_{n_i=k}$
s_k^2	Empirical variance of the number of males in clutches of size k
B_{01}	Bayes factor for comparing H_0 with H_1

[a] Care needs to be taken with interpretation of p in the multiplicative binomial model as p is no longer the expected sex ratio when $\psi \neq 0$.