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Facultative primary sex ratio variation: a lack of evidence in birds?

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The facultative control of primary sex ratio by breeding birds has become a major focus in evolutionary biology in recent years. A combination of well-developed theoretical literature and rapid publication of empirical results has created considerable confusion, with controversial claims for both extreme control of primary sex ratio versus no control around inherent random variability. We present a robust and quantitative summary of published empirical literature to assess clearly the body of evidence for female birds to control sex assignment in their offspring. Our meta-analytical approach reveals that published studies do not exhibit any variability beyond that which could be expected owing to sampling error. Therefore, we conclude that facultative control of offspring sex is not a characteristic biological phenomenon in breeding birds.

Keywords: birds; primary sex ratio; facultative adjustment; meta-analysis

1. INTRODUCTION

Adaptive primary sex ratio variation in birds is one of the most challenging and controversial fields in evolutionary biology. A scan of recent literature highlights a field with mixed empirical results and a complex array of theoretical predictions. It is therefore not surprising that scientists have questioned the potential for birds to bias primary sex ratios (e.g. Koenig & Dickinson 1996; Westerdahl *et al.* 1997; Pagliani *et al.* 1999; Radford & Blakey 2000; Koenig *et al.* 2001; Kasumovic *et al.* 2002) despite the fact that influential 'case studies' clearly exist (arguably the most influential of these being investigations of primary sex ratio in the Seychelles warbler, *Acrocephalus sechellensis* (Komdeur 1996; Komdeur *et al.* 1997, 2002)).

It is not unusual in studies of evolutionary biology to find that difficulties arise when evaluating the generality of the strength of research results (Møller & Jennions 2002). Nevertheless, the controversy is exaggerated in sex ratio studies owing to the recent development of molecular sexing techniques (Griffiths *et al.* 1996, 1998). These methodological advances have opened a previously restricted research field, which, combined with an already diverse body of adaptive theory, has led to the rapid publication of a large number of studies.

A potential problem associated with the rapid development of a new field relates to interpretations of effect size. Effect size is a standardized measure of the magnitude of a relationship. It is important to realize that weak or 'small' to 'intermediate' effects, explaining 1–10% of the variance (*sensu* Cohen 1988), are what scientists report in most fields of evolutionary biology (Møller & Jennions 2002). Explanations for weak effect size not only include biological constraints on optimality (Maynard Smith 1978) but also more problematic concerns of statistical limitation. Møller & Jennions (2002) have previously shown that sample sizes in evolutionary biology are typically far lower than those required for standard statistical confidence in rejecting the null hypothesis (resulting in increased type II error). Purely owing to sampling error (the larger the sample the more accurate the estimate) the variance in estimates of the 'true' effect size is higher for studies with smaller samples. This has sometimes led to the incorrect classification of small effects as having no effect and the consideration of studies with only large effect size as significant (Gontard-Danek & Møller 1999). This can result in a bias toward the publication of only significant results (either through editorial decisions or a failure to submit non-significant results). Publication bias is a real and well-documented issue in evolutionary biology (Palmer 2000; Jennions & Møller 2002) and it is therefore no surprise that it and considerations of statistical power are frequently referred to in the literature relating to adaptive primary sex ratios (Palmer 2000; Arnold *et al.* 2001; Hasselquist & Kempenaers 2002).

Despite these repeated cautions, the publication of empirical studies of primary sex ratio have recently increased dramatically (with 15 such publications in 2002 compared with between three and five each year between 1996 and 2001; see electronic Appendix A) and reviews now exist that attempt to summarize their results. By far the most common form of review is the qualitative summary of published literature. Although providing interesting perspectives, these reviews possess two major drawbacks: first, a lack of accountability for the primary literature they include, and second, they provide no quantitative conclusion regarding the body of evidence, for or against, a particular hypothesis (Hedges & Olkin 1985). Among the most recent qualitative reviews several areas in the primary sex ratio literature have been suggested to provide 'consistent' evidence for adaptive biases. These include the status of females in polygynous mating systems (Hasselquist & Kempenaers 2002), the laying order of eggs within a clutch (Krackow 1999; Cockburn *et al.* 2002; Hasselquist & Kempenaers 2002) and patterns within a breeding season (Komdeur & Pen 2002). The only way, however, to assess the true magnitude of

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adaptive primary sex ratio bias, and to quantify the extent to which this field has suffered from sociological issues in the publication process, is to conduct a statistically robust synthesis of the empirical literature. In this paper, we adopt a meta-analytical approach.

(a) *The meta-analytical approach to primary sex ratio: attempts and shortcomings*

The primary objective of a meta-analysis is to provide an estimate of the overall effect of a class of explanatory variables based on the collated information from available studies. To obtain this estimate, different test statistics are transformed into a standardized measure of the magnitude of the relationship—the ‘effect size’ (Rosenthal 1994).

Previously, two studies have used meta-analysis to address primary sex ratio variation in birds. First, Palmer (2000) analysed primary sex ratio literature, presenting an exemplary case highlighting publication bias in ecology. Recently, West & Sheldon (2002) provided not only strong support for adaptive primary sex ratio variation, but further, that chromosomal sex determination may not constrain the evolution of sex ratio adjustment. These two opposing conclusions reflect the very different literature incorporated within their respective analyses. The major difference between these two analyses is that the review of Palmer (2000) uses a database of Clutton-Brock (1986), who collated population-level sex ratios. By contrast, West & Sheldon (2002) focus on facultative control of offspring sex by individual breeding birds. It has been argued that, given the variable selective forces altering the primary sex ratio of individuals, it is difficult to predict population-level sex ratios (Frank 1990; West & Sheldon 2002). If so, this may provide a simple explanation for the above discrepancy.

There are, however, additional concerns with sex ratio data, not only in these meta-analyses but also within all forms of review in this field. Primary sex ratio was difficult to measure, especially before the advent of molecular sexing, and many studies claiming assessment of primary sex ratio cannot completely rule out the additional impacts of early mortality. Careful examination is therefore required to prevent the possibility that it is not secondary sex ratio that is being reported. In addition, if the goal of a meta-analysis is to generalize across a particular field of study then the analysis requires a complete unbiased set of empirical data if the conclusions are to represent the published literature and to facilitate accurate assessment of publication bias (Gurevitch *et al.* 2001). We believe that a shortcoming of the meta-analysis of West & Sheldon (2002) makes it erroneous to interpret their conclusions with respect to the current status of literature on primary sex ratio adjustment in birds. Notably, their study included only 16 parameters among 12 species. In fact, their analyses did not even incorporate all the parameters assessed within the literature they selected. Despite justification for ignoring a large majority of published results, their own decision rules for excluding studies (and parameters) violate the concept of the meta-analytic approach (Sharpe 1997), and weaken the generality of their conclusions. Literature on meta-analyses clearly advises that ‘methodological weakness’ (such as a decision to ignore studies with poor *a priori* predictions as in West and Sheldon’s 2002 analysis) should be explicitly addressed within a meta-analysis to quantify the potential impact on the collated results (Gurevitch *et al.* 2001).

Our aim was to quantitatively evaluate the evidence for facultative primary sex ratio variation in birds, using a thorough dataset of empirical studies. Recognizing the difficulties of investigating primary sex ratio and the associated limitations of past approaches we: (i) focus on the literature published since the development of accurate sexing techniques and that focuses on facultative sex ratio adjustment; (ii) include studies that analysed primary sex ratio; and (iii) include all putative parameters assessed.

2. MATERIAL AND METHODS

Studies were collated from literature searches of ISI and *Current Contents* databases using the terms ‘sex ratio’, ‘sex allocation’ and ‘bird’, followed by a thorough examination of the published bibliographies and email correspondence with the authors (see electronic Appendix A). To ensure that we included only results of primary sex ratio, studies were discarded if they did not analyse either: (i) the sex of all eggs laid in all broods; (ii) only broods that remained complete by the time of sampling; or (iii) both partial and complete broods if the authors precluded the possibility of sex-biased mortality.

Our measure of effect size was Pearson’s correlation coefficient. This metric is widely used in syntheses of correlational studies in ecology and evolution (Møller & Jennions 2002) and is the best-known index based on the variance accounted for owing to the introduction of an explanatory variable (Hedges & Olkin 1985). If the original sources did not provide a correlation coefficient, we transformed the published test statistics into a correlation coefficient using the formulae for transformation given by Rosenthal (1994). In a number of cases the published studies did not provide coefficient estimates or test statistics for non-significant results. In these cases the authors were contacted for their missing statistics.

Pearson correlation variates were subsequently transformed for analysis by Fisher’s Z-transformation:

$$Z_i = \tfrac{1}{2}\ln\frac{1 + r_i}{1 - r_i}. \tag{2.1}$$

The measure of effect size was weighted by sample size, based on the assumption that a larger sample size should provide a more reliable estimate of a true relationship. Studies of sex ratio adjustment have measured independent variables with respect to changes in either biological or temporal traits and bias toward the more costly sex. Biological traits include brood and clutch size, measures of female and male age, quality, size and weight, the presence and type of helpers, female status in polygynous breeding systems and finally measures of territory quality; whereas temporal traits include brood number, laying sequence, season and year. In total, we recognized 24 individual parameters. Only univariate parameters were included in the analysis and all of these parameters were independent, i.e. no two samples of explanatory variables X_i were the same. We estimated the common weighted average of the Z-transformed effect size variates for both biological and temporal traits as

$$Z_+ = \sum_{i=1}^{K} \frac{(n_i - 3)Z_i}{N - 3K}, \tag{2.2}$$

where K is the number of study samples in the analysis, n_i is the size of sample i, and $N = \Sigma n_i$. The large sample normal approximation to the distribution of Z_+ can subsequently be used to test the hypothesis that the common correlation is zero (Kraemer 1983) using the test statistic

$$Z_+\sqrt{N-3K}, \tag{2.3}$$

which is compared with the $\alpha = 0.05$ two-tailed critical value of the standard normal distribution. In the same manner, we constructed 95% confidence intervals around the mean effect size:

$$Z_+ \pm 1.96/\sqrt{N-3K}, \tag{2.4}$$

where 1.96 is the 95% two-tailed value of the standard normal distribution.

Because the studies used in our analyses obviously differ in many respects, such as the manner in which data were collected and the explanatory variables chosen for analysis, we used a random model to estimate the variance of the population of correlations (Hedges & Olkin 1985). The expected values of the mean squares are thus expressed as variance components of the mean effect sizes. We then tested whether the variance of the population of correlations differs from zero, using the large sample test for homogeneity of correlations given by Hedges & Olkin (1985):

$$Q = \sum (n_i - 3)(Z_i - Z_+)^2, \tag{2.5}$$

which is subsequently compared with the critical value from the χ^2 distribution with $K - 1$ degrees of freedom.

The homogeneity statistic determines whether the effect sizes from a series of studies exhibit any variability beyond that which could be expected owing to sampling error. In the case of significant heterogeneity, then *post hoc* multiple comparison methods can be used to partition the heterogeneous populations into more homogeneous groups in which the effect sizes within clusters are close, but the effect sizes between clusters are separated. Methods for *post hoc* disjoint cluster analysis follow Hedges & Olkin (1985). If the homogeneous model is consistent with the data, it implies that each study in essence conforms or replicates the findings of the other studies. Nevertheless, individual outliers, or aberrant results, are likely to remain and these can be identified by calculating standardized weighted residuals:

$$\check{e}_i = e_i \,/\, \sigma(e_i), \tag{2.6}$$

where e_i is the difference between the effect size of the ith study and the weighted mean with the ith study omitted, and $\sigma(e_i)$ is the square root of the approximate estimated variance. The residuals that have large absolute values (greater than 2) indicate a set of parameters with different effect sizes from the overall mean (Hedges & Olkin 1985).

Meta-analysis is based on the assumption that the literature reviewed is unbiased (Rosenthal 1994). Alternatively, publication bias occurs whenever the strength or direction of the results of published and unpublished studies differ. To examine publication bias we plotted effect size (z_i) against sample size (n_i) and conducted the rank correlation test of Begg & Mazumdar (1994) to investigate the relationship between the two. Publication bias is inferred if this relationship is significant such that there are fewer than expected studies with either negative or positive effects at low sample sizes (Møller & Jennions 2001).

3. RESULTS

We identified 40 studies (see electronic Appendix A), since the advent of molecular sexing techniques, that reported statistical analysis of facultative control in primary sex ratio adjustment of birds ($N = 214$ parameters).

The relationships between transformed effect size (Z_i) and sample size (N_i) across comparisons for biological and temporal traits are shown in figure 1*a* and *b*. The Begg and Mazumdar rank correlation tests between standardized effect size and sample size were non-significant (biological traits: $r = 0.04$, $n = 139$; temporal traits: $r = -0.19$, $n = 75$). This indicates that, in both cases, the number of expected negative (female-biased) and positive (male-biased) effects at low sample sizes was not significantly biased.

The common weighted averages (overall mean effect (95% confidence interval); equations (2.2) and (2.4)) in relation to biological traits (0.006 (−0.011, 0.023)) and temporal traits (−0.004 (−0.033, 0.025)) did not differ significantly from zero (test statistics from equation (2.3); biological traits = 0.66; temporal traits = −0.28). We subsequently used a random model (equation (2.5)) to estimate the variance of the population of correlations and tested whether the variance of the population of correlations was heterogeneous. The parameter variance components of the population of correlation coefficients in the random effects models were 0.24 across biological traits and 0.38 across temporal traits. Across both biological traits ($Q = 65.37$, $n = 139$) and temporal traits ($Q = 51.17$, $n = 75$) the tests of homogeneity, compared with the χ^2 distribution, were highly non-significant ($p > 0.5$), and we therefore infer that the published estimates of facultative sex ratio adjustment are estimating a single common population of effect sizes. Notably, there is no evidence that studies exhibit any variability beyond that which could be expected owing to sampling error.

Outlying parameters were identified from four studies where the effect sizes for laying sequence (temporal; $N = 1$ (from 32) reference 18 in electronic Appendix A) and habitat quality (biological; $N = 3$ (from 18) references 22, 19 and 9 in electronic Appendix A) deviated from those of the other studies in their respective homogeneous models (table 1; figure 1).

4. DISCUSSION

There are two clear conclusions to be drawn from our analysis. First, despite the small number of non-significant results from studies with low sample size (see below), the expected number of published negative (female-biased) and positive (male-biased) effects does not differ with respect to variability in sample size (figure 1). Therefore, despite the variability inherent among studies, the trend overall for producing either more sons or daughters is equal. Second, the published empirical evidence provides no consistent statistical pattern (i.e. heterogeneity in effect sizes) for facultative sex ratio manipulation across an ecological framework that differs with respect to both temporal and biological parameters. With increasing sample size the variability in effect sizes, rather than exhibiting significant heterogeneity among different studies, converges on a true effect of zero. Thus the large effects observed at small sample sizes represent random variation around the mean effect and their reporting is exaggerated by a greater publication of significant results at small

Table 1. Study parameters that were identified as outliers with aberrantly large standardized weighted residuals (equation (2.6)). (References are numbers 18, 22, 19 and 9 in electronic Appendix A.)

reference	species	trait	effect size	*N*
Heinsohn *et al.* (1997)	*Eclectus roratus*	laying sequence	−0.335	41
Komdeur (1996)	*Acrocephalus sechellensis*	territory quality	−0.374	54
Kasumovic *et al.* (2002)	*Molothrus ater*	territory quality	0.130	279
Byholm *et al.* (2002)	*Accipter gentilis*	territory quality	0.301	73

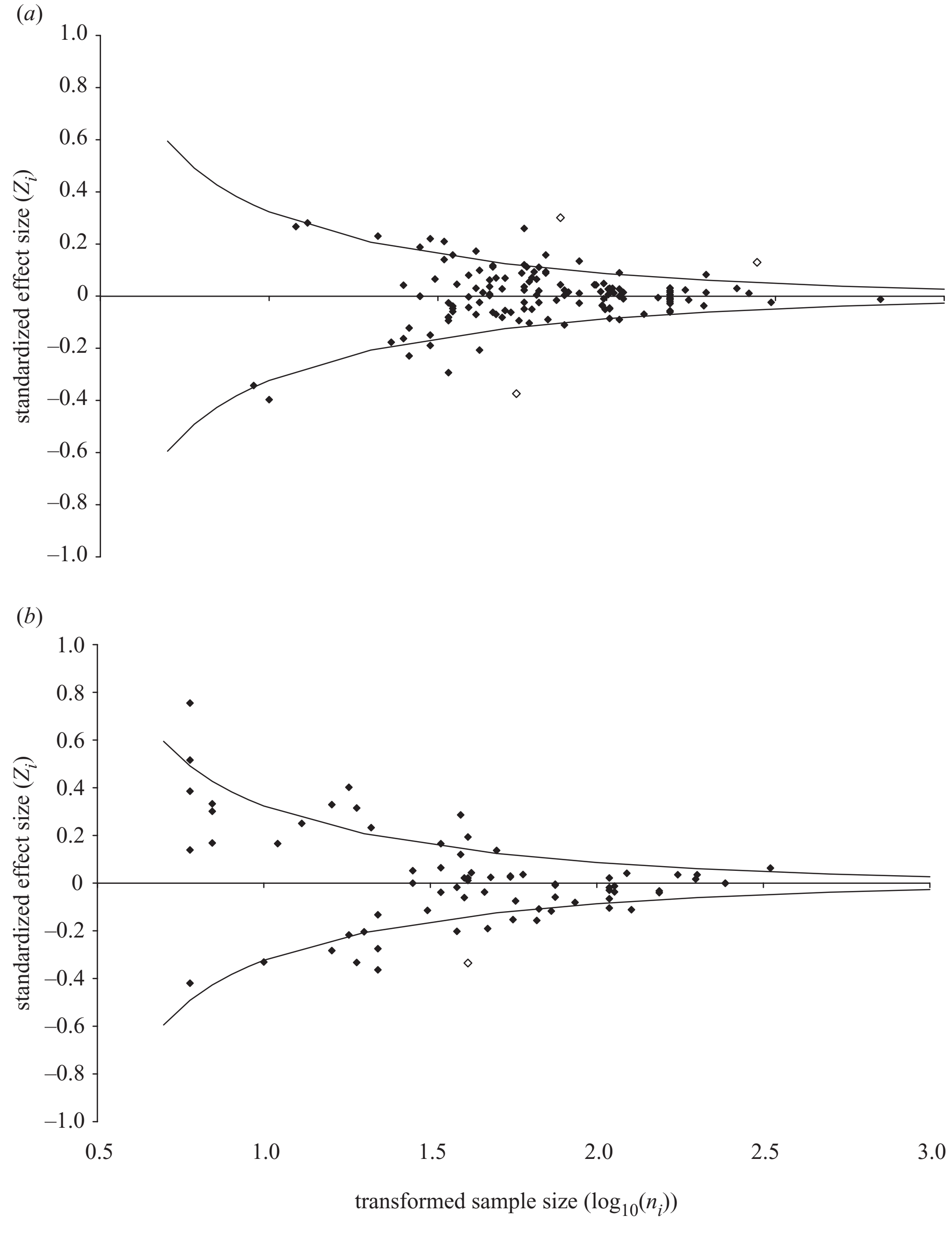

Figure 1. Funnel plots of the relationship between sex ratio adjustment and (*a*) biological or (*b*) temporal traits. Positive values reflect male-biased sex ratios and negative values female-biased sex ratios. Overlaid significance lines are calculated for $\alpha = 0.05$ following Sutton (1990). Open diamonds indicate study parameters with large standardized residuals.

sample sizes (figure 1). Notably, for sample sizes less than 100 there is a discernible absence of non-significant results being presented, although this may be a problem with editorial decisions rather than scientific reporting. Nevertheless, the inclusion of these ‘missing’ studies would only serve to add greater support to our conclusions.

This result is timely, given the numerous verbal reviews that suggest apparently consistent sex ratio biases in the empirical literature (Krackow 1999; Cockburn *et al.* 2002; Hasselquist & Kempenaers 2002; Komdeur & Pen 2002). Further, our results are in direct contrast to a recent review (West & Sheldon 2002) that concluded that female birds might control sex assignment to a similar degree to haplodiploid insects (a system assumed to provide females with precise sex allocation control). Their results, however, were strongly biased by an *a priori* decision to include only a small proportion of available empirical data (16 parameters in total). By contrast, our results seem to reflect those previously presented for tightly constrained 50 : 50 population-level sex ratios (Palmer 2000).

So, could the studies that have been presented as influential 'case studies' be true exceptions from the general patterns that are observed in birds? It is possible, for example, that certain species are present in an adaptive landscape whereby there is a net benefit accrued from biasing sex ratio, and that they in fact have the ability to do so. An overall mean effect of zero does not directly imply that there is no effect of facultative sex ratio adjustment but rather that among sample units and across studies the strength of producing both male- and female-biased sex ratios has not differed significantly. Nevertheless, if equal outcomes of male- and female-adjusted sex ratios negated the 'real' effects of each other this pattern would be robust under replication with increasing sample size and the effect sizes would exhibit significant heterogeneity, and not consistently converge to zero. This provides strong support for our conclusions given a lack of heterogeneity is extremely rare in meta-analyses conducted in the fields of ecology and evolution (Jennions & Møller 2002; Kotiaho & Tomkins 2002).

We have shown that the studies of primary sex ratio adjustment in birds do not exhibit any variability beyond that which could be expected owing to sampling error. Without variability among studies, there is thus no *a posteriori* clustering between groups of parameters that could consistently provide evidence for adaptive biases. We conclude that our study presents a robust and extensive summary of the current primary sex ratio literature on birds, and does not provide any evidence that facultative adjustment is a characteristic biological phenomenon. Individual studies have thus identified 'outliers', either statistical artefacts or very rare biological exceptions. Detection of outliers indicates that laying sequence and habitat quality (table 1), although not consistently associated with facultative sex ratio adjustment, have in the past both produced effect sizes that were not invariable with the homogeneous effect size model. We encourage biologists to provide further empirical evidence for testing against these conclusions.

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