Notes and Comments

Cooperative Breeders Adjust Offspring Sex Ratios to Produce Helpful Helpers

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ABSTRACT: Whether birds and mammals adaptively adjust their offspring sex ratios in response to their environment is much debated. A source of confusion is that different studies show different patterns, with sex ratio adjustment appearing to occur in some cases but not others. The extent to which this reflects interesting biological variation due to differences in the underlying selective forces, as opposed to statistical noise, is not clear. Cooperatively breeding species offer an opportunity to address this problem because the strength of selection on sex ratio adjustment can be estimated. When helping behavior is sex dependent, parents are predicted to overproduce the helping sex when this sex is rare or absent. We show here that the extent of this behavior depends on the benefit that helpers bring to parents: there is greater sex ratio adjustment when helpers bring larger benefits. Variable selection on sex ratio adjustment may thus explain variable empirical findings.

Keywords: local resource enhancement, meta-analysis, sex allocation, sex determination, Trivers and Willard.

Strong support for adaptive manipulation of offspring sex ratios has come from studies of invertebrates (Charnov 1982; Godfray 1994; Hardy 2002; West et al. 2005). However, the evidence is much less clear-cut for birds and mammals, where different studies show different patterns, and reviews of these studies have come to different conclusions even when utilizing overlapping data sets (van

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Schaik and Hrdy 1991; Palmer 2000; Brown and Silk 2002; Hardy 2002; West and Sheldon 2002; Ewen et al. 2004; Schino 2004; Sheldon and West 2004; Silk et al. 2005; West et al. 2005). A major difficulty in interpreting these variable empirical results is that it is often not clear how selection is acting on the sex ratio in vertebrates (Frank 1990; Cockburn et al. 2002; West and Sheldon 2002; Sheldon and West 2004). This means that it is often hard or impossible to predict the expected pattern of sex ratio adjustment for a given species or how it should vary across species.

A solution to this problem is offered by cooperatively breeding species, where it is possible to estimate the strength of selection for such sex ratio adjustment. In cooperative breeders, there is selection for parents to overproduce the helping sex when this sex is rare or absent (Gowaty and Lennartz 1985; Pen and Weissing 2000). The strength of selection for this sex ratio adjustment will be determined by the benefit provided by helpers, which varies across species (Griffin and West 2003). In some cases, helpers have been shown to have large positive effects on the fitness of their parents (Griffin and West 2003), in which case we would expect strong selection for sex ratio adjustment (Pen and Weissing 2000). At the other extreme, if "helpers" actually provide negligible help, there is no selection for parents to produce more of this sex (Pen and Weissing 2000). Consequently, we can predict that the extent of sex ratio adjustment should be positively correlated with the benefit that helpers provide.

We tested this prediction using meta-analysis, comparing standardized measures of two different relationships. The first is the relationship between offspring sex ratio and the number of helpers in a group (defined as r_{sex}), which assesses the extent to which parents overproduce the helping sex when that sex is rare or absent in a social group. The second is the relationship between offspring production or survival and the number of helpers (defined as r_{help}), which assesses the benefit of having helpers. Larger positive values represent either stronger overproduction of the helping sex when they are absent (r_{sex}) or a greater fitness benefit due to the presence of helpers (r_{help}). Con-

sequently, we predict a positive correlation between r_{sex} and r_{help}.

Methods

We included as many studies as possible in our analyses. We collected studies as part of a literature survey when writing book chapters on this topic (S. A. West, unpublished manuscript); from our previous articles in this area (West and Sheldon 2002; Griffin and West 2003; West et al. 2005); by searching for references in reviews of the subject (Sheldon 1998; Hardy 2002; Komdeur and Pen 2002; Ewen et al. 2004); by searching the Institute for Scientific Information Web of Science; by searching citations in all articles found by the above methods; and by directly contacting researchers. We know of (but could not include) additional unpublished studies of these relationships for three bird species; in all three cases, helpers have little effect on parental fitness, and there is no evidence for a sex ratio bias in favor of the helping sex, suggesting that inclusion of these data would further strengthen the relationship presented here.

We analyzed our data using the method of meta-analysis (Rosenthal 1991; Rosenberg et al. 2000), as we have described in detail elsewhere (Sheldon and West 2004; West et al. 2005). This methodology involves calculating from each study a standard measure of statistical effect size that can then be used as the response variable in comparative analyses. The effect size that we use is r, the correlation coefficient. The correlation coefficient from a study provides an estimate of how precisely individuals adjust their offspring sex ratios in response to local conditions: r ranges between 1 and -1, with values close to 1 (or -1) implying an extremely precise (low-scatter) positive (or negative) shift in the offspring sex ratio in response to variation in the relevant environmental variable; a value of 0 represents no correlation. More specifically, the r^2 from a study is the proportion of variance in the offspring sex ratio that is explained by the explanatory variable.

Effect sizes were calculated using standard methodology described in detail elsewhere (Rosenthal 1991; Rosenberg et al. 2000). Briefly, in some studies, the effect size is given as the correlation coefficient (r), the percentage of variance explained (r^2), or the Spearman rank correlation coefficient (r_s); in other cases, the effect size can be calculated from a test statistic (e.g., F, t, χ^2, or P values) and sample size using standard formulas (Rosenthal 1991; Rosenberg et al. 2000); in some cases, we used raw data given in figures or tables to calculate test statistics. If the test statistics were derived from ANOVA with more than two treatments, we applied an ordered heterogeneity test (Rice and Gaines 1994).

We calculated the effect size (r) for the relationships between offspring sex ratio and the number of helpers in a group (defined as r_{sex}), with a positive sign assigned to cases in which lower numbers of helpers led to a greater production of the helping sex, and between offspring production/survival and the number of helpers (defined as r_{help}), with a positive sign assigned to cases in which groups with more helpers produced more young. We did not include species where the effect of helper number was estimated for traits that are less clearly linked to fitness, such as feeding rates. The effect sizes used and details of how they were calculated are given in table 1.

All analyses were conducted on Z-transformed r values to correct for asymptotic behavior of large values of r. We conducted all analyses on species mean values, and so when required, we obtained a mean value from multiple studies on a single species by averaging Z_r, weighted for sample size, and summed sample sizes. All analyses were performed using MetaWin 2.0 (Rosenberg et al. 2000). We used random-effect models, because these are more appropriate for ecological data, and our underlying hypothesis is that effect sizes differ between species. Since sample sizes were small and error distributions of effect sizes unknown, we used randomization to obtain exact P values. Although we would ideally have also analyzed our data using a formal phylogeny-based comparative method to control for possible nonindependence of data points, this was not possible because of a lack of analytical tools that allow meta-analysis to be carried out in a phylogenetic framework (West et al. 2005). However, the species that we have examined are relatively widely dispersed, and all belong to different genera.

Results and Discussion

As predicted, we found greater sex ratio adjustment in species where the presence of helpers provides greater fitness benefits (fig. 1). We were able to obtain data on both the extent of sex ratio adjustment (r_{sex}) and the benefit provided by helpers (r_{help}) for 11 species, nine birds and two mammals (table 1). Across species, there was a significant positive correlation between r_{sex} and r_{help} (fig. 1), independently of whether the analysis was weighted according to the error variance in the estimates of r_{help} ($P = .007$; slope $\pm$ SE $= 0.89 \pm 0.31$) or r_{sex} ($P = .036$; slope $\pm$ SE $= 0.66 \pm 0.19$).

Although the sample size is small (because few studies have estimated both relationships), a relatively large proportion of the variance in sex ratio adjustment is explained by the benefits brought by helpers. Specifically, the P values given above would correspond to r^2 values of 0.66 and 0.40, respectively. The strength of this relationship is particularly striking, given that there are a number of additional factors that might be hypothesized to affect the

Table 1: Studies providing the effect sizes r_{sex} and r_{help}

Species	Sex ratio adjustment			Benefit of helping		
	Study	r_{sex}	Sample size	Study	r_{help}	Sample size
Birds:						
Acrocephalus sechellensis (Seychelles warbler)	Komdeur 1996	.546[a]	178	Komdeur 1994	.662[b]	15
Dacelo novaeguineae (laughing kookaburra)	Legge et al. 2001	−.239[c]	38	Legge 2000	−.187[b]	24
Manorina melanophrys (bell miner)	Ewen et al. 2003	.233[d]	59	Clarke 1989	.635[e]	12
Melanerpes formicivorus (acorn woodpecker)	Koenig et al. 2001	.031[f]	837	Koenig and Mumme 1987	.093[g]	160
Parabuteo borealis (Harris's hawk)	Bednarz and Hayden 1991	−.028[h]	261	Bednarz 1987	.039[i]	60
Philetairus socius (sociable weaver)	Doutrelant et al. 2004	−.316[d]	58	Doutrelant et al. 2004	.268[j]	77
Phoeniclus purpureus (green wood-hoopoe)	Ligon and Ligon 1990	.113[d]	128	Du Plessis 1993	.102[b]	144
Picoides borealis (red-cockaded woodpecker)	Gowaty and Lennartz 1985	.364[d]	41	Lennartz et al. 1987	.314[k]	93
Sialia mexicana (western bluebird)	Dickinson 2004	.235[d]	153	Dickinson 2004	.143[l]	613
Mammals:						
Lycaon pictus (African wild dog)	Creel et al. 1998	.720[a]	16	Malcolm and Marten 1982; Creel et al. 1998	.491[m]	47
Marmota marmota (alpine marmot)	Allainé 2004	.327[d]	82	Allainé et al. 2000	.193[n]	134

Note: Here r_{sex} is the effect size for the relationship between offspring sex ratio and the number of helpers in a group, and r_{help} is that for the relationship between offspring production/survival and the number of helpers. Figures and tables refer to those in the original articles.

[a] From West and Sheldon (2002).

[b] From Griffin and West (2003).

[c] Group size vs. sex ratio; $\chi^2_{(3)} = 6.2$.

[d] From West et al. (2005).

[e] Comparing the reproductive success of pairs with more or fewer than six helpers; $z = 2.2$.

[f] Table 3; comparing offspring sex ratio between groups with and without helpers gives $\chi^2_{(1)} = 0.79$.

[g] Table 6.5, chap. 6, p. 150; examining groups with two breeders, $\chi^2_{(2)} = 1.0$.

[h] Raw data on p. 122 give 56% males ($n = 152$) when no helpers, 59% males ($n = 109$) when helpers.

[i] Table 1 gives mean and SD for t-test, giving $t = 0.305$, $n = 60$.

[j] R. Covas, personal communication, from manuscript in preparation.

[k] Families with no helpers fledge on average 1.40 offspring/year (SD = 1.01, $n = 50$); families with helpers (1–2) fledge 2.05 offspring/year (SD = 0.97, $n = 43$).

[l] Carried out a t-test on the raw data provided for the offspring fledged with (3.87 ± 0.30) and without (2.75 ± 0.09) helpers, to obtain $t = 3.58$.

[m] This is the weighted average of two independent estimates. A reanalysis of the raw data from fig. 6 in Malcolm and Marten (1982), assuming Poisson errors, gives $\chi^2_{(1)} = 4.56$, $n = 17$; and fig. 1 in Creel et al. (1998) gives $r^2 = 0.234$, $n = 30$.
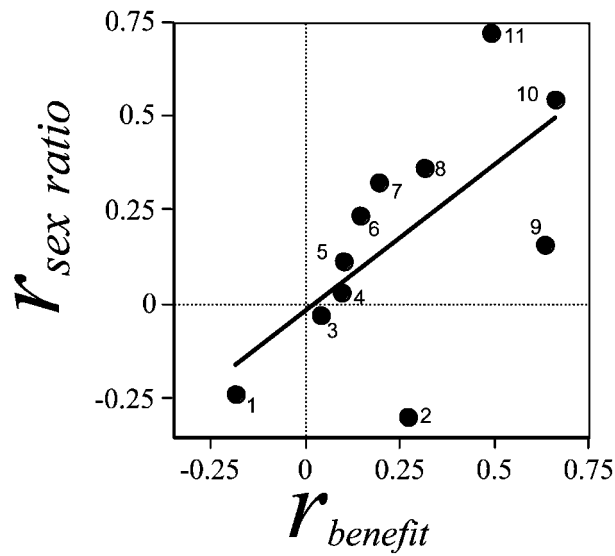
[n] Fig. 2*a*; $\chi^2_{(1)} = 5.01$.

Figure 1: Correlation between sex ratio adjustment and the benefits of helping. The effect size of the relationship between the offspring sex ratio and the number of helpers ($r_{\text{sex ratio}}$; r_{sex} in text) is plotted against the effect size of the relationship between the benefit of helping and the level of helping (r_{benefit}; r_{help} in text). The data points represent (*1*) laughing kookaburra, (*2*) sociable weaver, (*3*) Harris's hawk, (*4*) acorn woodpecker, (*5*) green wood-hoopoe, (*6*) western bluebird, (*7*) alpine marmot, (*8*) red-cockaded woodpecker, (*9*) bell miner, (*10*) Seychelles warbler, and (*11*) African wild dog. Across species, there was a significant positive correlation between r_{sex} and r_{help}, indicating that sex ratio adjustment is greater in species where the presence of helpers leads to greater fitness benefits.

skew in sex ratio, such as the extent to which sex biases in helping behavior are partial or absolute, diminishing returns from increasing helper number, the frequency with which helping occurs, and sex-differential influences of helper number on the quality of offspring reared (Frank 1990, 1998; Pen and Weissing 2000; Ewen et al. 2003; Doutrelant et al. 2004). The importance of these other factors has not been estimated in enough studies to allow an analysis of their effects.

Our results illustrate a possible limitation of using the mean effect size across a number of species to test for sex ratio adjustment. Overall, the mean effect size was not significantly different from 0 ($P > .05$; mean $r_{\text{sex}} = 0.168$; 95% confidence interval -0.007 to 0.345), which might be taken as evidence that facultative sex ratio adjustment in relation to helper number does not occur (although different conclusions are reached when the data set is not restricted to species where there are data on both sex ratio adjustment and the benefit of helping; West et al. 2005). Furthermore, there was no significant heterogeneity across species ($Q_t = 14.52$, df $= 10$, $P = .15$), which might suggest that variation in the extent of sex ratio adjustment across species was due only to sampling error. However,

our results suggest that sex ratio adjustment occurs in some species and not others and that this variation can be explained by variation in the strength of selection for sex ratio adjustment. It will be extremely interesting to determine whether a lack of a consistent sex ratio pattern in other cases, such as primates, can also be explained by variable selection (van Schaik and Hrdy 1991; Brown and Silk 2002; Ewen et al. 2004; Schino 2004; Silk et al. 2005).

Our result also illustrates two general points. First, it emphasizes the power of comparative statics when testing evolutionary theory (Frank 1998): it may be easier to predict how the extent of sex ratio adjustment should vary across species than what should occur in a particular species. Second, it provides an empirical link between the evolution of sex ratio adjustment and cooperation. Recent unification of social evolution theory emphasizes how the same selective forces should influence these traits (Frank 1998). We have previously shown that helpers are more likely to direct their helping behavior toward closer relatives (kin discrimination) in species where helpers provide a greater fitness benefit (higher r_{help}; Griffin and West 2003), as predicted by kin selection theory (Hamilton 1963, 1964). Taken together, these results show that the benefit provided by helpers (r_{help}) determines the extent of both kin discrimination when helping and sex ratio adjustment when producing those helpers.

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