SEX-RATIO ADJUSTMENT WHEN RELATIVES INTERACT: A TEST OF CONSTRAINTS ON ADAPTATION

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Abstract.—Studies of sex allocation offer excellent opportunities for examining the constraints and limits on adaptation. A major topic of debate within this field concerns the extent to which the ability of individuals to adaptively manipulate their offspring sex ratio is determined by constraints such as the method of sex determination. We address this problem by comparing the extent of sex-ratio adjustment across taxa with different methods of sex determination, under the common selective scenario of interactions between relatives. These interactions comprise the following: local resource competition (LRC), local mate competition (LMC), and local resource enhancement (LRE). We found that: (1) species with supposedly constraining methods of sex determination showed consistent sex-ratio adjustment in the predicted direction; (2) vertebrates with chromosomal sex determination (CSD) showed less adjustment then haplodiploid invertebrates; (3) invertebrates with possibly constraining sex-determination mechanisms (CSD and pseudo-arrhenotoky) did not show less adjustment then haplodiploid invertebrates; (4) greater sex-ratio adjustment was seen in response to LRC and LMC than LRE; (5) greater sex-ratio adjustment was seen in response to interactions between relatives (LRC, LMC, and LRE) compared to responses to other environmental factors. Our results also illustrate the problem that sex-determination mechanism and selective pressure are confounded across taxa because vertebrates with CSD are influenced primarily by LRE whereas invertebrates are influenced by LRC and LMC. Overall, our analyses suggest that sex-allocation theory needs to consider simultaneously the influence of variable selection pressures and variable constraints when applying general theory to specific cases.

Key words.—Local mate competition, local resource competition, local resource enhancement, sex allocation, sex determination.

Sex allocation has been a productive and successful area of evolutionary biology (West et al. 2000). Theory predicts a number of situations in which individuals are expected to adjust their relative allocation to male and female reproduction, and there is a huge empirical literature supporting these predictions across a wide range of organisms (Charnov 1982; Godfray 1994; Bourke and Franks 1995; Frank 1998; Hardy 2002). However, the striking successes of sex allocation theory seem to be limited to a number of taxonomic groups. For example, considering facultative adjustment of offspring sex ratios (defined as proportion of males) in response to local conditions, striking patterns are frequently observed in insects, especially the Hymenoptera (ants, bees, wasps), and less frequently in vertebrates. Explaining these broad taxonomic patterns is one of the major outstanding problems for the field of sex allocation (West et al. 2002).

It has commonly been assumed that variation in the extent of sex-ratio adjustment can be primarily explained by the method of sex determination. Specifically, clear patterns are most frequently seen in the Hymenoptera because their haplodiploid sex determination allows precise control of the sex ratio, whereas chromosomal (genetic) sex determination (CSD) is presumed to act as a constraint that precludes control of offspring sex ratios in taxa such as vertebrates (Maynard Smith 1978; Williams 1979; Charnov 1982; Clutton-Brock 1986; Clutton-Brock and Iason 1986; Palmer 2000). However, there is very little concrete support for this assumption, and increasing evidence against it. Specifically: (1) studies of a wide range of taxa with CSD have reported examples that suggest significant control of offspring sex ratios (re-

viewed by Hardy 2002; West et al. 2002); (2) there are consistent patterns of sex-ratio adjustment across vertebrates, including cases where clear a priori predictions can be made for how offspring sex ratios should be adjusted (Badyaev et al. 2001; West and Sheldon 2002; Schino 2004; Sheldon and West 2004).

In addition, there are several alternative explanations of why extreme sex-ratio skews are less often seen in vertebrates (West et al. 2000, 2002; West and Sheldon 2002). First, selection for sex-ratio adjustment in vertebrates may be weaker. In agreement with this, many of the most convincing examples in insects occur in cases in which there is intense competition for mates between related males and selection for extremely female-biased sex ratios, as low as 5% males (Hamilton 1967; Godfray 1994). Sex-ratio shifts in vertebrates can depend upon factors with weaker fitness consequences such as the heritability of fitness between fathers and offspring (Burley 1981; Pen and Weissing 2000a). Second, the longer life span and more complex life history of vertebrates (e.g., multiple breeding attempts, overlapping generations) may lead to multiple selective forces acting on the sex ratio at different times (West et al. 2000; Cockburn et al. 2002). For example, it has been argued that ungulate, marsupial, and primate sex ratios can be shaped by the influence of polygynous mating systems, competition among related females, cooperation among related females, inheritance of maternal rank by daughters, and overlapping generations (Trivers and Willard 1973; Clark 1978; Simpson and Simpson 1982; Hiraiwa-Hasegawa 1993; Silk 1983, 1988; West and Godfray 1997; Cockburn et al. 2002). Third, en-

vironmental predictability may influence the benefit of sex-ratio adjustment, and vertebrates may be less able to assess the relevant environmental factors that influence the optimum sex ratio (West et al. 2000; West and Sheldon 2002). For example, female parasitoid wasps need merely to determine factors such as whether there are other females on a patch, or the size of the host in which they are laying eggs, whereas vertebrate females might need to assess factors such as the heritable genetic quality of mates, or the amount of parental investment mates are able to provide. In short, the problem with understanding the causes of variation in adaptive sex-ratio adjustment is that there are multiple confounding factors operating when the comparison is restricted to vertebrates and haplodiploid invertebrates.

Our aim here is to carry out a quantitative test of whether the mechanism of sex determination constrains sex-ratio adjustment. An ideal test would examine the extent of sex-ratio adjustment across species with different methods of sex determination when the same behavior is examined in all species, and all species are subject to the same selective regime. This is obviously not possible. However, it is possible to examine a situation in which sex ratios are adjusted in response to one general type of effect, and for which there should be relatively similar selection pressures across species. Specifically, we examine situations in which sex ratios are influenced by interactions between relatives. These interactions can have positive (competitive) or negative (cooperative) fitness effects, and include: (1) local resource competition (LRC), when related individuals of one sex compete more for resources; (2) local mate competition (LMC), when related individuals compete for mates, representing a much studied special case of LRC; (3) local resource enhancement (LRE), when individuals of one sex have greater positive fitness effect on relatives, such as through cooperation (Hamilton 1967; Clark 1978; Taylor 1981; Schwarz 1988; Frank 1998). Studies of these forms of sex allocation include many of the most striking examples of sex-ratio adjustment in insects, birds, and mammals (Godfray 1994; Komdeur et al. 1997; Creel et al. 1998; West et al. 2002).

Focusing our attention on this area has several other advantages. First, we are able to examine species with a variety of sex determination systems: diploid vertebrates with CSD (birds, mammals, snakes), haplodiploid invertebrates (ants, bees, wasps, beetles, spider mites, thrips), diploid invertebrates with CSD (aphids, spiders), pseudo-arrhenotokous invertebrates (phytoseiid and other mites, beetles, mealy bugs; haplodiploid mechanisms such as paternal genome loss that require male eggs to be fertilized and which have thus been suggested to constrain sex-ratio manipulation), and simultaneous hemaphrodites (a wide range of taxa). Second, following Hamilton (1967), theory is particularly well developed in this area, and there are clear a priori predictions that can be made for how sex ratios should vary, so that the effect sizes can be examined using meta-analysis (see Methods). This is important because it is necessary to study the extent to which individuals shift sex ratios, and not population sex ratios (West and Sheldon 2002). Population sex ratios can be very hard to predict and the extent of any deviation from 50% males does not reflect the precision with which indi-

viduals are adjusting sex ratios (Frank 1987a, 1990; Pen and Weissing 2000b, 2002; West and Sheldon 2002).

The specific questions that we address are: (1) Does CSD prevent adaptive sex-ratio adjustment? We test this by examining whether organisms with CSD show consistent patterns of sex-ratio adjustment in the direction predicted by theory. (2) Does CSD constrain sex-ratio adjustment to be less precise or weaker then in haplodiploid organisms? (3) Have LRC and LMC selected for more (or less) precise sex-ratio adjustment than LRE? This might be expected because: (a) the magnitude of the selective force may vary between competitive (fitness decrement) and cooperative (fitness increment) interactions between relatives; (b) interactions can be between different classes of individuals—primarily between siblings with LMC and LRC and between mothers and offspring with LRE; (c) the fitness consequences of LRE vary across species, and can be low or negligible in some cooperative breeders (Griffin and West 2003). (4) Do the data on sex-ratio adjustment in response to LMC suggest a role of environmental predictability in determining the precision of sex-ratio adjustment? We test this by examining the extent to which sex ratios are manipulated in response to two different cues that should differ in their relative predictability—number of females on a patch or relative fecundity (see methods). (5) Is the precision of sex-ratio adjustment in response to interactions between relatives (LRE, LRC, and LMC) greater than that in response to environmental variation influencing the fitness of offspring of each sex (including factors such as mate quality in birds, host size in solitary wasps, maternal condition of rank in ungulates; these represent different forms of what is termed the Trivers and Willard (1973) hypothesis)? This would be expected if the selective forces arising from interactions between relatives are stronger, and select for more extreme sex ratios (Frank 1998).

METHODS

Predicted Patterns of Sex-Ratio Adjustment

We are testing the extent to which different organisms facultatively adjust their offspring sex ratios in response to interactions between relatives. Theory predicts a number of ways in which individuals are predicted to adjust their offspring sex ratios in response to such interactions. The unifying principle in all these cases is that individuals are selected to produce a lower proportion of the competitive sex when the degree of LMC or LRC increases, or more of the cooperative sex when the degree of LRE increases. Considering local mate competition (LMC): (1) females should lay a less female-biased sex ratio as the number of females laying eggs on a patch increases (variable foundress number: Hamilton 1967); (2) for a constant number of females laying eggs on a patch, the sex ratio produced by each female should be negatively correlated to the relative number of offspring that they contribute to the patch (variable fecundity: Werren 1980; Yamaguchi 1985; Stubblefield and Seger 1990); (3) the sex ratios of wingless offspring should be more female biased than that of winged offspring because mate competition will be greater between wingless males (wing status: Hamilton 1979; Frank 1986); (4) when multiple generations occur in a patch, the sex ratio should become relatively female-biased

at the time of dispersal from that patch, because this is when competition between related females will be least (haystack model: Frank 1986; Nagelkerke and Sabelis 1996); (5) females should produce a more female-biased sex ratio if they are born on a patch, rather than an immigrant, because natal females will be more related to the other females on a patch (natal or immigrant: Taylor and Crespi 1994). Considering other cases of local resource competition (LRC): (6) if LRC occurs among sisters, then the sex ratio should be positively correlated with brood size (i.e., produce more males) because larger broods lead to greater potential for LRC (variable fecundity: Frank 1987b); (7) if the extent of LRC among sisters varies across patches, then relatively female-biased sex ratios should be produced in the patches with lower LRC, for example, when some colonies of a social insect species reproduce by budding and others do not, or if queen replenishment occurs (variable LRC: Pamilo 1990, 1991; Brown and Keller 2000). Considering local resource enhancement (LRE): (8) when offspring of one sex stay and help raise other offspring, mothers should produce that sex when they have no or relatively few helpers (to obtain helpers), and the other sex when they have relatively large numbers of helpers (Gowaty and Lennartz 1985; Pen and Weissing 2000b); (9) when offspring of one sex cooperate after dispersal, the sex ratio should be decreasingly biased towards that sex as brood size increases, because of diminishing returns to extra cooperation (Schwarz 1987, 1994; Greeff 1999).

Collection and Inclusion of Studies

We collected studies that tested the above predictions using a number of methods. Specifically: (1) as part of a literature survey when writing three book chapters on these topics (S. A. West, unpubl. ms); (2) searching for references in reviews of the subject (e.g., Charnov 1982; Wrensch and Ebbert 1993; Godfray 1994; Bourke and Franks 1995; Hardy 2002); (3) searching the Institute for Scientific Information web of science on 25 November 2003, for all articles referring to local resource competition or local resource enhancement or local mate competition from 1981–2003; (4) searching citations in all papers found by the above methods. Altogether, this method produced over 500 potentially related articles, but only a fraction of these contained relevant sex-ratio data.

We have included as many studies as possible in our analyses. We excluded studies where there was no clear a priori pattern of sex-ratio adjustment being tested for. This included a number of studies from primates, ungulates, marsupials, and rodents where LRC had been discussed as a potentially important factor, but where there may have been other factors acting (see introduction). We also excluded studies of social insects, in which variation across colonies in relatedness asymmetry (Boomsma and Grafen 1990, 1991) could provide an alternative explanation for sex-ratio variation (discussed by Chan et al. 1999; Murakami et al. 2000; Brown et al. 2002). Finally, we excluded studies of LMC with variation in relatedness between females on a patch or between females and mates, because such sex-ratio shifts: (a) may not always be selected for; and (b) may not be possible if there is no mechanism of kin recognition, because they rely upon in-

dividuals assessing relatedness (Herre et al. 1997; Reece et al. 2004; Shuker et al. 2004a,b).

From the subject areas for which we have included studies and there was sex-ratio data, we were forced to exclude studies in which appropriate effect sizes (see below) could not be calculated. This included studies in which (1) no appropriate test statistics were given or could be calculated (e.g., Kuno 1962; Holmes 1972; Hamilton 1979; Zaher et al. 1979; Rojas-Rousse et al. 1983; Yamaguchi 1985; Orzack 1986; Orzack and Parker 1986; Herre 1987, 1988; Strand 1988; van Dijken et al. 1993; Hardy and Cook 1995; Gauthier et al. 1997; Herre et al. 1997; Hardy et al. 1998, 1999; Hardy and Mayhew 1998; van Baaren et al. 1999; Molbo et al. 2003; Tsuchida and Ohguchi 1998; Nishimura and Jahn 1996; Tagawa 2000); (2) the appropriate test statistics were pseudoreplicated (see below), or data that could be used in calculating test statistics would lead to pseudoreplication (e.g., Velthuis et al. 1965; Wylie 1965a,b, 1966, 1967, 1973, 1976a,b, 1979; Walker 1967; Kochetova 1978; Kondo and Takafujii 1982; Owen 1983; Narasimham 1984; Bednarz 1987; Schwarz 1987; Dinh et al. 1988; Holekamp and Smale 1995; Koenig and Dickinson 1996; Nunn and Pereira 2000; Koenig et al. 2001; Wool and Sulami 2001); (3) the data are a subset of that in other studies we have included (Sabelis and Nagelkerke 1987; Orzack and Parker 1990; Rispe et al. 1999; Brown and Keller 2000); (4) there are no relevant data in the paper (Wiackowski 1962; Shiga and Nakanishi 1968; Waage 1982; Suzuki and Hiehata 1985; Cipollini 1991; Higgins and Myers 1992; Orzack and Gladstone 1994; Monge-Najera 1995; Izraylevich and Gerson 1996; West and Herre 1998a,b; Antolin 1999; Arnold et al. 2001; Oku and Nishida 2001; Jordal et al. 2002; Santolamazza-Carbone and Rivera 2003). In addition, we excluded data from three parasitoid wasp species where the relationship between sex ratio and foundress number has been examined, but the appropriate biology for LMC does not apply. These were two species where LMC does not occur because there is inbreeding avoidance and related males do not appear to compete (van Dijken et al. 1989; Cook et al. 1994; Ode et al. 1995), and one species where brood guarding and ovicide means that the foundress number never varies and so will always be one (Griffiths and Godfray 1988; Legner and Warkentin 1988; Hardy and Blackburn 1991). The inclusion of these three wasp species made no difference to our results and conclusions, merely reducing the mean effect size (r) for the haplodiploid invertebrates by ≈ 0.03.

Data Analysis

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; see also West and Sheldon 2002; Griffin and West 2003). Briefly, this methodology involves calculating a standard measure of statistical effect size from each study 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, 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 zero 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, these are (1) 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); (2) in other cases the effect size can be calculated from a test statistic (F, t, χ^2, P-value, etc) and sample size using standard formulae (Rosenthal 1991; Rosenberg et al. 2000); (3) 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 >2 treatments, we applied an ordered heterogeneity (OH) test (Rice and Gaines 1994). In some cases with the data from wasps we could not apply an OH test because the P-values were too low for the existing statistical tables, and therefore in these cases the r-value is a conservative underestimate (see Appendix).

We did not include studies where the analyses where pseudoreplicated, or where the available data only allow a pseudoreplicated analysis (Hurlbert 1984; Cook et al. 1994). The reason for this is that pseudoreplication can decrease the estimate of the effect size r, because it can increase the variance per treatment (while increasing sample size and the chance of obtaining a significant result). This is most easily illustrated with the following example: Consider a species where each female produces four offspring, and where 10 females in environment A each produce a sex ratio of 0.25 (one male, three females), and 10 females in environment B each produce a sex ratio of 0.75 (three males, one female). If the data are analyzed appropriately with mothers as the independent data point, then $r = 1$ would be obtained (sample size $n = 20$); whereas if the analysis treats all offspring as independent, this gives $\chi^2_{(1)} = 20.93$, $n = 80$, and hence the much lower effect size of $r = 0.51$, which would also incorrectly be given more weight in the overall analysis due to its larger sample size.

In all cases we assigned a positive value to the effect size (r) if the sex-ratio shift was in the predicted direction, and a negative value if it was in the opposite direction. 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 thus 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. Because sample sizes were sometimes small and error distributions of effect sizes unknown, we bootstrapped to obtain confidence intervals around mean effect sizes and used randomization to obtain exact P-values for specific comparisons of groups.

Meta-analysis allows several tests to see whether the published studies, and therefore the mean effect size observed, have been influenced by a tendency not to publish nonsignificant results (publication bias: Rosenthal 1991; Duvall and Tweedie 2000; Palmer 2000; Rosenberg et al. 2000; Møller and Jennions 2001). We tested for publication bias in three ways. First, we tested for a significant negative correlation between effect size and sample size, which would indicate publication bias (a lack of nonsignificant results with small sample sizes). Second, we calculated the ''fail-safe number'' X, which is the number of unpublished studies with an effect size of zero that would have to exist in order for the overall mean effect size to be not significantly different from zero. Interpretation of the meaning of X depends in part on subjective assessment of whether it is likely that so many unpublished studies exist. A quantitative criterion is that a result is robust if $X > 5n + 10$, where n is the number of studies on which the meta analysis was based, although this criterion is extremely hard to reach with relatively small sample sizes (Rosenberg et al. 2000). Third, we used the trim-and-fill method of Duvall and Tweedie (2000). This method estimates the number (L_0) and effect size of studies that are missing from a meta-analysis due to publication bias against nonsignificant results. These are then added to the dataset, the mean effect size recalculated, and its statistical significance derived (Jennions and Møller 2002).

There is a large literature on carrying out statistical analyses with phylogeny-based comparative methods such as independent contrasts (Felsenstein 1985; Grafen 1989; Harvey and Pagel 1991; Mayhew and Pen 2002). However, there are as yet no methodologies for carrying out phylogenetically controlled meta-analyses (Schino 2004), thus phylogeny has generally been ignored in meta-analyses (though see West and Sheldon 2002), and it is even common that multiple studies on a species are used as independent data points. In some cases the question being addressed means that the lack of a formal comparative method is not a problem. For example, if we are testing taxon-based questions such as whether vertebrates manipulate sex ratios less then invertebrates, it is appropriate to use data from multiple species to test this in a meta-analysis, despite there being only one phylogenetically independent contrast between them. However, in other cases it would be useful to carry out an independent contrast analysis. For example, when comparing the extent to which individuals adjust sex ratio in response to either the number of females on a patch or relative fecundity, it is both appropriate and possible to make independent contrasts within species or within taxonomic groups. Here, we address these problems in two ways. First, when addressing taxon-based questions, we have analyzed the data in multiple ways to show the importance of including or omitting different taxa. Second, when an independent contrast approach is appropriate and possible we have utilized one. Because the statistics of incorporating effect sizes into the method of independent contrasts is not clear, we have taken the conservative approach of applying sign tests to only the branch tip contrasts (detailed below). Future studies aimed at taxa in which different sex determination mechanisms have evolved independently (Normark 2003) would be very useful.

RESULTS

We obtained data from 87 studies of 64 species (Appendix). These comprise data from five groups: 12 vertebrates

TABLE 1. Summary of mean effect sizes for studies of individual sex-ratio adjustment in response to local resource competition (LRC), local mate competition (LMC), and cooperative local resource enhancement (LRE) interactions between relatives. X is the fail-safe number, which is the number of unpublished studies averaging zero effect that would have to exist for the overall mean effect size to be not significantly different from zero and CI is the confidence interval. The effect size versus sample size column shows the Spearman rank correlation coefficient and significance for the relationship between effect size and sample size.

Class of study	Mean effect size r	95% CI	N (species)	Fail-safe number (X)	Effect size versus sample size
All	0.528*	0.458–0.596	64	4257	$R_s = -0.19, P = 0.14$
Haplodiploid invertebrates	0.564*	0.488–0.638	36	2320	$R_s = -0.15, P = 0.37$
Pseudo-arrhenotokous invertebrates	0.605*	0.390–0.742	5	18	$R_s = 0.10, P = 0.87$
CSD vertebrates	0.253*	0.087–0.415	12	29	$R_s = -0.12, P = 0.71$
CSD invertebrates	0.671*	0.449–0.863	4	5	$R_s = 0.20, P = 0.80$
Simultaneous hermaphrodites	0.551*	0.430–0.699	7	95	$R_s = -0.39, P = 0.38$
CSD and pseudo-arrhenotokous invertebrates	0.638*	0.476–0.764	9	48	$R_s = 0.27, P = 0.49$
CSD vertebrates, CSD and pseudo-arrhenotokous invertebrates	0.446*	0.289–0.587	21	121	$R_s = -0.10, P = 0.68$
LMC and LRC (All)	0.575*	0.509–0.635	50	3739	$R_s = -0.22, P = 0.12$
LMC and LRC (Separate sexes)	0.578*	0.507–0.642	43	2650	$R_s = -0.17, P = 0.28$
LRE	0.276*	0.106–0.525	13	47	$R_s = -0.14, P = 0.65$

* $P < 0.01$.

with CSD (nine birds, two mammals, one snake); four diploid invertebrates with CSD (three aphids, one spider); five pseudo-arrhenotokous invertebrates (one beetle, one mealy bug, three mites); 36 haplodiploid invertebrates (eight ants, two bees, 15 parasitoid wasps, six fig wasps, one beetle, three spider mites, one thrip); and seven simultaneous hemaphrodites (one each of barnacle, cestode, fish, flatworm, leech, polychaete, trematode). Overall the mean effect size is significantly greater than zero, suggesting that individuals consistently adjust their offspring sex ratios as predicted by theory (Table 1, Fig. 1).

Sex Determination and Sex Ratios

Our data do not support the hypothesis that the method of sex determination poses such a constraint that it prevents facultative adjustment of offspring sex ratios. Considering just the species with potentially constraining methods of sex determination, the mean effect size was significantly greater then zero, implying that they consistently adjust their offspring sex ratios as predicted by theory (Table 1, Fig. 2). This result holds when considering vertebrates (diploids with CSD) or invertebrates (diploids with CSD and pseudo-arrhenotokous species) separately (Table 1). Furthermore, several analyses suggest that these patterns are not due to publication bias. For example, in all cases the effect size is not significantly negatively correlated with the sample size (Table 1), the calculated fail-safe numbers are relatively large (Table 1), and the mean effect size is still greater then zero when carrying out a trim and fill analysis (CSD vertebrates, CSD and pseudo-arrhenotokous invertebrates: $n = 21$, number of missing studies $L_0 = 0$; CSD vertebrates: $n = 12$,
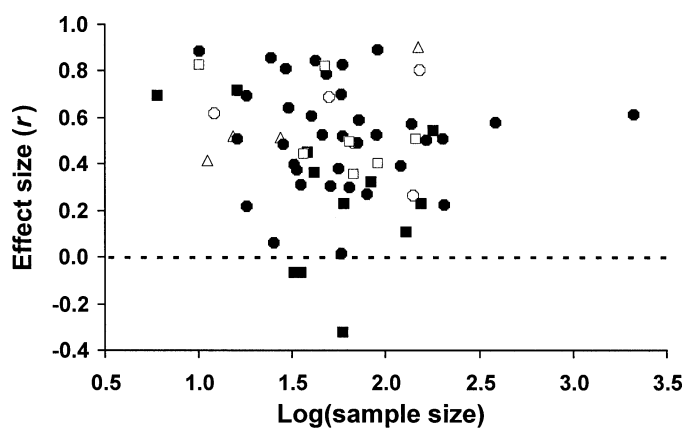

FIG. 1. Facultative sex-ratio adjustment in response to interactions between relatives. The effect size (r) is plotted against the sample size of the study. A positive value of r corresponds to an observed sex-ratio shift in the predicted pattern. The significant tendency towards positive values indicates a consistent trend to adjust offspring sex ratios as predicted by theory. The different symbols represent vertebrates with CSD (filled squares), invertebrates with CSD (open triangles), pseudo-arrhenotokous invertebrates (open circles), haplodiploid invertebrates (filled circles), and simultaneous hermaphrodites (open squares).
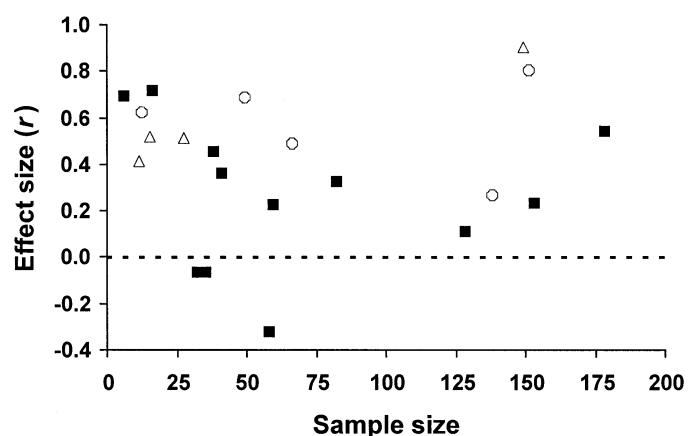

FIG. 2. Facultative sex-ratio adjustment by organisms with supposedly constraining methods of sex determination. The effect size (r) is plotted against the sample size of the study. A positive value of r corresponds to a sex-ratio shift in the predicted pattern. The significant tendency towards positive values indicates a consistent trend to adjust offspring sex ratios as predicted by theory. The different symbols represent vertebrates with CSD (filled squares), invertebrates with CSD (triangles), and pseudo-arrhenotokous invertebrates (circles).
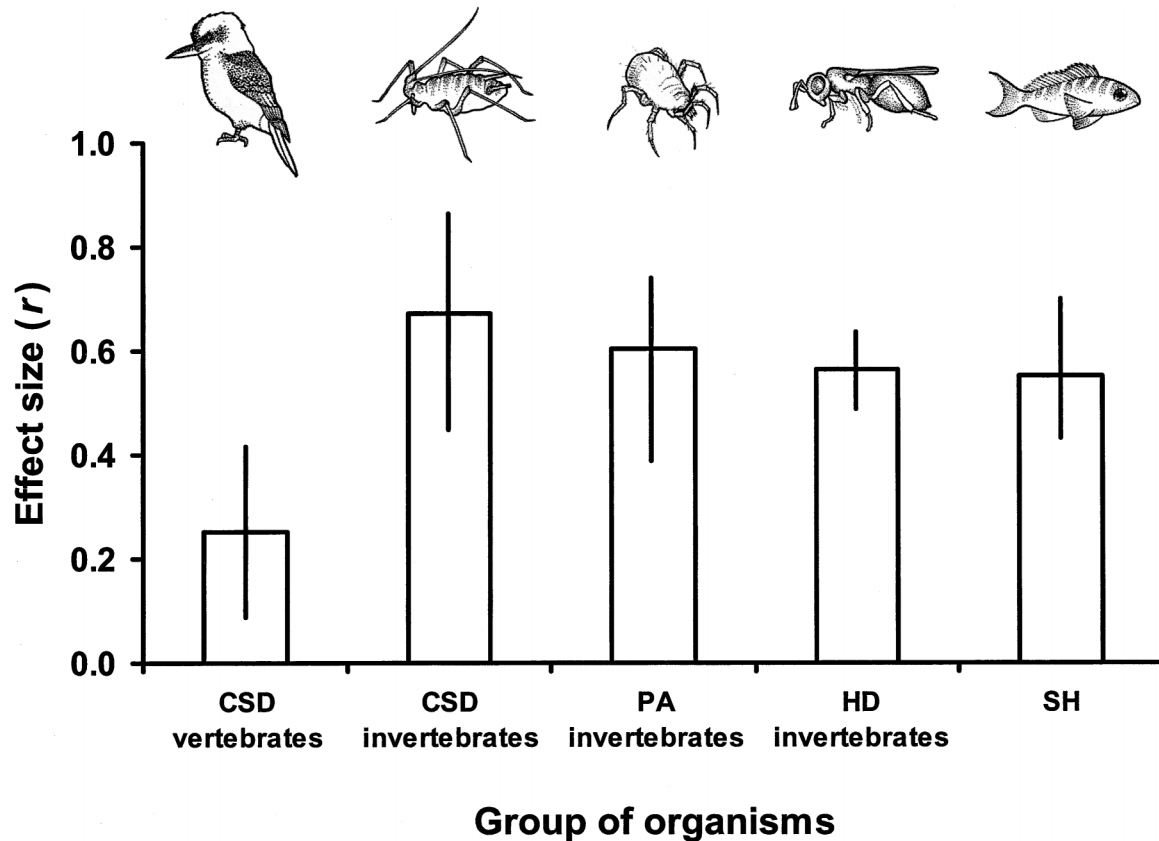
FIG. 3. Sex-ratio adjustment across species with different methods of sex determination. Plotted are the mean and 95% CI of the effect size (r) for different groups of organisms. A positive value of r corresponds to a sex-ratio shift in the predicted pattern. The different columns show the pattern for vertebrates with CSD, invertebrates with CSD, pseudo-arrhenotokous invertebrates, haplodiploid invertebrates, and simultaneous hermaphrodites. The mean effect size is significantly lower in vertebrates with CSD than in other groups. The animals illustrated are laughing kookaburra (*Dacelo novaeguineae*), aphid (*Uroleucon cirsii*), predatory mite (*Phytoseiulus persimilis*), parasitoid wasp (*Nasonia vitripennis*) and chalk bass (*Serranus tortugarum*); drawing not to scale.

number of missing studies $L_0 = 2$, adjusted mean $r = 0.203$, 95% confidence interval (CI): 0.011–0.371, $P < 0.04$).

We found mixed support for the hypothesis that the precision of sex-ratio adjustment is greater in haplodiploid species than in species with potentially constraining methods of sex determination (Table 1, Fig. 3). There was significant variation across the different groups (all five groups: randomization test, $P = 0.011$, $n = 64$; four groups with separate sexes: $P = 0.004$, $n = 57$). This variation was explained by vertebrates with CSD showing significantly lower effect sizes then the other four groups (randomization test, $P = 0.004$, $n = 64$). The other four groups do not differ significantly from each other (randomization test, $P = 0.537$, $n = 52$). This is mixed support because, although vertebrates with CSD have lower effects sizes, the invertebrates with potentially constraining methods of sex determination (diploid CSD and haplodiploid pseudo-arrhenotoky) do not. Specific comparisons are: (1) the vertebrates with CSD have significantly lower effect sizes then the haplodiploid invertebrates (randomization test, $P = 0.003$, $n = 48$); (2) there is no significant difference comparing the haplodiploid invertebrates with the CSD and pseudo-arrhenotokous invertebrates (randomization test, $P = 0.304$, $n = 45$); and (3) the CSD and pseudo-arrhenotokous invertebrates have significantly

larger effect sizes then the vertebrates with CSD (randomization test, $P = 0.006$, $n = 21$).

Selective Pressure and Sex Ratios

Considering all species, the mean effect size was significantly larger in response to LMC and LRC than in response to LRE (Fig. 4, Table 1; all five groups: randomization test, $P = 0.004$, $n = 63$; four groups with separate sexes: randomization test, $P = 0.002$, $n = 56$). In this analysis the data from the mealy bug species was not included, because it could be argued to be a response to either LRC or LRE (Varndell and Godfray 1996).

Considering species subject to LMC, we are able to compare the effect size when the sex ratio is adjusted in response to either the number of females laying eggs on a patch simultaneously (variable foundress number), or the relative brood size of females that visit a patch sequentially (variable fecundity). Furthermore, we are able to examine this question using independent contrasts (Harvey and Pagel 1991) between and within species. There are four parasitoid and fig wasp species in which both these situations have been examined, and in all cases the data show greater effect sizes in response to the number of females on a patch (Fig. 5, Ap-
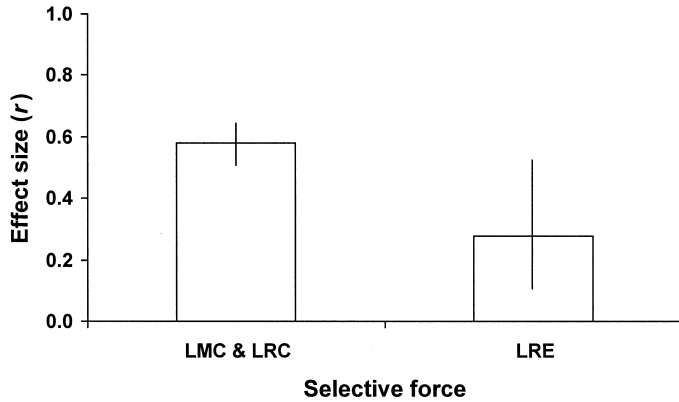
FIG. 4. Sex-ratio adjustment across species in response to different selective forces. Plotted are the mean and 95% CI of the effect size (r). A positive value of r corresponds to a sex-ratio shift in the predicted pattern. The two groups represent sex-ratio manipulation in response to: (a) competitive interactions, LMC and LRC ($n = 43$ species, one vertebrate and 42 invertebrates); (b) cooperative interactions, LRE ($n = 13$ species, nine birds, two mammals, and two bees). Significantly larger effect sizes are seen in response to competitive interactions (see Discussion).

pendix). Furthermore, the same pattern occurs if we also consider cases in which relative fecundity is assessed simultaneously, which allows comparison among the simultaneous hermaphrodite species, within an ant species (wing status rather than foundress number), and among three other ant species (two-tailed sign test, $P = 0.063$, $n = 5$ within species comparisons; $P = 0.013$, $n = 7$ including all comparisons; Fig. 5, Appendix).

Finally, we compared the effect sizes in this study with those in response to other proposed selective pressures on sex allocation. Specifically, we divided the reasons for sex-ratio manipulation into two broad categories: (1) responses to interactions between relatives (LRE, LRC, and LMC; this study), and (2) responses to variation in other local resources/conditions—the Trivers and Willard (1973) hypothesis. This hypothesis assumes that variation in some environmental factor has different fitness consequences for the two sexes—examples previously investigated include mate quality in birds, host size in solitary wasps, and maternal condition or rank in ungulates and primates (Brown and Silk 2002; West and Sheldon 2002; Schino 2004; Sheldon and West 2004). For the latter group, we consider only cases in which clear predictions can be made for the direction of sex-ratio shift (see Discussion), for which we have data on 62 species—56 solitary parasitoid wasps in response to host size, and six birds in response to mate quality (West and Sheldon 2002). Our result below would be even stronger if we included the other data. The mean effect size in response to interactions between relatives (mean $r = 0.525$) is almost twice that in response to other local conditions (mean $r = 0.306$; randomization test, $P = 0.002$, $n = 119$; Fig. 6). This same pattern holds if we consider haplodiploids or vertebrates separately, although the difference is not statistically significant in vertebrates (haplodiploids: $P = 0.002$, $n = 101$; vertebrates: $P = 0.70$, $n = 18$).
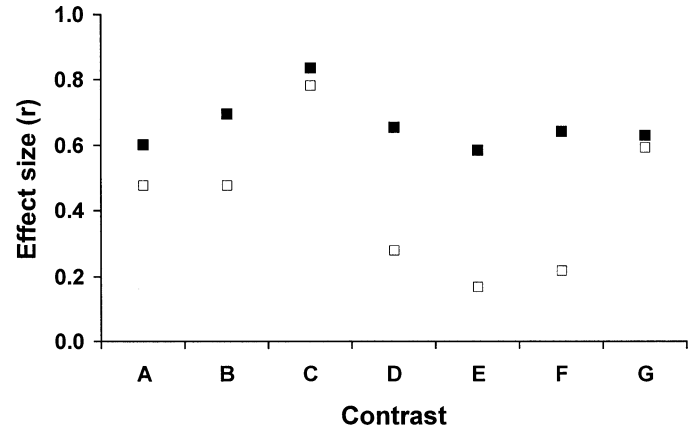

FIG. 5. Sex-ratio adjustment in response to LMC, with different cues. The effect size (r) is plotted for sex-ratio adjustment in response to variable foundress number (filled squares) and fecundity (open squares) for seven independent contrasts. The different contrasts are either within species (A) *Blastophaga nipponica*; (B) *Nasonia vitripennis*; (C) *Telenomus remus*; (D) *Trichogramma evanescens*; (E) *Technomyrmex albipes*), or within groupings (F) Ants, *Cardiocondyla obscurior* versus *Epimyrma kraussei*; (G) simultaneous hermaphrodites, *Serranus tortugarum* and *Schistocephalus solidus* versus other hermaphrodites). In all cases the effect size is larger for sex-ratio manipulation in response to foundress number, suggesting greater sex-ratio shifts in response to more diverse and predictable cues.

DISCUSSION

We have shown that across 64 species individuals adjust their offspring sex ratio as predicted by theory, in response to competitive or cooperative interactions between relatives (Fig. 1, Appendix). Furthermore, this pattern is very strong, reinforcing the impression that sex allocation is an unusually successful area of empirical evolutionary biology. Specifically:
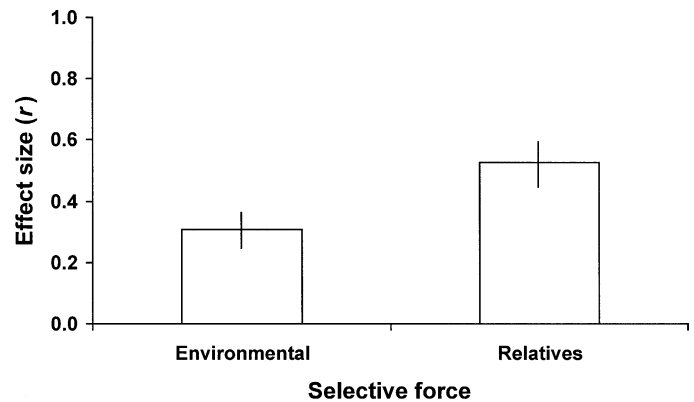

FIG. 6. Sex-ratio adjustment across species in response to different selective forces. Plotted are the mean and 95% CI of the effect size (r). A positive value of r corresponds to a sex-ratio shift in the predicted pattern. The two groups represent sex-ratio manipulation in response to: (1) environmental variation—Trivers and Willard (1973) hypothesis ($n = 62$ species, six bird species in response to mate quality, and 56 parasitoid wasp species in response to host size from West and Sheldon 2002); and (2) cooperative or competitive interactions between relatives, LRE, LRC, and LMC ($n = 57$ species, 12 vertebrates and 45 invertebrates from this study). Significantly larger effect sizes are seen in response to interactions between relatives.

(1) the mean effect size of $r = 0.53$ is very high compared to the average value of $r = 0.19$ from evolutionary and ecological studies (Møller and Jennions 2002), and (2) there are only three negative effect sizes at the level of the species—these were all birds in response to LRE (Appendix). Overall, studies of sex-ratio adjustment in response to interactions between relatives explain eight times the amount of variance in the data (28%) than the average (3.6%) achieved in evolutionary and ecological studies (Møller and Jennions 2002).

Sex Determination

Our data do not support the hypothesis that the method of sex determination poses such a strong constraint that it prevents facultative adjustment of offspring sex ratios. We examined three groups with potentially constraining methods of sex determination: vertebrates with CSD, invertebrates with CSD, and pseudo-arrhenotokous invertebrates. In all cases the mean effect size was significantly greater than zero, showing consistent adjustment of offspring sex ratios in the direction predicted by theory (Fig. 2, Table 1). Indeed, the mean effect size for these supposedly constrained groups: $r = 0.45$ (separate groups: $r = 0.25$–0.67), was rather large.

Our data provide mixed support for the hypothesis that the precision of sex-ratio adjustment is greater in haplodiploid species than in species with potentially constraining methods of sex determination such as CSD. The mean effect size for haplodiploids was significantly greater than that for vertebrates with CSD (supporting the hypothesis of constraint), but not significantly different from that for invertebrates with potentially constraining methods of sex determination (diploids with CSD and pseudo-arrhenotokous haplodiploids) (Fig. 3; Table 1). Furthermore, even the result with vertebrates does not provide unequivocal support for a role of sex determination, because it could equally be explained by confounded differences in selective pressure—predominantly LRE in vertebrates and predominantly LMC and LRC in haplodiploids (see below).

Selective Force and Environmental Predictability

The mean effect size in species subject to LRE was significantly lower than that in species subject to LMC and LRC (Fig. 4; Table 1). As we discussed in the introduction, there are a number of reasons why selection could be weaker with LRE. However, a crucial point here is that taxa and selective force are confounded in the available data. Studies from vertebrates are primarily (11/12) on LRE, whereas the invertebrate studies are primarily (42/44) on LRC and LMC, and this difference in the proportion of studies on LRE is highly significant ($G = 37.53$, $P < 0.0001$). Consequently, these differences could be explained as being due either to the mechanism of sex determination or to different forces of selection favoring different degrees of sex-ratio skew. However, our result that the mean effect size does not vary across invertebrates with different methods of sex determination (Fig. 3; Table 1) supports a role of different selective force, rather than constraints imposed by sex determination.

It would be extremely useful to obtain targeted additional data, such as estimates of the effect of LRE in a wider range of invertebrates (if it occurs; Martins et al. 1999), or LRC/

LMC in vertebrates and other invertebrate taxa with possibly constraining methods of sex determination (Normark 2003), especially if this allowed the use of a phylogenetic perspective (Harvey and Pagel 1991; Mayhew and Pen 2002). For example, when comparing LRC/LMC with LRE there are currently only two phylogenetically independent comparisons, one in the vertebrates (snakes vs. the rest) and one in the invertebrates (bees vs. all the rest)—both show a lower effect size with LRE (Appendix). However, although additional data relating to these comparisons are needed, such data may not be obtainable. For instance, avian mating systems and life histories, with overlapping generations and offspring dispersal are incompatible with any but the weakest form of LMC.

We have provided support for the idea that the amount of sex-ratio adjustment can be determined by environmental predictability and the mechanistic cues involved (West and Sheldon 2002). We tested this by considering species subject to LMC, in which the sex ratio is adjusted in response to either the number of females laying eggs on a patch simultaneously or the relative brood size of females that visit a patch sequentially. Females laying eggs on a patch simultaneously will have: (1) a greater number of cues (cues from interactions with other females, plus cues from eggs that those other females are laying); and (2) possibly more reliable cues (females may only be able to determine if a host (patch) has eggs laid in it, and not the actual number of eggs that the previous female has laid; Orzack and Parker 1990; King and Skinner 1991a; Shuker and West 2004). Consistent with a role of environmental predictability, the data show greater effect sizes in response to the number of females on a patch (Fig. 5).

Our analyses suggest that sex-ratio manipulation is more precise in response to interactions between relatives (LRE, LRC, and LMC) than in response to environmental variation differentially influencing male and female fitness (sometimes termed the Trivers and Willard hypothesis) (Fig. 6). We found that the mean effect size in response to interactions between relatives (LMC, LRC, and LRE; this study) was significantly greater than in response to environmental variation (Trivers and Willard hypothesis), considering cases where clear a priori predictions could be made (mate quality in birds, host size in parasitoid wasps; West and Sheldon 2002). We found this pattern in general, but also when examining just haplodiploid species. This pattern would be expected if selection is stronger, or more predictable, in response to interactions between relatives. For example, the appropriate response with LMC can be determined by local conditions (e.g., number of females present), whereas with environmental variation it can depend upon the spectrum of environments encountered by the entire population (e.g., the distribution of mate quality or host size). Although this verbal argument seems plausible, it requires specific theoretical modeling (West et al. 2002).

Overall Patterns of Sex-Ratio Adjustment Across All Animals

In this final section we synthesize the recent meta-analyses that have examined the extent to which individuals adjust offspring sex ratios. These studies divide into two categories: those in which clear a priori predictions could be given for

the mean effect size (West and Sheldon 2002; this study) and those in which they could not (Brown and Silk 2002; Cameron 2004; Ewen et al. 2004; Schino 2004; Sheldon and West 2004). The former show consistent patterns of sex-ratio manipulation in the predicted direction, with effect sizes significantly greater than zero (West and Sheldon 2002; this study). This demonstrates that the method of sex determination is not a constraint that prevents adaptive sex-ratio manipulation.

In contrast with the studies where no clear a priori predictions could be given, the effect size is very small, or not significantly greater then zero, suggesting no consistent pattern of sex-ratio manipulation (Brown and Silk 2002; Cameron 2004; Ewen et al. 2004; Schino 2004; Sheldon and West 2004). These studies investigated the importance of maternal condition in ungulates (Cameron 2004; Sheldon and West 2004) and primates (Brown and Silk 2002; Schino 2004), and a variety of factors in birds (Ewen et al. 2004). These studies are not unambiguous tests of sex-ratio theory, because it is generally not clear if sex-ratio manipulation is selected for in the species studied, and if so, in what direction (West and Sheldon 2002; Sheldon and West 2004).

Considering ungulates and primates, Trivers and Willard (1973) originally suggested that mothers in better condition (or higher rank) should be more likely to produce sons, because they can provide more resources to their offspring, and sons gain greater benefit from these extra resources than daughters. However, an argument can also be made for sex-ratio adjustment in the opposite direction: if maternal rank is inherited by daughters (but not sons) or not transmitted from fathers to offspring, it can select for high quality mothers to produce daughters, as may occur in some primates and ungulates (Silk 1983; Leimar 1996; Sheldon and West 2004). Furthermore, there are a variety of other factors that could influence how sex ratio should vary with maternal condition, such as LRC or LRE (Hiraiwa-Hasegawa 1993). Therefore, without detailed data from each species, it will rarely be clear what the expected pattern of sex-ratio adjustment is.

This problem is illustrated very clearly by a recent meta-analysis of all published relationships involving brood sex ratios in birds (Ewen et al. 2004). This analysis used data on 214 correlations from 40 studies of 31 species, examining the correlation between the sex ratio and a wide range of factors, including brood size, brood number, age, quality, body size, body weight, season, laying sequence, and year. The sign of expected effect size was assigned in Ewen et al. (2004) based on excess of males being a positive effect and excess of females a negative effect. In the majority of these cases there is no clear prediction that the factor examined should influence offspring sex ratios, let alone in what direction. This makes assigning positive or negative signs to effect sizes an ad hoc process, even when ignoring the problem of pseudoreplication at the species level. Indeed, even considering single traits, the same pattern is not necessarily expected across species, except in some cases (West and Sheldon 2002). This has been clearly demonstrated by work on the house finch *Carpodacus mexicanus* which showed that opposite patterns of sex-ratio adjustment were favored in two populations of the same species (Badyaev et al. 2001). Although Ewen et al. (2004) point out the advantage of using

a large dataset, and then using statistics to look for consistent patterns, this is only useful if the sign of effect sizes can be logically assigned. In addition, the conclusion that there are no significant effects because an indiscriminate analysis shows no general pattern is analogous to concluding that no character is an adaptation simply because not all characters are adaptations.

What can we learn from these studies where there is no clear a priori prediction for the mean effect size? The first use of these studies is that they can test for consistent patterns that could suggest the relative strength of different potential selective forces. In ungulates, females in better condition tend (weakly) to produce sons, suggesting that the Trivers and Willard effect outweighs that of other factors such as maternal inheritance of female condition (Sheldon and West 2004). Within primates, there is no consistent pattern across species, suggesting that either different forces dominate in different species, there is weak overall selection, or that a constraint such as CSD prevents sex-ratio manipulation (Brown and Silk 2002; Schino 2004).

The other use of these studies is that predictions can be made for how the effect size should vary across species. For example, in species where the Trivers and Willard effect is stronger, we should expect relatively greater production of sons from high quality mothers (Leimar 1996). Consistent with this, larger effect sizes are found in species with greater sexual dimorphism in both ungulates and primates (Schino 2004; Sheldon and West 2004). In primates it has also been shown that the effect size is consistent across multiple studies of the same population and that high quality mothers are more likely to produce sons when population growth rates are lower, which as consistent with the idea that LRC at high population densities can remove the benefit of inheritance of maternal rank (van Schaik and Hrdy 1991; Schino 2004). These results suggest that the pattern in primates is shaped by different selective forces acting in different species (Schino 2004; see also Johnson 1988; van Schaik and Hrdy 1991). More generally, this illustrates that it may be easier to understand how effect sizes should vary across species rather than what the overall effect size should be, emphasising the power of comparative statics when testing evolutionary theory (Frank 1998).

These different meta-analyses also illustrate two other factors that can influence the extent of sex-ratio adjustment. First, greater sex-ratio adjustment is shown in more predictable environments. This influence is shown most clearly in the data from solitary wasps adjusting their offspring sex ratio in response to host size—larger effect sizes are seen in species that kill the host when laying an egg, relative to species where the host is not killed and continues to grow after parasitism, with the result that host size is less predictable (West and Sheldon 2002). Additional evidence for a role of environmental predictability comes from the observation of larger effect sizes in ungulates with shorter gestation periods (Sheldon and West 2004), primates with shorter maturation times (Schino 2004), and larger responses to LMC based upon number of females rather than relative fecundity (this study, Fig. 5). Longer gestation and development times could lead to greater unpredictability because it

will be harder for a female to predict the amount of resources she will have available for lactation.

Second, the effect size can depend upon the quality of the data. Although this may seem a trivial point, its importance is demonstrated clearly in the ungulate data, where considerably larger effect sizes are seen in studies based upon behavioral data and observations of maternal condition prior to conception (mean $r = 0.17–0.29$), than in studies based upon morphological data and measures of maternal condition taken postconception (mean $r = 0.05–0.06$; Sheldon and West 2004; see also Cameron 2004). The manner in which data have been collected could also explain some of the variation in this study. In some LMC experiments females are forced to remain on a patch (e.g., Orzack 1990; Orzack et al. 1991), and it has been argued that this results in unnatural superparasitism and less precise sex-ratio adjustment (Godfray 1994). Consistent with this, studies in the wasp *Nasonia vitripennis* show larger effect sizes in experiments in which females are allowed to disperse (e.g., Werren 1980, 1983), considering sex-ratio shifts in response to the number of females laying eggs on a patch or their fecundity (Appendix).

Conclusions

The anecdotal observation of striking sex-ratio shifts in haplodiploid invertebrates, and less often in vertebrates with CSD, has led to the suggested role of sex determination mechanism in constraining sex ratio manipulation. Here, we have brought together the vertebrate and invertebrate literature, and made a quantitative comparison of the precision of sex-ratio adjustment across species with different methods of sex determination. We have shown that when considering sex-ratio manipulation in similar selective scenarios, the difference between vertebrates with CSD and haplodiploid invertebrates can be explained equally by confounded differences in selection pressure (LRE vs. LRC/LMC). Indeed, a consistent pattern to come out of sex-allocation meta-analyses is that the extent of sex-ratio adjustment depends on the form of selection on sex allocation.

A major task for the future is to develop theoretical models that can predict the observed variation in the amount and precision of sex-ratio manipulation in response to environmental uncertainty and other factors that influence the selection pressure. Most theoretical models predict threshold (step-function) adjustment of offspring sex ratios, rather than the gradual shifts that are observed (Leimar 1996; Pen et al. 1999; Pen and Weissing 2002; West et al. 2002), and little attention has been given to examining the intensity of selection and predicting the degree of precision (Herre 1987; Orzack 1990; Greeff 1998; West and Herre 1998b). Consequently, predictions and explanations for the variation across species in precision of sex-ratio adjustment have been based on verbal arguments, such as those in this paper. For example, we lack formal theory for an influence of environmental predictability on sex-ratio adjustment or for whether larger effects are predicted with LRC and LMC than with LRE. It is not yet clear to what extent these problems can be solved with evolutionarily stable strategy (optimality) models, or whether a quantitative or population genetic approach to sex ratio theory is required, incorporating complications such as mutation-selection balance and antagonistic pleiotropy.

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Studies from which data for meta-analysis were extracted. Type gives the predicted pattern being tested in that study—see Methods section (predicted patterns of sex-ratio adjustment) in main text for details.

Species	Study	Type	r	Sample size n
Vertebrates				
Birds, CSD				
Acrocephalus sechellensis (Seychelles warbler)	Komdeur 1996	LRE	0.546[1]	178
Calocitta formosa (white-throated magpie-jay)	Berg 2004	LRE	−0.064[2]	32
Dacelo novaeguineae (laughing kookaburra)	Legge et al. 2001	LRE	0.455[1]	38
Malurus leucopterus (white-winged fairy wren)	Rathburn and Montgomerie 2004	LRE	−0.063[3]	35
Manorina melanophrys (Bell miner)	Ewen et al. 2003	LRE	0.233[4]	59
Philetairus socius (sociable weaver)	Doutrelant et al. 2004	LRE	−0.316[5]	58
Phoeniculus purpureus (green wood-hoopoe)	Ligon and Ligon 1990	LRE	0.113[1]	128
Picoides borealis (red-cockaded woodpecker)	Gowaty and Lennartz 1985	LRE	0.364[1]	41
Sialia mexicana (western bluebird)	Dickinson 2004	LRE	0.235[6]	153
Mammals, CSD				
Lycaon pictus (African wild dog)	Creel et al. 1998	LRE	0.720[1]	16
Marmota marmota (Alpine marmot)	Allaine 2004	LRE	0.327[7]	82
Snakes, CSD				
Vipera berus	Madsen and Shine 1992	LMC, fecundity	0.698[8]	6
Invertebrates				
Ants, Haplodiploid				
Cardiocondyla obscurior	Cremer and Heinze 2002	LMC, foundress number	0.646[9]	30
Epimyrma kraussei	Winter and Buschinger 1983	LMC, fecundity	0.220[10]	18
Formica exsecta	Brown et al. 2002	LRC, variable LRC	0.383[11]	55
Formica truncorum	Sundström 1995	LRC, fecundity	0.700[12]	18
Leptothorax acervorum	Chan and Bourke 1994	LRC, fecundity	0.510[13]	16
Messor aciculatus	Hasegawa and Yamaguchi 1995	LRC, fecundity	0.812[14]	29
Messor pergandei	Ode and Rissing 2002	LRC, fecundity	0.496[15]	70
Technomyrmex albipes	Tsuji and Yamauchi 1994	LMC, wing status	0.602[16]	37
Technomyrmex albipes	Tsuji and Yamauchi 1994	LRC, fecundity	0.168[17]	30
Technomyrmex albipes	Tsuji and Yamauchi 1996	LMC, wing status	0.672[18]	53
Technomyrmex albipes	Tsuji and Yamauchi 1996	LMC, wing status	0.481[19]	79
Technomyrmex albipes	Mean	LMC	0.514	199
Aphids, CSD				
Pemphigus spyrothecae	Foster and Benton 1992	LMC, fecundity	0.906[20]	149
Rhopalosiphum padi	Dagg and Vidal 2004	LRC, fecundity	0.519[21]	27
Uroleucon cirsii	Dagg and Vidal 2004	LMC, fecundity	0.420[22]	11
Bees, Haplodiploid				
Exoneura richardsoni	Cronin and Schwarz 1997	LRE	0.490[23]	85
Xylocopa sulcatipes	Stark 1992	LRE	0.332[24]	40
Beetles, Haplodiploid				
Xylosandrus germanus	Peer and Taborsky 2004	LMC, foundress number	0.531[25]	89
Beetles, Pseudo-arrhenotokous				
Hypothenemus hampei	Borsa and Kjellberg 1996	LMC, foundress number	0.270[26]	138
Mealy Bugs, Pseudo-arrhenotokous				
Planococcus citri	Varndell and Godfray 1996	LRC or LRE	0.806[27]	151
Mites, Spider, Haplodiploid				
Oligonychus pratensis	Stiefel and Margolies 1992	LMC, haystack	0.380[28]	33
Tetranychus cinnabarinus	Wrensch and Young 1978	LMC, foundress number	0.400[29]	120
Tetranychus urticae	Roeder et al. 1996	LMC, foundress number	0.641[30]	34

APPENDIX. Continued.

Species	Study	Type	r	Sample size n
Tetranychus urticae	Roeder et al. 1996	LMC, foundress number	−0.056[31]	32
Tetranychus urticae	Roeder 1992	LMC, foundress number	0.936[32]	54
Tetranychus urticae	Young et al. 1986	LMC, haystack	0.288[33]	117
Tetranychus urticae	Wrensch and Young 1983	LMC, haystack	0.553[34]	148
Tetranychus urticae	Mean	LMC	0.584	385
Mites, Pseudo-arrhenotokous				
Hemisarcoptes coccophagus	Izraylevich and Gerson 1996	LMC, foundress number	0.624[35]	12
Phytoseiulus persimilis	Nagelkerke and Sabelis 1998	LMC, foundress number	0.602[36]	31
Phytoseiulus persimilis	Nagelkerke and Sabelis 1998	LMC, foundress number	0.797[37]	18
Phytoseiulus persimilis	Mean	LMC, foundress number	0.693	49
Typhlodromus occidentalis	Nagelkerke and Sabelis 1998	LMC, foundress number	0.495[38]	66
Spiders, CSD				
Anelsimus domingo	Aviles et al. 2000	LMC, fecundity	0.522[39]	15
Thrips, Haplodiploid				
Hoplothrips pedicularius	Taylor and Crespi 1994	LMC, natal or immigrant	0.401[40]	32
Wasps, Fig, Haplodiploid				
Blastophaga nipponica	Kinoshita et al. 2002	LMC, fecundity	0.667[41]	20
Blastophaga nipponica	Kinoshita et al. 2002	LMC, fecundity	0.289[42]	45
Blastophaga nipponica	Kinoshita et al. 1998	LMC, foundress number	0.605[43]	71
Blastophaga nipponica	Mean	LMC	0.575	136
Liporrhopalum tentacularis	Moore et al. 2002	LMC, foundress number	0.594[44]	71
Pegoscapus assuetus	Frank 1985	LMC, foundress number	0.701[45]	57
Pegoscapus (*citrifolia*)	Herre 1985	LMC, foundress number	0.523[46]	58
Pegoscapus (*insipida*)	Herre 1985	LMC, foundress number	0.898[47]	90
Pegoscapus (*popenoei*)	Herre 1985	LMC, foundress number	0.846[48]	42
Wasps, Parasitoid, Haplodiploid				
Anagyrus kamali	Sagarra et al. 2000	LMC, foundress number	0.307[49]	50
Caraphractus cinctus	Jackson 1966	LMC, foundress number	0.893[50]	10
Diaeretiella rapae	Abidi et al. 1988	LMC, foundress number	0.608[51]	40
Melittobia australica	Abe et al. 2003	LMC, foundress number	0.859[52]	24
Melittobia digitata	Cooperband et al. 2003	LMC, foundress number	0.019[53]	57
Muscidifurax raptor	King and Seidl 1993	LMC, foundress number	0.271[54]	79
Nasonia giraulti	King and Skinner 1991b	LMC, foundress number	0.529[55]	45
Nasonia vitripennis	Werren 1980	LMC, fecundity	0.597[56]	68
Nasonia vitripennis	Werren 1983	LMC, foundress number	0.824[57]	71
Nasonia vitripennis	King and Skinner 1991b	LMC, foundress number	0.723[58]	43
Nasonia vitripennis	Flanagan et al. 1998	LMC, fecundity	0.447[59]	86
Nasonia vitripennis	Shuker and West 2004	LMC, foundress number	0.683[60]	180
Nasonia vitripennis	Orzack 1990	LMC, fecundity	0.391[61]	529
Nasonia vitripennis	Orzack et al. 1991	LMC, foundress number	0.547[62]	1108

APPENDIX. Continued.

Species	Study	Type	r	Sample size n
Nasonia vitripennis	Molbo and Parker 1996	LMC, foundress number	0.718[63]	13
Nasonia vitripennis	Mean	LMC	0.616	2098
Pteromalus puparum	Takagi 1986	LMC, foundress number	0.793[64]	48
Spalangia cameroni	King 1989	LMC, foundress number	−0.306[65]	35
Spalangia cameroni	King 1989	LMC, foundress number	0.759[66]	20
Spalangia cameroni	Mean	LMC, foundress number	0.317	35
Telenomus fariai	Rabinovich et al. 2000	LMC, foundress number	0.490[67]	28
Telenomus remus	van Welzen and Waage 1987	LMC, foundress number	0.879[68]	22
Telenomus remus	van Welzen and Waage 1987	LMC, fecundity	0.787[69]	21
Telenomus remus	Schwartz and Gerling 1974	LMC, foundress number	0.795[70]	15
Telenomus remus	Mean	LMC	0.830	58
Trichogramma chilonis	Suzuki et al. 1984	LMC, fecundity	0.065[71]	25
Trichogramma evanescens	Waage and Lane 1984	LMC, fecundity	0.389[72]	30
Trichogramma evanescens	Waage and Lane 1984	LMC, foundress number	0.537[73]	35
Trichogramma evanescens	van Dijken 1987	LMC, fecundity	0.176[74]	49
Trichogramma evanescens	Salt 1936	LMC, foundress number	0.779[75]	50
Trichogramma evanescens	Mean	LMC	0.508	164
Trichogramma pretiosum	Luck et al. 2001	LMC, foundress number	0.227[76]	203
Simultaneous Hermaphrodites				
Catomerus polymerus (Barnacle)	Raimondi and Martin 1991	LMC, foundress number	0.448[77]	36
Echinostoma caproni (Trematode)	Trouve et al. 1999	LMC, foundress number	0.499[78]	63
Helobdella papillornata (Leech)	Tan et al. 2004	LMC, foundress number	0.410[79]	90
Macrostomum sp. (Flatworm)	Scharer and Ladurner 2003	LMC, foundress number	0.825[80]	47
Ophryotrocha diadema (Polychaete worm)	Lorenzi et al. submitted	LMC, foundress number	0.512[81]	144
Schistocephalus solidus (Cestode)	Scharer and Wedekind 2001	LMC, fecundity	0.831[82]	10
Serranus tortugarum (Fish)	Petersen and Fischer 1996	LMC, fecundity	0.360[83]	67

Notes on calculation of r values: [1] From West and Sheldon 2002. [2] Table 1, $\chi^2_{(1)} = 0.13$, direction of effect (sign), E. Berg, pers. comm. [3] Mainland data, where helpers occur, $\chi^2_{(1)} = 0.14$, sample size and direction of effect, M. Rathburn, pers. comm. [4] Presence of any helpers, $\chi^2_{(1)} = 3.2$. [5] Day 9, with helpers versus no helpers, $P = 0.008$. [6] T-test on data in Table 2, comparing ''breeding, not helping'' with ''nonbreeding helper,'' gave $t = 2.97$. [7] Table 1, $\chi^2_{(1)} = 8.7$. [8] Sex ratio in first versus second litter, $t = 18$. [9] Sex ratio versus number queens, $F_{(4,29)} = 3.32$, OH test with $r_s = 1$ gave $P = 0.0002$. [10] Sex ratio versus investment in sexuals, analysis of data (transformed) in Table 2 gave $F_{(1,17)} = 0.8678$. [11] Sex ratio versus queen number, $F_{(1,49)} = 8.41$. [12] Sex ratio versus sexual brood production, $r^2 = 0.49$. [13] Sex ratio versus productivity in polygynous colonies that bud, $r = 0.51$. [14] Sex ratio versus sexual brood production, $r^2 = 0.659$. [15] Sex ratio versus resource (hence fecundity) manipulation, $F_{(3,66)} = 9.28$. [16] Sex ratio versus winged or wingless offspring, did a t-test on data from page 158, assuming sample sizes from Table 2. [17] Sex ratio versus investment in winged sexuals, Table 4. [18] Sex ratio versus winged or wingless offspring, Table 1, 1990, analysis gave $t = 6.49$. [19] Sex ratio versus winged or wingless offspring, Table 1, 1991, analysis gave $t = 4.81$. [20] Sex ratio versus offspring in brood, raw data in Fig. 4 gave $F_{(1,147)} = 677$. [21] Sex ratio versus total offspring, $r^2 = 0.269$. [22] Sex ratio versus total offspring, $r^2 = 0.176$. [23] Sex ratio versus brood size, Spearman $r_s = 0.490$. [24] Sex ratio versus brood size, $F_{(1,38)} = 4.69$. [25] Sex ratio versus foundress number, $\chi^2_{(1)} = 25.13$. [26] Sex ratio versus foundress number, Table II gave $\chi^2_{(2)} = 8.58$, upon which performed an OH test. [27] Sex ratio versus juvenile and adult crowding, $r^2 = 0.65$. [28] Sex ratio versus leaf quality during paternal development, $P = 0.029$. [29] Sex ratio versus number of females, analysed data in Table 2 to give $F_{(1,117)} = 21.50$. [30] Sex ratio versus number of females on a patch, OP1, reconstructed data in Fig. 1 and 2 to give $t = 4.720$. [31] Sex ratio versus number of females on a patch, LP, reconstructed data in Fig. 1 and 2 to give $t = 0.31$. [32] Sex ratio versus number of females, used data in Table 1 (low-low and high-low versus low-high and high-high), to give $t = 19.16$. [33] Sex ratio versus environment when ovipositing, analysis of data in Table 1, gives effect of environment when ovipositing, $t = 3.224$. [34] Sex ratio versus leaf quality, analysis of mean squares from Table 2 gave $F_{(1,144)} = 64.26$. [35] Sex ratio at high or low mite density, $F_{(1,10)} = 6.38$. [36] Culture A, sex ratio versus foundress number, Table 2 gives $Z = 3.35$. [37] Culture B, sex ratio versus foundress number, Table 2 gives $Z = 3.38$. [38] Sex ratio versus foundress number, Table 1 gives $Z = 3.38$. [39] Sex ratio versus number embryos scored, regression on raw data in Table 1 gave $F_{(1,13)} = 4.88$. [40] Sex ratio versus wingless or dealate (had wings, but lost them), $t = 2.4$. [41] Sex ratio versus first or second female, 4 h, reconstructed data from Fig. 2, gave $t = 3.80$. [42] Sex ratio versus first or second female, 24 h, reconstructed data from Fig. 2, gave $t = 1.98$. [43] Sex ratio versus foundress number, reconstructed data in Fig. 1, gave $F_{(1,69)} = 39.93$. [44] Sex ratio versus foundress number, $\chi^2_{(1)} = 28.76$. [45] Raw data is in Table 3.8 of Frank 1983, logistic regression analysis of sex ratio versus foundress number gave $F_{(1,55)} = 53.23$. [46] Sex ratio versus foundress number, analysis of data summary in Leigh et al. 1985 gave $F_{(1,56)} = 21.12$. [47] Sex ratio versus foundress number, analysis of data summary in Leigh et al. 1985 gave $F_{(5,84)} = 30.38$. [48] Sex ratio versus foundress number, analysis of data summary in Leigh et al. 1985 gave $F_{(3,38)} = 20.66$. [49] Sex ratio versus foundress number, data in Table 1, ANOVA and then OH test, giving $F_{(4,45)} = 0.78$, $P_c = 0.73$, $r_s = 1$, and final $P = 0.015$. [50] Sex ratio versus foundress number, analysed

APPENDIX. Continued.

raw data in Table IX with logistic regression, gives $\chi^2_{(1)} = 7.97$, with $HF = 2.34$. [51] Sex ratio versus foundress number, analysed data in Table 1 to give $F_{(3,36)} = 9.97$. [52] Sex ratio versus foundress number, *Wolbachia* (naturally) infected strain, r_s given on page 35. [53] Sex ratio versus foundress number, Table 4. [54] Sex ratio versus foundress number, analysed data in Table 2A, averaging over days 1–3. [55] Sex ratio versus foundress number, H value in Table 1 is equivalent to $\chi^2_{(5)} = 22.67$. [56] Sex ratio versus relative brood size, r_s value provided in reanalysis by Orzack 1990. [57] Sex ratio versus foundress number, used means and standard errors from Figure 1 to do an ANOVA, giving $F_{(6,64)} = 18.06$. [58] Sex ratio versus foundress number, H value in Table 1 is equivalent to $\chi^2_{(5)} = 34.27$. [59] Sex ratio versus relative brood size, gives $r^2 = 0.2$. [60] Sex ratio versus foundress number, gives $r^2 = 0.467$. [61] Sex ratio versus relative fecundity, meta-analysis of data from different lines in Table 1. [62] Observed sex ratio versus predicted, meta-analysis of data from different lines in Table 8. [63] Sex ratio versus foundress number, r_s given. [64] Sex ratio versus foundress number, used raw data from figure 6 to give $F_{(1,47)} = 79.45$. [65] Sex ratio versus foundress number (2,4,6, or 10), paper gives $P = 0.17$, and then did OH test. [66] Sex ratio versus foundress number (1 or 2), paired t-test, $t = 4.95$. [67] Sex ratio versus foundress number, gave $\chi^2_{(1)} = 6.72$. [68] Sex ratio versus foundress number, gave $\chi^2_{(2)} = 20.4$. [69] Sex ratio versus first or second person to oviposit, when second female forced to lay a smaller clutch size (15 versus 5), $\chi^2_{(1)} = 13$. [70] Sex ratio versus foundress number, data in Table 1 gave $F_{(1,13)} = 22.29$. [71] Sex ratio in parasitised or unparasitised hosts, $t = 0.31$ given in Table II. [72] Sex ratio versus relative brood size, r_s value provided in reanalysis by Orzack (1990). [73] Sex ratio versus foundress number, means and standard errors obtained from Figure 1, used to do ANOVA, giving $F_{(4,30)} = 6.44$, and then did OH test on that to give $P = 0.00075$. [74] Sex ratio when first or second (superparasitising), $F_{(1,47)} = 1.5$. [75] Sex ratio versus foundress number, raw data given in Table V, analyzed to give $F_{(1,48)} = 73.90$. [76] Comparing sex ratio of one and two versus three foundresses, $G_{(2)} = 15.0$. [77] Ratio of egg/sperm mass versus group size, $F_{(1,33)} = 8.268$. [78] Ovary size versus group size, $F_{(2,59)} = 11.2$. [79] Testisac volume versus group size, $F_{(3,67)} = 5.85$; OH test on $P = 0.0013$, $R_s = 1$, gave $r_s P_c = 0.9987$, $P = 0.0001$. [80] Testes area versus group size, $r^2 = 0.68$ given in Table 1. [81] Number of cocoons laid versus group size, Table 1 gives $F_{(1,140)} = 49.69$. [82] Sex allocation versus group size, $r^2 = 0.6$ given in Table 2. [83] Proportion of gonad to male function versus size, $r_s = 0.36$ given.