

Constraints in the evolution of adaptive adjustment of offspring sex ratios: (Supplementary Online Information)

Stuart A. West & Ben C. Sheldon

Further details of which data can be used

A clear example of the problems that arise when considering whether population sex ratios can be used to test for adaptive sex allocation is provided with helper at the nest models. Originally, ‘repayment’ models (1, 2) attempted to predict how such behaviour would influence the sex ratio bias expected at the level of the population, and suggested that population sex ratios would be biased towards the sex that provides greater levels of help. It has been argued that some data support these models (3). However, more recently, Pen & Weissing (4) showed that the population sex ratio is predicted to depend on additional factors such as whether clutch size is adjusted in response to the number of helpers, something that cannot be assumed.

This contrasts with the situation for species that change sex or have environmental sex determination, where theory has been relatively successful in predicting population sex ratios (a bias towards the first sex or that produced in poorer conditions) (5-8). Despite relying on the same basic theory, the situation in these organisms is simpler because individuals control their own sex and so some of the complicating factors that may also influence sex allocation (other reproductive decisions of the parent, parent-offspring conflict over the sex ratio) are removed.

We have stated in the main text that there are a number of areas in which it is extremely hard to make clear a priori predictions for the direction of sex ratio skew (e.g. maternal condition and the sex ratio in mammals). However, we emphasise that whether there are consistent patterns in such sex ratio skews remains a valid and important question for study (and one that should be addressed with meta-analysis). However, the crucial point is that in the absence of empirical data that also tests the underlying assumptions of theoretical predictions, the discovery of an overall pattern could not be said to constitute strong support for any theoretical model.

Obtaining data and analyses

We obtained data on bird and mammal species by searching the ISI Web of Science (WOS), using the key words “bird/mammal” + “sex ratio/allocation”, and by forward-searching based on citations of refs. (1, 9-11), and the citations within papers citing these references. We used all studies published up to 1 September 2001 (see appendix table 1). One of the studies on helper status (12) involved a subset of the data in another study (13), so we used only the larger study in the analysis. We obtained data on parasitic wasp species by: (a) searching Bath Information and Data Services (BIDS) during July 2000 for the words/phrases “sex ratio/allocation” + “host size/quality/age” + “parasitoid/parasitic wasp”, and also by searching WOS in June 2001; (b) references given in reviews on the topic (14-16); (c) references in all papers found with a & b. We

found >120 papers dealing with host size dependent sex allocation, and from these we were able to obtain r values from 65 studies on 56 solitary species.

We did not include data from two further studies in mammals that also support the hypothesis that sex ratios should be adjusted in response to helper status. These studies were on spotted hyenas (*Crocuta crocuta*) (17) and ringtailed lemurs (*Lemur catta*) (18). We did not include these studies because their low replication at the level of breeding group ($N=1$ and $N=3$ respectively), and lack of sex ratio data from concurrent breeding groups meant that r values could not be calculated.

We followed standard meta-analysis practices, described in detail elsewhere (19-21). Briefly, r values were calculated as described in Rosenthal (19), chapter 2; in most cases this was determined by the equation for r (page 19 of (19)), which is Pearson's r applied to dichotomous data, and can be calculated easily from r^2 values (either published values, or in a large fraction of the parasitic wasps studies, we used the raw data to estimate r^2); analyses were conducted on Z -transformed r -values to correct for asymptotic behaviour of large values of r . When required, we obtained a mean value from multiple studies on a single species by averaging Z_r . All analyses were performed using MetaWin 2.0 (21). Since sample sizes were often quite small, and error distributions of effect sizes unknown, we bootstrapped to obtain confidence intervals around mean effect sizes, and used randomisation to obtain exact P -values for specific comparisons of groups.

We carried out a formal comparative analysis (using independent contrasts on species mean effect sizes) to determine whether the pattern with parasitic wasp species was a phylogenetic artefact (for example, whether it was driven by data from a single clade) (22). We constructed a phylogeny following Basibuyuk, Quicke, Rasnitsyn & Fitton (www.bio.ic.ac.uk/staff/dlq/tree.rtf) and Belshaw et al. (23), which provided six independent contrasts, and calculated independent contrasts using the brunch routine of the programme Comparative Analysis by Independent Contrasts (CAIC) (24).

Sex ratio adjustment in idiobiont and koinobiont wasps

King (14) examined a related question in 1989, by surveying the number of idiobiont and koinobiont species that do and do not show significant shifts in sex ratio with host size (see also (25)). However, this 'vote-counting' approach suffers from a number of problems that can often lead to erroneous conclusions, and which are solved by the use of meta-analytic procedures (21, 26). For example, vote-counting reduces a continuous variable (statistical effect size) to a binary variable with an arbitrary cut off point ($P = 0.05$), which is largely determined by sample size. In addition, King made no attempt to control for phylogenetic artefacts (22), and there have been a large number of further studies published since, facilitating a more detailed and rigorous study.

Supplementary Information Table 1: Studies of individual variation in the sex ratio in response to mate attractiveness (MATE) and the presence/absence of helpers (HELP) in co-operatively breeding birds and mammals.

Species	Type of Study	Effect Size (r)	Sample Size (N)
Zebra finch <i>Taeniopygia guttata</i> ¹	MATE	0.352	30
Zebra finch <i>Taeniopygia guttata</i> ²	MATE	0.452	26
Blue tit <i>Parus caeruleus</i> ³	MATE	0.376	31
Collared flycatcher <i>Ficedula albicollis</i> ⁴	MATE	0.394	79
Great reed warbler <i>Acrocephalus arundinaceus</i> ⁵	MATE	-0.159	47
Barn swallow <i>Hirundo rustica</i> ⁶	MATE	-0.040	54
Great tit <i>Parus major</i> ⁷	MATE	0.140	57
Blue tit <i>Parus caeruleus</i> ⁸	MATE	0.439	21
Great tit <i>Parus major</i> ⁹	MATE	0.137	84
Mallard <i>Anas platyrhynchos</i> ¹⁰	MATE	0.250	16
Dark-eyed Junco <i>Junco hyemalis</i> ¹¹	MATE	0.027	48
Red-cockaded Woodpecker <i>Picoides borealis</i> ¹²	HELP	0.364	41.49
Seychelles warbler <i>Acrocephalus sechellensis</i> ¹³	HELP	0.546	178
Seychelles warbler <i>Acrocephalus sechellensis</i> ¹⁴	HELP	0.563	116
Green wood-hoopoe <i>Phoeniculus purpureus</i> ¹⁵	HELP	0.113	128
Laughing kookaburra <i>Dacelo novaeguineae</i> ¹⁶	HELP	0.455	38
African wild dog <i>Lycaon pictus</i> ¹⁷	HELP	0.720	16

Notes:

1. Trait is band colour, and test-statistic calculated from table 1, assuming a sample size of 30 males (27).
2. Trait is band colour, and test statistic is derived from the P -value associated with figure 1a (11).
3. Trait is male over-winter survival, shown previously to be correlated with female preference and subsequently with male UV plumage brightness (28).
4. Trait is male forehead patch width (29): see (30) for a reanalysis.
5. Trait is male song repertoire size (31).
6. Trait is male tail length (32).
7. Trait is male breast-stripe size, controlling for the effect of tarsus length (33) - p. 70, a univariate model with breast stripe width gives a standardised $r = 0.270$.
8. Relationship between UV-chroma and sex ratio within controls (34).
9. Trait is male breast-stripe width (35).
10. Trait is male attractiveness determined by choice trials, test-statistic from table 1 (36), with the sign of the relationship provided by A.F. Russell (pers. comm, 15 August 2001).

11. Trait is testosterone implant status (with T-implant males assumed to be more attractive) (37).
12. Sample size calculated as the number of offspring divided by mean clutch size (3).
13. Relationship is between sex ratio and territory quality for the first offspring produced by a pair (13).
14. Data are a subset of (13), so were not used in the meta-analysis (12).
15. Comparison of small and large flock sex ratios (38).
16. Association between clutch sex ratio and the type of helpers present (39).
17. Association between litter sex ratio and parity (40).

References (Text and Supplementary Table 1)

1. S. T. Emlen, M. Emlen, S. A. Levin, *Am. Nat.* **127**, 1-8 (1986).
2. C. M. Lessells, M. I. Avery, *Am. Nat.* **129**, 610-620 (1987).
3. P. A. Gowaty, M. R. Lennartz, *Am. Nat.* **126**, 347-353 (1985).
4. I. Pen, F. J. Weissing, *Proc. Roy. Soc. Lond. B* **267**, 539-544 (2000).
5. E. L. Charnov, *The Theory of Sex Allocation* (Princeton University Press, Princeton, 1982).
6. S. A. Frank, I. R. Swingland, *Journal of theoretical Biology* **135**, 415-418 (1988).
7. E. L. Charnov, J. J. Bull, *Nature* **338**, 148-150 (1989).
8. E. L. Charnov, *Life History Invariants* (Oxford University Press, Oxford, 1993).
9. R. L. Trivers, D. E. Willard, *Science* **179**, 90-92 (1973).
10. J. L. Blank, V. Nolan Jr, *Proc. Natl. Acad. Sci. U.S.A.* **80**, 6141-6145 (1983).
11. N. Burley, *Evolution* **40**, 1191-1206 (1986).
12. J. Komdeur, S. Daan, J. Tinbergen, C. Mateman, *Nature* **385**, 522-525 (1997).
13. J. Komdeur, *Proc. Roy. Soc. Lond. B* **263**, 661-666 (1996).
14. B. H. King, *Oecologia* **78**, 420-426 (1989).
15. B. H. King, in *Evolution and Diversity of Sex Ratio in Insects and Mites* D. L. Wrensch, M. A. Ebbert, Eds. (Chapman & Hall, New York, 1993) pp. 418-441.
16. H. C. J. Godfray, *Parasitoids. Behavioural and Evolutionary Ecology* (Princeton University Press, Princeton, 1994).
17. K. E. Holekamp, L. Smale, *Am. Nat.* **145**, 261-278 (1995).
18. C. L. Nunn, M. E. Pereira, *Behav. Ecol. Sociobiol.* **48**, 18-28 (2000).
19. R. Rosenthal, *Meta-analytic Procedures for Social Research* (Sage Publications, Thousand Oaks, 1991).
20. J. Gurevitch, L. V. Hedges, *Ecology* **80**, 1142-1149 (1999).
21. M. S. Rosenberg, D. C. Adams, J. Gurevitch, *MetaWin: Statistical Software for Meta-Analysis. Version 2.0* (Sinauer Associates, Sunderland, Mass, 2000).
22. P. H. Harvey, M. D. Pagel, *The Comparative Method in Evolutionary Biology*. R. M. May, P. H. Harvey, Eds., Oxford Studies in Ecology and Evolution (Oxford University Press, Oxford, 1991).
23. R. Belshaw, M. Fitton, E. Herniou, C. Gimeno, D. L. J. Quicke, *Syst. Ent.* **23**, 109-123 (1998).
24. A. Purvis, A. Rambaut, *CABIOS* **11**, 247-251 (1995).
25. J. K. Waage, *Ann. Appl. Biol.* **101**, 159-164 (1982).

26. G. Arnqvist, D. Wooster, *Trends Ecol. Evol.* **10**, 236-240 (1995).
27. N. Burley, *Science* **211**, 721-722 (1981).
28. E. Svensson, J. A. Nilsson, *Proc. Roy. Soc. Lond. B* **263**, 357-361 (1996).
29. H. Ellegren, L. Gustafsson, B. C. Sheldon, *Proc. Natl. Acad. Sci. USA* **93**, 11723-11728 (1996).
30. B. C. Sheldon, H. Ellegren, *Anim. Behav.* **57**, 285-298 (1999).
31. H. Westerdahl, S. Bensch, B. Hansson, D. Hasselquist, T. von Schantz, *Molec. Ecol.* **6**, 543-548 (1997).
32. N. Saino, H. Ellegren, A. P. Moller, *Molec. Ecol.* **8**, 399-406 (1999).
33. M. Kolliker, et al., *Behav. Ecol.* **10**, 68-72 (1999).
34. B. C. Sheldon, S. Andersson, S. C. Griffith, J. Ornborg, J. Sendecka, *Nature* **402**, 874-877 (1999).
35. A. N. Radford, J. K. Blakeley, *Behav. Ecol.* **11**, 294-298 (2000).
36. E. J. A. Cunningham, A. F. Russell, *Nature* **412**, 498-499 (2001).
37. J. L. Grindstaff, C. A. Buerkle, J. M. Castro, V. Nolan, E. D. Ketterson, *Behav. Ecol. Sociobiol.* **50**, 312-316 (2001).
38. J. D. Ligon, S. H. Ligon, *Auk* **107**, 765-771 (1990).
39. S. Legge, R. Heinsohn, M. C. Double, R. Griffiths, A. Cockburn, *Behav. Ecol.* **12**, 524-533 (2001).
40. S. Creel, N. Marusha Creel, S. L. Monfort, *Animal Reproduction Science* **53**, 315-320 (1998).

Supplementary Table 2: Studies of variation in sex ratio in response to host size in parasitic wasps.

Species	Sample size (N)	Effect size (r)
<i>Idiobionts</i>		
<i>Anisopteromalus calandrae</i> (1)	1665	0.270
<i>Anisopteromalus calandrae</i> (2)	297	0.179
<i>Avetianella longoi</i> (3)	30	0.390
<i>Brachymeria intermedia</i> (4)	127	0.362
<i>Bracon mellitor</i> (5)	128	0.277
<i>Catolaccus grandis</i> (6)	30	0.376
<i>Coccygomimus turionella</i> (7)	50	0.503
<i>Coeloides brunneri</i> (8)	82	0.373
<i>Coeloides sordidator</i> (9)	757	0.262
<i>Dendrocerus carpenteri</i> (10)	261	0.224
<i>Dinarmus basalis</i> (2)	1329	0.213
<i>Dolichomitus</i> sp. (11)	204	0.764
<i>Eupelmus vuilleti</i> (12)	161	0.361
<i>Eurytoma goidanichi</i> (13)	118	0.540
<i>Eurytoma morio</i> (14)	1299	0.256
<i>Heterospilis prosopidis</i> (15)	1207	0.536
<i>Heterospilus prosopidis</i> (2)	993	0.221
<i>Itoplectis cocquisitor</i> (16)	86	0.284

<i>Itopectis naranyae</i> (17)	96	0.560
<i>Lariophagus distinguendis</i> (18)	1362	0.644
<i>Lariophagus distinguendis</i> (19)	1324	0.285
<i>Metacolus unifasciatus</i> (14)	3764	0.152
<i>Metaphycus helvolus</i> (20)	85	0.231
<i>Metaphycus helvolus</i> (20)	91	0.191
<i>Muscidifurax raptor</i> (21)	610	0.101
<i>Muscidifurax raptor</i> (22)	22	0.400
<i>Pachycrepoideus vindemiae</i> (23)	2609	0.798
<i>Pimpla parnarae</i> (24)	242	0.354
<i>Pimpla turionellae</i> (25)	455	0.256
<i>Roptrocercus zylophagorum</i> (26)	70	0.544
<i>Spalagia cameroni</i> (27)	24	0.754
<i>Spalangia endius</i> (28)	1489	0.036
<i>Spalangia endius</i> (29)	519	0.147
<i>Spalangia endius</i> (Florida) (30)	55	0.575
<i>Spalangia endius</i> (india) (30)	62	0.062
<i>Tiphia popilliavora</i> (31)	2225	0.660
Koinobionts		
<i>Aenasius vexans</i> (32)	55	0.310
<i>Alysia manducator</i> (33)	262	0.541
<i>Anagyrus pseudococci</i> (34)	480	0.451
<i>Aphelinus abdominalis</i> (35)	290	0.637
<i>Aphelinus mali</i> (36)	16098	0.359
<i>Aphidius ervi</i> (37)	159	0.234
<i>Aphidius nigripes</i> (38)	19543	-0.131
<i>Aphidius smithi</i> (39)	113	0.051
<i>Aphidius sonchi</i> (40)	107	0.131
<i>Biosteres tryoni</i> (41)	4362	0.221
<i>Campoletis sonorensis</i> (42)	85	0.004
<i>Casitaria arjuna</i> (43)	1935	-0.160
<i>Cotesia melanoscela</i> (44)	132	0.097
<i>Dacnusa sibirica</i> (45)	436	0.128
<i>Encyrtus saliens</i> (46)	488	0.429
<i>Ephedrus californicus</i> (47)	510	0.299
<i>Ephedrus californicus</i> (48)	454	0.042
<i>Ephedrus cerasicola</i> (49)	179	-0.009
<i>Epidinocarsis lopezi</i> (50)	496	0.408
<i>Hyposoter lymantriae</i> (43)	2800	0.064
<i>Leiophron uniformis</i> (51)	551	0.080
<i>Leptomastix abnormis</i> (52)	26	0.187
<i>Leptomastix dactylopii</i>	116	0.261
<i>Leptomastix epona</i> (53)	87	0.275
<i>Microcharops anticarsiae</i> (54)	318	0.221
<i>Microplitis croceipes</i> (55)	191	0.075

<i>Opius concolor</i> (56)	1377	0.368
<i>Pnigalio flavipes</i> (57)	502	0.314
<i>Trybliographa rapae</i> (58)	155	0.013

References (Supplementary Table 2)

1. van den Assem, J., Putters, F. A. & Prins, T. C. (1984) *Neth. J. Zool.* **34**, 33-62.
2. Nishimura, K. & Jahn, G. C. (1996) *J. Ethol.* **14**, 27-33.
3. Hanks, L. M., Gould, J. R., Paine, T. D., Millar, J. G. & Wang, Q. (1995) *A. Ent. Soc. Am.* **88**, 666-671.
4. Barbosa, P. & Frongillo, E. A. (1979) *Entomophaga* **24**, 139-143.
5. Tillman, P. G. & Cate, J. R. (1993) *Environ. Entomol.* **22**, 1161-1165.
6. Heinz, K. M. (1998) *Bull. Ent. Res.* **88**, 37-45.
7. Sandlan, K. (1979) *Ecol. Ent.* **4**, 365-378.
8. Ryan, R. B. & Rudinsky, J. A. (1962) *Can. Entomol.* **94**, 748-763.
9. Kenis, M. (1996) *Entomophaga* **41**, 217-224.
10. Mackauer, M. & Lardner, R. M. (1995) *Ecol. Ent.* **20**, 118-124.
11. Kishi, Y. (1970) *Appl. Ent. Zool.* **5**, 126-132.
12. Terrasse, C., Nowbahari, B. & Rojas-Rousse, D. (1996) *J. Ins. Behav.* **9**, 251-263.
13. Tagawa, J., Aoki, S. & Kiyosue, T. (2000) *Appl. Entomol. Zool.* **35**, 541-547.
14. Mendel, Z. (1986) *Entomophaga* **31**, 127-137.
15. Jones, W. T. (1982) *Behav. Ecol. Sociobiol.* **10**, 207-210.
16. McGugan, B. M. (1955) *Can. Entomol.* **87**, 178-187.
17. Ueno, T. (1998) *Evol. Ecol.* **12**, 643-654.
18. Simbolotti, G., Putters, F. A. & Assem, J. v. d. (1987) *Behaviour* **100**, 1-31.
19. van den Assem, J. (1971) *Neth. J. Zool.* **21**, 373-402.
20. Lampson, L. J., Morse, J. G. & Luck, R. F. (1996) *Environ. Entomol.* **25**, 283-294.
21. Wylie, H. G. (1967) *Can. Entomol.* **99**, 742-748.
22. Seidl, S. E. & King, B. H. (1993) *Evolution* **47**, 1876-1882.
23. van Alphen, J. J. M. & Thunnissen, I. (1983) *Neth. J. Zool.* **33**, 497-514.
24. Ueno, T. (1999) *A. Ent. Soc. Am.* **92**, 609-614.
25. Arthur, A. P. & Wylie, H. G. (1959) *Entomophaga* **4**, 297-301.
26. Samson, P. R. (1984) *Entomophaga* **29**, 287-298.
27. King, B. H. (1988) *Evolution* **42**, 1190-1198.
28. Donaldson, J. S. & Walter, G. H. (1984) *Ecol. Ent.* **9**, 395-402.
29. King, B. H. (2000) *Behav. Ecol. Sociobiol.* **48**, 316-320.
30. Napoleon, M. E. & King, B. H. (1999) *Behav. Ecol. Sociobiol.* **46**, 325-332.
31. Brunson, M. H. (1938) *J. Agric. Res.* **57**, 379-387.
32. Bertschy, C., Turlings, T. C. J., Bellotti, A. & Dorn, S. (2000) *Entomol. Exp. Appl.* **95**, 238-291.
33. Holdaway, F. G. & Fairfield Smith, H. (1935?), 247-259.
34. Chandler, L. D., Meyerdirk, D. E., Hart, W. G. & Garcia, R. G. (1980) *Southwestern Entomologist* **5**, 99-103.
35. Honek, A., Jarosik, V., Lapchin, L. & Rabasse, J. M. (1998) *J. Agric. Entomol.* **15**, 209-221.
36. Asante, S. K. & Danthanarayana, W. (1993) *Entomophaga* **38**, 391-403.

37. Wellings, P. W., Morton, R. & Hart, P. J. (1986) *Ecol. Ent.* **11**, 341-348.
38. Cloutier, C., McNeil, J. N. & Regniere, J. (1981) *Can. Entomol.* **113**, 193-198.
39. Mackauer, M. & Kambhampati, S. (1988) *Entomol. Exp. Appl.* **49**, 167-173.
40. Shu-sheng, L. (1985) *Entomol. Exp. Appl.* **37**, 41-48.
41. Wong, T. T. Y., Ramadan, M. M., McInnis, D. O. & Mochizuki, N. (1990) *J. Econ. Entomol.* **83**, 779-783.
42. Gunasena, G. H., Vinson, S. B. & Williams, H. J. (1989) *A. Ent. Soc. Am.* **82**, 187-191.
43. Fuester, R. W. & Taylor, P. B. (1991) *A. Ent. Soc. Am.* **84**, 429-435.
44. Kolodny-Hirsch, D. M. (1988) *Environ. Entomol.* **17**, 127-131.
45. Croft, P. & Copland, M. J. W. (1995) *Entomol. Exp. Appl.* **74**, 121-124.
46. Wright, E. J. & Kerr, J. D. (1988) *Entomol. Exp. Appl.* **48**, 51-59.
47. Cloutier, C., Levesque, C. A., Eaves, D. M. & Mackauer, M. (1991) *Can. J. Zool.* **69**, 1489-1495.
48. Kouame, K. L. & Mackauer, M. (1991) *Oecologia* **88**, 197-203.
49. Hagvar, E. B. & Hofsvang, T. (1986) *Entomophaga* **31**, 337-346.
50. van Dijken, M. J., Neuenschwander, P., van Alphen, J. J. M. & Hammond, W. N. O. (1991) *Ecol. Ent.* **16**, 233-240.
51. Debolt, J. W. (1981) *A. Ent. Soc. Am.* **74**, 334-337.
52. Cadee, N. & van Alphen, J. J. M. (1997) *Entomol. Exp. Appl.* **83**, 277-284.
53. Karamaouna, F. & Copland, M. J. W. (2000) *Entomol. Exp. Appl.* **97**, 301-308.
54. Patel, P. N. & Habib, M. E. M. (1993) *Entomophaga* **38**, 511-517.
55. Harrison, W. W., Herbert, D. A. & Hardee, D. D. (1993) *J. Entomol. Sci.* **28**, 343-349.
56. Avilla, J. & Albajes, R. (1984) *Entomol. Exp. Appl.* **35**, 43-47.
57. Barrett, B. A. & Brunner, J. F. (1990) *Environ. Entomol.* **19**, 803-807.
58. Neveu, N., Krespi, L., Kacem, N. & Nenon, J.-P. (2000) *96*, 231-237.