

How is sexual conflict over parental care resolved? A meta-analysis

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Abstract

Biparental care of offspring is both a form of cooperation and a source of conflict. Parents face a trade-off between current and future reproduction: caring less for the current brood allows individuals to maintain energy reserves and increase their chances of remating. How can selection maintain biparental care, given this temptation to defect? The answer lies in how parents respond to changes in each other's effort. Game-theoretical models predict that biparental care is evolutionarily stable when reduced care by one parent leads its partner to increase care, but not so much that it completely compensates for the lost input. Experiments designed to reveal responses to reduced partner effort have mainly focused on birds. We present a meta-analysis of 54 such studies, and conclude that the mean response was indeed partial compensation. Males and females responded differently and this was in part mediated by the type of manipulation used.

Introduction

Conflicts of interest over care

Biparental care of offspring is rare across the animal kingdom, but among birds, cichlid fishes and primates it is the predominant mode of parenting (Lack, 1968; Clutton-Brock, 1991; Bennett & Owens, 2002; Reynolds *et al.*, 2002). Biparental care is a form of cooperation between an adult male and female, but it is not free from conflict. Caring for young is essential for the offspring to become independent in many organisms, but it is also costly, both in terms of resources used and in terms of lost opportunities for remating. Therefore, in attempting to maximize their lifetime reproductive success, parents face a trade-off between current and future offspring (e.g. Smith, 1995). The net result of this is a conflict of interest between parents (post-fertilization sexual conflict: Royle *et al.*, 2004; van Dijk & Székely, 2008), as each parent will benefit from shifting more of the burden of care for

the current offspring onto its partner (Trivers, 1972; Lessells, 1999; Houston *et al.*, 2005).

An early theoretical investigation of parental care, by Houston & Davies (1985), modelled responses to changes in care effort over evolutionary time. The model assumed that each parent displays a fixed level of effort that maximizes its fitness given the effort of its mate. Biparental care was shown to be an evolutionarily stable strategy (ESS) if a decrease in care by one parent selected for an increase in care of a smaller magnitude by its partner (and vice versa in the case of increased care). In Houston and Davies' model, each parent brings to the relationship a 'sealed bid' of how much care effort they will invest in the offspring. Later models (e.g. McNamara *et al.*, 1999, 2003; Johnstone & Hinde, 2006) allowed parents to respond to one another's behaviour in real time – to negotiate care levels. If one parent decreases its parental effort, its partner has four options: abandon the family; reduce its own effort; increase its own effort; or continue caring at the same level. McNamara *et al.* (1999, 2003) predicted a similar 'partial compensation' response to Houston and Davies, but in behavioural as opposed to evolutionary time: if one parent decreases its effort, the ESS response by its partner is to increase its own care effort, but not so much that it completely compensates for the lost care (for a review, see Houston *et al.*, 2005).

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Later, Jones *et al.* (2002) and Johnstone & Hinde (2006) developed models that predicted that negotiation could lead to partial, full or even no compensation (or desertion) depending on the shapes of the cost and benefit functions of parental care, and on how well each parent is informed of offspring needs. Numerous ecological and life-history variables (e.g. mating system, developmental mode, levels of extra-pair paternity, strength of sexual selection, brood size) have also been proposed to affect patterns of parental care and responses to reduced partner effort (Lack, 1968; Wilson, 1975; Skutch, 1976; Silver *et al.*, 1985; Clutton-Brock, 1991; Houston & McNamara, 2002; Reid *et al.*, 2002; Kokko & Jennions, 2008; Olson *et al.*, 2008; McGraw *et al.*, in press).

With these models in mind, many empiricists have sought to determine how parents make decision about offspring desertion (e.g. Székely, 1996; Székely & Cuthill, 1999; McNamara *et al.*, 2002; Griggio *et al.*, 2005; Szentirmai *et al.*, 2007), or whether parents compensate for reduced parental investment by their partner.

Experimental studies of parental effort

Two types of experiment have been used to investigate responses to reduced partner care effort. First, to find out whether a single parent can match or better the care provided by two parents, researchers have removed one parent (henceforth, the target parent), and determined whether the remaining parent (henceforth, widow or respondent) compensated for the lost care (e.g. Greenlaw & Post, 1985; Duckworth, 1992; Whittingham *et al.*, 1994; Székely & Cuthill, 1999; Gubernick & Teferi, 2000; Itzkowitz *et al.*, 2001; Royle *et al.*, 2002; Smiseth *et al.*, 2005). Second, researchers have used experimental manipulations to reduce the care effort of one parent and investigated how its partner responded to a reduction in care. These manipulations are of two broad types. On the one hand, the target parent may be handicapped to make care provision more energetically demanding (e.g. Wright & Cuthill, 1990; Sanz *et al.*, 2000; Griggio *et al.*, 2005; Paredes *et al.*, 2005; Suzuki & Nagano, 2009; Lendvai *et al.*, in press). On the other hand, researchers have used manipulations intended to divert male behaviour from care provision to courtship: these include testosterone implants (e.g. Ketterson *et al.*, 1992; Stoehr & Hill, 2000; Van Roo, 2004; Schwagmeyer *et al.*, 2008), manipulations of sexual signals (Qvarnstrom, 1997; Nakagawa *et al.*, 2007) and increased nest box availability (Smith, 1995).

An extensive literature search revealed 124 experiments that investigated the effect of mate removal or manipulation to reduce parental care in animals (Fig. 1). Various authors have noted that the results of such experiments are not consistent, as some studies reported no change by the responding parent, whereas others reported partial or full compensation (Sanz *et al.*, 2000; Houston *et al.*, 2005). We wished to conduct a meta-

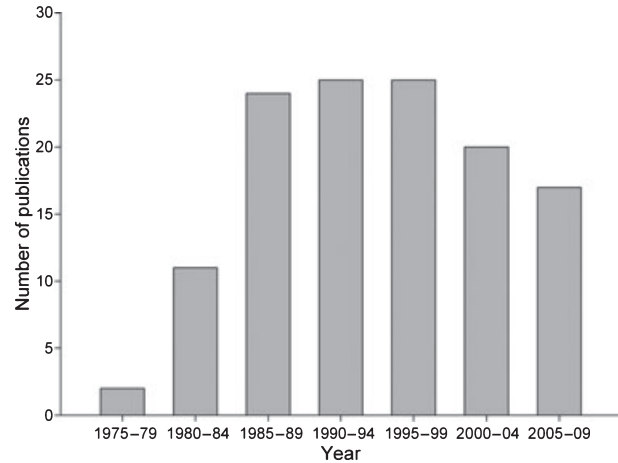


Fig. 1 Published papers reporting effect on brood success and/or parental effort following mate removal or manipulation to reduce care effort. Numbers were obtained following a search of the ISI Web of Knowledge.

analysis of the results of such experiments to explore whether and to what extent individuals compensate for lowered partner investment in offspring. Although published results have been compared in review articles, or in the discussion sections of research papers (Bart & Tornes, 1989; Mock & Fujioka, 1990; Sanz *et al.*, 2000; Houston *et al.*, 2005; Hinde, 2006), we are not aware of any formal meta-analysis.

We chose to restrict our analysis to avian studies for several reasons. First, the key theoretical models in this area were formulated with birds in mind (Maynard Smith, 1977; Houston & Davies, 1985; Johnstone & Hinde, 2006). Second, and more importantly, the vast majority of published experimental studies are on birds. A number of important experiments have been carried out on fish (e.g. Raadik *et al.*, 1990; Itzkowitz *et al.*, 2001), mice (e.g. Cantoni & Brown, 1997; Gubernick & Teferi, 2000), and invertebrates (e.g. Robertson, 1998; Jenkins *et al.*, 2000; Hunt & Simmons, 2002; Rauter & Moore, 2004; Smiseth *et al.*, 2005; Suzuki & Nagano, 2009), but most of these proved to be unsuitable, either because they did not report the change in behaviour of the remaining parent or because we could not calculate effect sizes from the data presented (see Materials and methods). Further, very different measures of care were used, and we only found one nonavian manipulation study (Suzuki & Nagano, 2009). We therefore decided not to include the small number remaining as we felt this would not add significant value to the data set (the 'apples and oranges' problem of meta-analysis: Lipsey & Wilson, 2001). The studies included in our data set are listed in Table S1.

Our objective was to address quantitatively two questions. First, do parents change their care behaviour in response to a reduction in partner effort and, if so, is partial compensation the norm? Second, can we identify

any variables that influence responses? We predicted that birds may respond differently to partner removal vs. manipulation (McNamara *et al.*, 2003). Further, even if different manipulations reduce the target parent's effort by a similar degree, they may have qualitatively different effects on the respondent's behaviour. This is because different manipulations may have different effects on perceived partner quality. Females may perceive weighted or clipped males differently from those whose attractiveness has been manipulated by a testosterone implant or increased badge size: females may invest more in the offspring of more attractive males, regardless of his care effort (Burley, 1988; Møller & Thornhill, 1998; Houston *et al.*, 2005).

Materials and methods

Data collection

We undertook a thorough search of the literature for avian studies of parental removal or manipulation of effort, using previously compiled lists and online citation databases. We also sought unpublished studies using the group email list of Association for the Study of Animal Behaviour. Our primary goal was to collect studies that reported the effect of experimental treatment on (a) care by the respondent parent and (b) total care by the target and respondent parents. Care behaviours used were incubation, brooding of young and/or food provisioning for the brood, as these are by far the most commonly reported measures of care in birds. A major function of both incubating the eggs and brooding of the young is thermoregulation, therefore we combined these in a single behaviour (henceforth, incubation). We discarded studies that did not include data on either (a) or (b), did not specify the sex of the individuals used, or where the manipulation did not have a significant effect on parental behaviour of the target parent (as defined by the reported *P*-values: we used this criterion as we were interested in the effect specifically of reduced parental effort, not of manipulation *per se*). We also recorded the effects of experimental treatment on reproductive output (hatching or fledging success, chick mass or growth, brood mass, chick survival). We discarded studies for which we could not calculate effect sizes for changes in care using available data, because effect sizes are the foundation of meta-analysis (see below). From an initial list of 96 studies using these filters, 53 published studies and one manuscript in preparation met our criteria for inclusion in the meta-analysis data set. In one case, we combined three studies published by the same group of researchers in order to gain all information required for the study population. The studies in our data set are detailed in Appendix S1 and Table S1 in the Supporting Information.

Where available, we also recorded the time at which the target parent was removed or manipulated (before egg laying, during incubation or after hatching), clutch or

brood size at the time of manipulation and the proportion of total feeding and/or incubation undertaken by the female in control pairs.

Our data set included data on 25 male removals, 11 female removals, 26 manipulations of male care and 11 manipulations of female care. Manipulations included handicapping by the addition of weights (representing 2–10% of the individual's body mass), feather clipping, inducing stress by a capture-handle-release protocol, implanting males with testosterone, increasing the size of a sexually selected signal (male facial badge) and providing extra nest boxes to induce males to pair with a second female. Table 1 summarizes the sample sizes for each treatment. Our data set includes information on 33 species, comprising 26 Passeriformes, four Charadriiformes, two Anseriformes and one Falconiformes. Following the definitions in the Introduction, we will refer to the parent that was removed or manipulated as the target parent, and the remaining or unmanipulated parent as the respondent.

Different subsets of these studies yielded effect sizes for target parent, respondent and total feeding and/or incubation behaviour (see Table S1). When calculating mean effect sizes, the number of studies used ranged from 7 to 52 (Table 2). A literature search for other meta-analyses in the fields of behaviour and ecology revealed the occasional data set comprising over 100 effect sizes, but meta-analytic data sets in these fields typically included 20–60 data points. Although some of our calculations of mean effect sizes therefore rely on small numbers of data points, our full data set appears to be a respectable size.

As stated in the section Experimental studies of parental effort, various ecological and life-history variables are predicted to affect parental care. However, data on most of these variables were only available for a subset of species in our data set. Further, we could not analyse the effect of time in the breeding season as most studies carried out experimental treatments over a wide range of dates (several weeks). Therefore, we do not include analyses of these variables in the present study. Results of interim analyses are available from the authors on request, and are expected to form the basis of a follow-up study (F. Harrison, Z. Barta, T. Székely &

Table 1 Summary of sample sizes for different experimental treatments in our data set (see Table S1).

Treatment	Target parent = female	Target parent = male
Removal	11 cases (8 species)	25 cases (21 species)
Weighting	7 cases (5 species)	6 cases (4 species)
Feather clipping	4 cases (4 species)	3 cases (3 species)
Testosterone implant	–	14 cases (11 species)
Increase badge size	–	1 case
Provision of extra nest boxes	–	1 case
Stress	–	1 case

Table 2 Calculation of overall mean effect sizes.

	<i>N</i>	<i>d</i> ₊₊	SE	<i>P</i>	<i>Q</i>	<i>P</i>	Power (one-tailed)	Power (two-tailed)	Failsafe sample size
(a) Respondent effort									
<i>Full data set</i>									
Feeding (fixed-effects)	52	1.03	0.057	< 0.001					
Feeding (mixed model)		1.26	0.162	< 0.001	389.8	< 0.001	0.87	0.96	275
Incubation (fixed-effects)	27	0.17	0.071	0.017					
Incubation (mixed model)		0.22	0.118	0.060	61.5	< 0.001	0.60	0.82	2
<i>Removals</i>									
Feeding (fixed-effects)	25	1.69	0.086	< 0.001					
Feeding (mixed model)		1.97	0.237	< 0.001	169.1	< 0.001	0.63	0.84	221
Incubation (fixed-effects)	16	0.28	0.091	0.757					
Incubation (mixed model)		0.07	0.181	0.698	46.6	< 0.001	0.39	0.66	0
<i>Manipulations</i>									
Feeding (fixed-effects)	27	0.50	0.076	< 0.001					
Feeding (mixed model)		0.61	0.164	< 0.001	111.9	< 0.001	0.62	0.84	55
Incubation (fixed-effects)	11	0.39	0.113	< 0.001					
Incubation (mixed model)		0.39	0.113	< 0.001	8.8	0.555	0.36	0.63	10
(b) Total effort									
<i>Full data set</i>									
Feeding (fixed-effects)	43*	-0.76	0.063	< 0.001					
Feeding (mixed model)		-1.11	0.235	< 0.001	564.7	< 0.001	0.81	0.94	195
Incubation (fixed-effects)	19	-0.39	0.082	< 0.001					
Incubation (mixed model)		-0.58	0.146	< 0.001	45.3	< 0.001	0.48	0.74	36
<i>Removals</i>									
Feeding (fixed-effects)	23	-0.98	0.093	< 0.001					
Feeding (mixed model)		-1.62	0.437	< 0.001	463.9	< 0.001	0.58	0.81	163
Incubation (fixed-effects)	12	-0.45	0.098	< 0.001					
Incubation (mixed model)		-0.76	0.202	< 0.001	33.1	< 0.001	0.34	0.62	33
<i>Manipulations</i>									
Feeding (fixed-effects)	20*	-0.58	0.085	< 0.001					
Feeding (mixed model)		-0.63	0.191	< 0.001	90.7	< 0.001	0.52	0.77	43
Incubation (fixed-effects)	7	-0.24	0.147	0.102					
Incubation (mixed model)		-0.31	0.208	0.140	10.8	0.094	0.26	0.53	3

*One case had variance = 0.

I. Cuthill, unpublished data). We were able, however, to include data on brood or clutch size in our meta-analytic models. Reproductive value of the current brood is likely to influence the direct benefits of caring for a brood and, where available, we recorded clutch and/or brood size at the time of experimental manipulation. Some authors recorded the range of clutch or brood sizes included in the study, others reported an average. Unfortunately, most studies that used a range of clutch or brood sizes did not provide a breakdown of results across different clutch or brood sizes. This generally seemed to be due to small sample size. Therefore, we used the average clutch or brood size in each study in our meta-analysis.

Meta-analytic techniques

Meta-analysis is a formal framework that tests whether the results of different studies are consistent with one another. It also calculates the mean magnitude of the response to experimental manipulation across studies. This relies on the calculation of standardized measures of

change in response variables (effect sizes: Nakagawa & Cuthill, 2007). Effect sizes can be adjusted such that studies with larger sample sizes (or smaller variance) are given more weight in the calculation of overall mean effect size. We present here a short explanation of our meta-analysis: for a more detailed introduction to this technique, see Fernandez-Duque & Vaggia (1994), Côté & Sutherland (1997) and Lipsey & Wilson (2001).

Our effect size was the standardized mean difference between levels of a given care type (total or respondent feeding, incubation or brooding) in control and experimental pairs. This is Cohen's *d* (Cohen, 1977) and is calculated for the *i*th study as

$$d_i = \left(\frac{\bar{X}_{\text{Tmt}} - \bar{X}_{\text{Ctrl}}}{\text{PooledSD}} \right) \left(1 - \frac{3}{4(n_{\text{Tmt}} + n_{\text{Ctrl}} - 2) - 1} \right) \quad (1)$$

where n_{Tmt} and n_{Ctrl} are the number of individuals (or pairs) that contributed to calculating the group means \bar{X}_{Tmt} and \bar{X}_{Ctrl} , for experimental and control groups respectively. PooledSD is the pooled standard deviation across experimental and control groups.

The variance of d_i is calculated as

$$s^2(d_i) = \left(\frac{n_{\text{Tmt}} + n_{\text{Ctrl}}}{n_{\text{Tmt}}n_{\text{Ctrl}}} \right) + \left(\frac{d_i^2}{2(n_{\text{Tmt}} + n_{\text{Ctrl}})} \right) \quad (2)$$

A 95% confidence interval for d_i may then be calculated; if d_i is significantly different from zero, then we conclude that there is a significant difference between control and experimental groups in that study.

We calculated d_i and $s^2(d_i)$ either from means and standard deviations reported in papers or by converting reported z -scores, F -ratios or correlation coefficients using Wilson's effect size determination programme (ES Calculator, available from <http://mason.gmu.edu/~dwilsonb/ma.html>). We also calculated the statistical power of our estimates of mean effect size using the method detailed by Hedges & Pigott (2001).

Full compensation, partial compensation and no compensation all occurred with regard to feeding or incubation behaviour (Table S1). We classified full compensation as having occurred when the effect sizes for the target parent, respondent parent and their total effort were significantly < 0 , significantly > 0 and not significantly different from 0 respectively. Partial compensation was concluded when the corresponding values were significantly < 0 , significantly > 0 and significantly < 0 . There were two cases of overcompensation (effect size for total feeding effort significantly > 0). We then explored the mean responses across studies using meta-analysis.

The weighted mean effect size across studies d_{++} and its variance $s^2(d_{++})$ may then be calculated:

$$d_{++} = \left[\sum_{i=1}^N d_i / s^2(d_i) \right] / \left[\sum_{i=1}^N 1 / s^2(d_i) \right] \quad (3)$$

$$s^2(d_{++}) = 1 / \left[\sum_{i=1}^N 1 / s^2(d_i) \right] \quad (4)$$

where N is the number of studies. This calculation of d_{++} assumes that all variation between the values of d calculated from different studies is due to sampling error alone and is thus a 'fixed-effect' calculation; however, it is possible to estimate the random or between-studies variance component, and include this in the calculation of d_{++} . The method of moments estimate of the random variance component was used in these calculations (Lipsey & Wilson, 2001).

We also calculated the failsafe sample size N_n . This is the number of unpublished, nonsignificant studies that would need to exist in order to make the results of a meta-analysis nonsignificant; the higher the value of N_n , the more reliable the results of the meta-analysis:

$$N_n = N(d_{++}/d_c - 1) \quad (5)$$

where d_c is the minimum meaningful effect size. We set d_c to 0.2 as values of $d \leq 0.2$ are generally considered small (Cohen, 1977).

We then determined whether there was significant variation (heterogeneity) among the effect sizes of studies using Q statistics (Côté & Sutherland, 1997; Lipsey & Wilson, 2001). If the value of Q is significantly large, then a single mean effect size d_{++} is not the best way to describe the effects of experimental manipulation, because there are differences in estimated effect size between study populations. These may be due to identifiable factors that vary among studies, such as differences in the life history of species or in experimental techniques. Such factors may be identified using statistical tests that are analogous to ANOVA or weighted regression (but that do not rely on the assumption of homogeneity of variance). We used random-effect calculations of d_{++} to calculate Q as this reduces the chances of committing a Type I error when testing for the significance of Q . (For further explanation of this methodology, see Lipsey & Wilson, 2001.)

Just as ANOVA partitions total variance in a data set into variance due to explanatory variables and variance due to error (between- and within-group variance), so Q can be partitioned into between- and within-group heterogeneity. The data were split into categories (e.g. mate removal vs. mate manipulation studies) and heterogeneity between (Q_B) and within (Q_W) categories calculated using an analogue to the ANOVA. If Q_B is significant, this indicates that the grouping factor (in the preceding example, experimental treatment) explains a significant proportion of the total heterogeneity in effect sizes. The mean effect sizes within each group can then be calculated (denoted d_+). Alternatively, an analogue to a weighted multiple regression model can be used to determine whether fitting one (or more) continuous explanatory variables (e.g. share of feeding undertaken by the female in control pairs) explains a significant amount of heterogeneity (Q_{Model} vs. Q_{Residual}). In this case, for each variable treated as continuous, an estimate of the slope of its effect (beta) and a corresponding P -value are also returned.

We used freely-available SPSS macros developed by Lipsey & Wilson (2001) to carry out these analyses (macros available from <http://mason.gmu.edu/~dwilsonb/ma.html>). We effectively used mixed models by weighting effect sizes of each study by the method of moments estimate of the random effects variance component. Simple fixed effects models assume that any heterogeneity remaining after a model has been fitted (Q_{Residual} or Q_W) is entirely due to sampling error, but a mixed model does not exclude the possibility that this is due to systemic but unidentified sources of heterogeneity. This gives a more robust test of the significance of Q_{Model} or Q_B (for details, see Lipsey & Wilson, 2001).

Constraints and caveats

Some species were the subject of multiple removal or manipulation studies. As studies were generally separated geographically, published several years apart or used manipulation at different time points (before laying, during incubation or after hatching), we considered these results as independent data points. One study (Sasvári, 1986) included data on two species and we considered these results to be independent data points. As we weighted the analyses for the random effects variance component, we were not overly concerned about potential problems of nonindependence.

Calculating effect sizes for the effect of experimental treatment on reproductive output was challenging, because there was little consistency in which measure (one or more of hatching success, fledging success, chick mass, brood mass, chick growth or chick survival) was reported. Therefore, we simply scored whether a given study reported complete failure to hatch or fledge (-2), a significant decrease (-1), significant increase (1) or no change (0) in whichever measure(s) of reproductive output the authors used.

Results

Do parents change their care behaviour in response to a reduction in partner effort?

We first analysed removal and manipulation data together, and tested for a significant change in respondent behaviour (Fig. 2a, Table 2). Respondents increased their feeding effort in response to reduced partner effort ($d_+ = 1.26 \pm 0.162$, $N = 52$, $P < 0.001$); however, the total feeding effort decreased compared with control levels ($d_+ = -1.11 \pm 0.235$, $N = 43$, $P < 0.001$). Therefore, parents do not compensate fully for reduced partner effort in terms of feeding effort. The failsafe sample sizes for the change in respondent and total feeding were 275 and 195 respectively. The failsafe sample size is the number of unpublished, nonsignificant studies that would need to exist in order to make the results of a meta-analysis nonsignificant; the higher the failsafe sample size, the more confident we can be that significant results are not Type I errors.

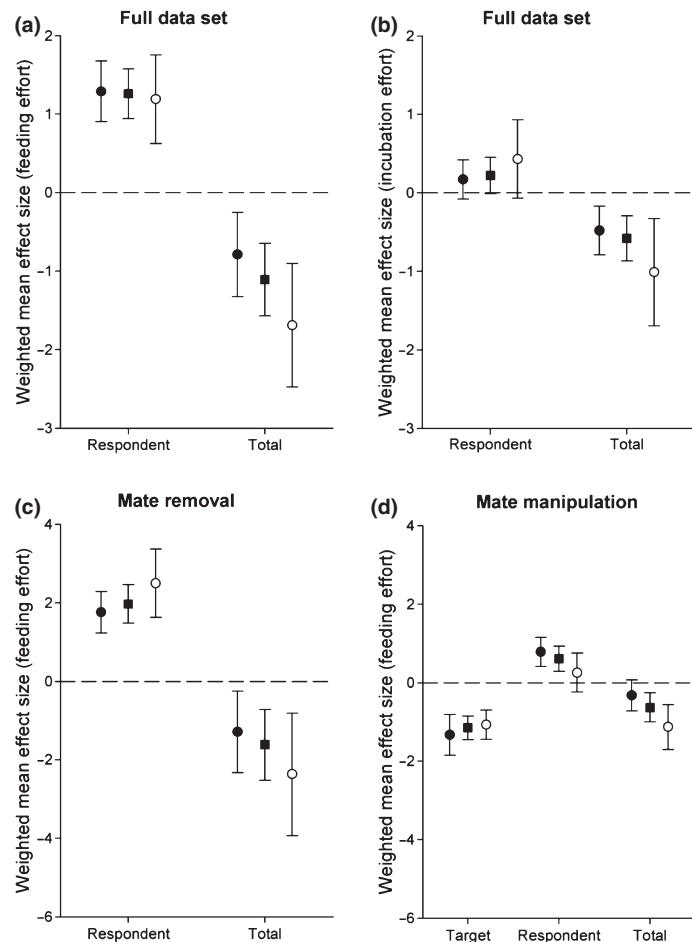


Fig. 2 Weighted mean effect sizes (Cohen's d) computed from our data set. In all graphs, squares show mean across both sexes, black circles show mean for females and white circle mean for males. Error bars show 95% confidence intervals. (a) Effect sizes for changes in feeding effort calculated from the full data set. (b) Effect sizes for changes in incubation or brooding effort calculated from the full data set. (c) Effect sizes for changes in feeding effort calculated from mate removal studies only. (d) Effect sizes for changes in feeding effort calculated from mate manipulation studies only.

Respondents also showed a nonsignificant increase in incubation behaviour (Fig. 2b, $d_+ = 0.22 \pm 0.118$, $N = 27$, $P = 0.060$). The effect of partner removal or manipulation on incubation was much smaller than the effect on feeding behaviour. As with feeding, the total incubation decreased ($d_+ = -0.58 \pm 0.146$, $N = 19$, $P < 0.001$), hence respondents did not fully compensate for reduced partner effort. The failsafe sample sizes for the change in respondent and total incubation were 2 and 36 respectively. Therefore, conclusions drawn regarding incubation effort are less robust than those from the feeding data.

What are the causes of heterogeneity in responses to reduced partner effort?

Q statistics revealed significant heterogeneity in respondent and total feeding and in respondent and total

incubation (Table 2, all P -values < 0.001). We therefore hypothesized that variation between studies or species in experimental, ecological or life-history variables may explain some of this heterogeneity. Models referred to in the following paragraphs are given in Table 3.

Analyses of the full data set

Treatment (removal vs. manipulation) explained a significant amount of heterogeneity both in respondent feeding and total feeding (Fig. 2c,d, Table 3). Widows increased feeding effort more than did partners of manipulated birds, and this result held when respondent sex was included in the model (treatment beta = -0.48 , $P < 0.001$; sex beta = -0.009 , $P = 0.936$). When treatment (removal vs. manipulation) was included in the model, there was a nonsignificant tendency for total feeding effort to decrease more when the female was

Table 3 Results of meta-analytic models 'Treatment' is coded as 1 = removal, 2 = manipulation; 'respondent sex' is coded as 1 = female, 2 = male; 'treatment (weight/other)' is coded as 1 = weight, 0 = other. For clarification of any other variables, see Materials and methods section or Supporting Information.

(a) Results of models predicting d (respondent feeding)							(b) Results of models predicting d (total feeding)						
Terms in model	Beta	P	Q_{Model}	P	Q_{Residual}	d.f. P	Terms in model	Beta	P	Q_{Model}	P	Q_{Residual}	d.f. P
<i>Full data set</i>							<i>Full data set</i>						
Treatment	-0.484	<0.001	21.2	<0.001	69.7	49 0.028	Treatment	0.243	0.034	7.9	0.019	68.7	41 0.004
Respondent sex	-0.009	0.936					Respondent sex	-0.217	0.058				
<i>Removals</i>							<i>Removals</i>						
Respondent sex	0.216	0.174	2.0	0.365	38.1	22 0.177	Respondent sex	-0.279	0.087	6.7	0.036	33.2	20 0.032
Mating system	0.038	0.809					Mating system	0.372	0.022				
Respondent sex	0.097	0.619	10.0	0.007	16.9	13 0.203	Respondent sex	-0.143	0.524	0.6	0.740	19.7	13 0.104
Feeding skew to female	0.588	0.003					Feeding skew to female	0.120	0.594				
Respondent sex	0.049	0.798	1.4	0.484	25.8	15 0.040	Respondent sex	-1.211	0.617	1.6	0.460	15.8	12 0.198
Time of removal	0.224	0.242					Time of removal	-0.257	0.288				
Respondent sex	0.264	0.122	2.4	0.302	32.5	18 0.019	Respondent sex	-0.238	0.202	3.9	0.142	25.4	17 0.086
Chick score (< 0 vs. ≥ 0)	0.047	0.783					Chick score	0.248	0.183				
Respondent sex	0.433	0.038	4.6	0.100	20.9	12 0.053	Respondent sex	0.108	0.729	2.4	0.302	8.6	12 0.737
Brood size	-0.247	0.237					Brood size	-0.481	0.122				
<i>Manipulations</i>							<i>Manipulations</i>						
Respondent sex	-0.496	0.006	12.4	0.002	21.8	20 0.354	Respondent sex	-0.413	0.075	4.1	0.128	18.0	17 0.387
Feeding skew to female	0.549	0.003					Feeding skew to female	-0.039	0.866				
Respondent sex	-0.376	0.032	8.4	0.015	24.4	22 0.327	Respondent sex	-0.465	0.025	6.7	0.034	17.0	16 0.387
Time of manipulation	0.380	0.031					Time of manipulation	-0.200	0.336				
Respondent sex	-0.529	0.006	13.1	0.001	14.5	13 0.337	Respondent sex	-0.457	< 0.001	44.2	< 0.001	12.2	12 0.428
Chick score	-0.518	0.007					Chick score	0.667	< 0.001				
Respondent sex	-0.491	0.003	13.4	0.001	28.0	24 0.260	Respondent sex	-0.358	0.070	10.2	0.006	18.8	18 0.407
Treatment (weight/other)	-0.506	0.002					Treatment (weight/other)	0.367	0.063				
Respondent sex	-0.343	0.042	5.2	0.075	31.0	24 0.153	Respondent sex	-0.325	0.034	26.8	< 0.001	19.1	18 0.388
d (partner feeding effort)	-0.230	0.173					d (partner feeding effort)	0.612	< 0.001				
Respondent sex	-0.299	0.084	3.4	0.182	29.9	24 0.188	Respondent sex	-0.436	0.033	5.8	0.054	18.1	18 0.450
Partner feeding score	-0.118	0.500					Partner feeding score	0.199	0.332				
Respondent sex	-0.318	0.415	0.67	0.715	6.0	6 0.425	Respondent sex	0.179	0.702	0.3	0.845	4.8	4 0.304
Brood size	-0.006	0.988					Brood size	0.129	0.783				
<i>(c) Results of models predicting d (respondent incubation)</i>							<i>(d) Results of models predicting d (total incubation)</i>						
<i>Full data set</i>							<i>Full data set</i>						
Treatment	0.309	0.075	4.2	0.125	30.5	24 0.167	Treatment	0.191	0.377	2.6	0.270	21.8	16 0.150
Respondent sex	0.233	0.179					Respondent sex	-0.207	0.339				

removed or manipulated than when the male was removed or manipulated (treatment $\beta = -0.24$, $P = 0.034$; sex $\beta = -0.22$, $P = 0.058$).

Although these models explained a significant proportion of the total heterogeneity in effect sizes ($P < 0.001$ and $P = 0.019$), significant residual heterogeneity remained ($P = 0.028$ and 0.004). We therefore split the data into removals and manipulations to explore the possible causes of this heterogeneity (see Table 3 and below). Neither treatment nor sex was a significant cause of heterogeneity in respondent incubation or total incubation ($\beta \leq 0.19$, $P \geq 0.075$).

Mate removal experiments

The mean response was again partial compensation. Widows increased their feeding effort (Fig. 2c; $d_+ = 1.97 \pm 0.237$, $N = 25$, $P < 0.001$), but the total feeding effort decreased ($d_+ -1.62 \pm 0.437$, $N = 23$, $P < 0.001$). Taking into account random effects variance, there was no effect of sex on respondent or total feeding ($Q_B = 2.02$, $P = 0.155$, d.f. = 1 for 18 females and 7 males and $Q_B = 1.28$, $P = 0.258$, d.f. = 1 for 16 females and 7 males; Fig. 2c).

Respondent sex became a significant predictor of the change in respondent feeding if brood size was included in the model (males showed a greater increase in feeding than females: $P = 0.038$, brood size $P = 0.237$). In a model that included respondent sex, there was a significant effect of time of removal such that later removal promoted a greater increase in effort by the respondent ($\beta = 0.380$, $P = 0.031$).

Reduced reproductive performance was not associated with a smaller increase in respondent feeding effort or a larger decrease in total feeding rate: reproductive output score (-1 or -2 vs. 0 or 1) did not explain a significant amount of heterogeneity in either of these variables (respondent feeding $Q_B = 0.006$, $P = 0.939$, d.f. = 1, total $N = 21$; total feeding $Q_B = 2.2$, $P = 0.136$, d.f. = 1, total $N = 20$).

Manipulation experiments

Target birds reduced their parental effort, as expected (Fig. 2d). As with mate removal experiments, partners of manipulated birds showed partial compensation with regard to feeding effort (Fig. 2d; respondent $d_+ = 0.61 \pm 0.164$, $N = 27$, $P < 0.001$; total $d_+ = -0.63 \pm 0.191$, $N = 20$, $P < 0.001$). Overall, respondents showed increased incubation effort, but total incubation was unaffected (respondent $d_+ = 0.39 \pm 0.113$, $N = 11$, $P < 0.001$; total $d_+ = -0.31 \pm 0.208$, $N = 7$, $P = 0.141$). There was significant heterogeneity in respondent and total feeding ($P < 0.001$), but not in respondent or total incubation ($P \geq 0.094$).

Type of manipulation explained a significant amount of heterogeneity in respondent feeding ($Q_B = 10.4$, $P = 0.035$, d.f. = 4, $N = 27$). This was mainly due to a difference between handicapping by weighting and all

other treatments. Weighted males reduced feeding to a greater extent than did males that received another type of manipulation (Fig. 3, $Q_B = 9.3$, $P = 0.002$, d.f. = 1, $N = 18$). However, their partners increased feeding to a similar extent (Fig. 3, weight vs. other; $Q_B = 1.0$, $P = 0.31$, d.f. = 1, $N = 17$). As a result, there was no significant difference in the change in total feeding effort between the two treatment groups when females responded ($Q_B = 3.6$, $P = 0.060$, d.f. = 1, $N = 14$). Interestingly, males increased feeding effort if the female was weighted, but did not change it if she was clipped (Fig. 3, $Q_B = 9.0$, $P = 0.003$, d.f. = 1, $N = 10$), even though weighted females and those that received a different manipulation (clipping) reduced feeding effort to a similar extent (Fig. 3, $Q_B = 3.71$, $P = 0.054$, d.f. = 1, $N = 10$). The latter conclusions were unchanged when we excluded cases where the feeding effect size for the target parent was not significantly different from zero.

Type of manipulation (weighting vs. clipping) and the proportion of feeding done by the female in control pairs together explained a large amount of heterogeneity in male feeding response; males showed a greater response if their partner was weighted and if she normally undertook a greater proportion of chick feeding (Fig. 4; $Q_{\text{Model}} = 20.8$, $P < 0.001$; $Q_{\text{Residual}} = 7.4$, $P = 0.287$; $R^2_{\text{adj}} = 65.0\%$; $N = 9$). This result was unchanged by the exclusion of one outlier (Griggio *et al.*, 2005; $Q_{\text{Model}} = 13.9$, $P = 0.001$; $Q_{\text{Residual}} = 5.1$, $P = 0.400$; $R^2_{\text{adj}} = 62.2\%$; $N = 8$).

When manipulations that were expected to alter the male's attractiveness (testosterone, increased badge size and extra nest boxes) were compared with those that were not (weighting, clipping, stress), there was no

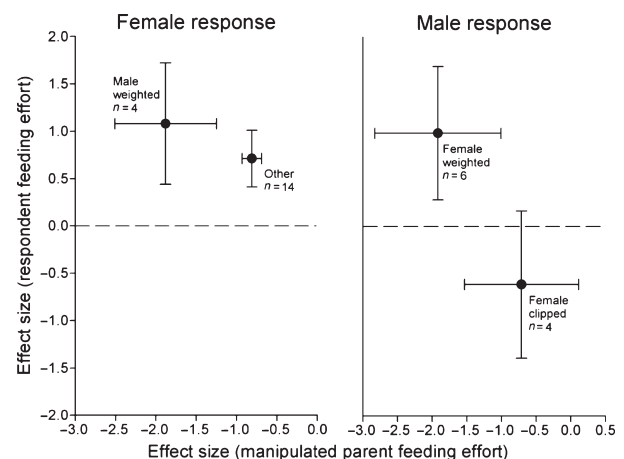


Fig. 3 Female respondents increased feeding effort to a similar extent regardless of the type of manipulation (weight vs. other) that their partner received ($Q_B = 1.0$, $P = 0.31$, d.f. = 1, $N = 17$). Males increased feeding effort if their partner was weighted but not if she was clipped ($Q_B = 9.0$, $P = 0.003$, d.f. = 1, $N = 10$). Graphs show weighted mean effect size (Cohen's d) and 95% confidence interval.

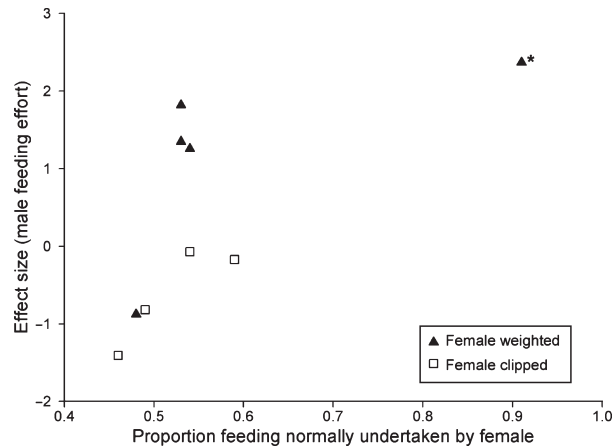


Fig. 4 Type of manipulation (weighting, triangles vs. clipping, squares) and the proportion of feeding done by the female in control pairs together explained a large amount of heterogeneity in male feeding response ($Q_{\text{Model}} = 20.8$, $P < 0.001$). This result was unchanged by the exclusion of one outlier marked * (Griggio *et al.*, 2005; $Q_{\text{Model}} = 13.9$, $P = 0.001$). The graph shows effect sizes (Cohen's d) from individual studies.

significant effect of treatment type on change in feeding by either the male or the female (male: $Q_B = 2.0$, $P = 0.158$, d.f. = 1, $N = 18$ and female: $Q_B = 0.03$, $P = 0.865$, d.f. = 1, $N = 17$ respectively). The latter results were unchanged when we excluded cases where the effect size for the male was not significantly different from zero.

Reduced total feeding was associated with reduced reproductive output although this result was based upon a small number of studies ($d_+ = -1.60 \pm 0.277$, $P < 0.016$, $N = 4$), and unchanged reproductive outputs were associated with no change in total feeding rate ($d_+ = -0.28 \pm 0.155$, $P = 0.069$, $N = 11$). These results held when respondent sex was included in the model (Table 3).

Discussion

We have presented the first meta-analysis of a large body of data relating to a question of significant biological interest. Biparental care is generally predicted to be stable if one parent cannot successfully rear offspring alone (Maynard Smith, 1982), or if each parent compensates partially for changes in care by its partner (Houston & Davies, 1985; McNamara *et al.*, 1999, 2003). Overall, our results reveal that birds can and do respond to partner removal and reduced partner effort by altering the level of parental care (incubation or providing food to their chicks). Consistent with theoretical predictions, the mean response was partial compensation for reduced partner effort. However, there was considerable variation in the direction and magnitude of this response, and our

analyses highlight potential sources of variation which could benefit from future experimental study.

Sources of variation in respondent behaviour

Birds responded differently to partner removal vs. partner manipulation, and in feeding vs. incubation effort. Notably, the effect sizes for change in incubation were smaller than those for feeding (though it should be noted that the sample sizes for incubation were smaller). This may be explained by greater costs being incurred by reducing feeding rate than by reducing incubation constancy.

Focusing on responses via feeding effort, it is clear that there is sex difference in response: females appeared to be better at compensating than males, but we were surprised that females did not respond differently to manipulations that may have made their mates more attractive. This suggests that females may respond more strongly to paternal investment than to any 'good genes' signified by attractiveness (Burley, 1988; Møller & Thornhill, 1998; Houston *et al.*, 2005). Alternatively, a female's view of what constitutes an attractive trait may be different from that of the investigators. Interestingly, males responded to weighted females by increasing feeding effort, but did not alter feeding effort in response to a clipped female, whereas females increased feeding to a similar extent regardless of the type of manipulation their partner received.

It is possible that males perceive weighted females differently from those with clipped feathers: in a study of rock sparrows (*Petronia petronia*), Griggio *et al.* (2005) suggested that males may perceive a weighted female as ready to lay a new clutch, and so increase their care effort in an attempt to ensure paternity of her next brood. Bart & Tornes (1989) and Wagner (1992) have also suggested that male birds may provide care in order to increase their chances of remating, and a similar strategy has been suggested in various organisms including arthropods and primates (Ens *et al.*, 1996; Tallamy, 2001; Reichard, 2007). In addition to increasing provisioning rate, male partners of weighted female rock sparrows in the Griggio *et al.* study also showed increased mate guarding and courtship behaviour: this and the data presented in Fig. 4 suggest that males will increase feeding behaviour (a) if they were doing less work to begin with and (b) if they perceive that increasing effort may bring increased reproductive success. Certainly an improvement in flight ability has been observed in female birds after laying (Kullberg *et al.*, 2005), but it is not known whether the flight ability of gravid females is similar to that of experimentally weighted females. Further, although weighted females did not reduce their feeding to a greater extent than clipped females, the P -value for this difference was close to 0.05 and we do not feel able to reject an alternative explanation for the difference in male responses.

Suggestions for future work

Biparental care is an excellent model system with which to investigate conflict and cooperation between two unrelated individuals. First, it is a common behaviour at least in certain group of animals, and it is easy to measure in the field. Second, the outcome of the parental interactions – offspring – is a Darwinian measure of fitness. Third, it is one of the few aspects of life-histories and ecology that has been frequently manipulated in the field in various ecological settings.

However, a potential problem with interpreting the data of parental care manipulations is that it is difficult to gain a consistent measure of ‘compensation’. A parent may compensate for reduced partner effort in terms of maintaining overall food delivery levels, but in strict terms full compensation may only be said to occur if there is no detrimental effect on the chicks. We could not determine reliably the effects on the chicks in the vast majority of cases used in our data set. Further, most studies measured only feeding rates, without taking into account the quality or quantity of food delivered (see Table S1). A widowed parent may face a trade-off between foraging and remaining close enough to the nest to defend it from predators, and this trade-off could affect the quality of food delivered to the brood (Weatherhead, 1979; Sasvári, 1986; Aho *et al.*, 1997; but see also Lifjeld & Slagsvold, 1988). A trade-off between feeding and brooding is also expected (e.g. Wolf *et al.*, 1990). Perhaps incubation or brooding behaviour may provide a more unambiguous care variable in future studies.

Future work should also address the effects of brood size, brood age and time in the breeding season. All of these are predicted to affect the trade-off between current and future reproductive success, and therefore the cost : benefit ratio of compensating for reduced partner effort. Although a few experiments and theoretical models have addressed these factors (Emlen & Oring, 1977; Greenlaw & Post, 1985; Sasvári, 1986; Wolf *et al.*, 1990, 1991; Wright & Cuthill, 1990; Whittingham, 1994; Markman *et al.*, 1995; Barta *et al.*, 2002; Webb *et al.*, 2002; Emlen & Wrege, 2004), data availability prevented us from including these variables in our analyses. More experimental work on male responses and precocial (nonpasserine) species could also prove valuable, given that the majority of experiments we found were from altricial birds, especially on passerines.

Experiments that effectively ‘titrate’ the amount of care provided by one parent would be significant improvement over studies that simply apply a fixed handicap. What is the response of the female if the male’s care is reduced to, say, 75%, 50% or 25% of his normal level? Also, with regard to the possible existence of negotiation, experiments where individuals are alternately handicapped and relieved would reveal whether their partners can track changes in effort and alter their

care patterns repeatedly. Certainly birds can dynamically alter provisioning in response to experimental changes in brood size (Wright & Cuthill, 1990), but do they respond similarly to changes in partner behaviour? Paredes *et al.* (2005) provide preliminary results pertinent to this area. Thick-billed murres (*Uria lomvia*) equipped with data loggers decreased chick provisioning and their partners responded by increasing their own provisioning rate (Table S1). However, when the data loggers were removed and the target birds’ provisioning levels returned to normal, their partners continued provisioning rates at elevated rates.

Comparison with other animal taxa

A limited number of published studies have investigated the effects of partner removal in cichlid fish (Raadik *et al.*, 1990; Itzkowitz *et al.*, 2001) and beetles (Robertson, 1998; Hunt & Simmons, 2002; Rauter & Moore, 2004; Smiseth *et al.*, 2005; Jenkins *et al.*, 2000; Suzuki & Nagano, 2009). Some of these studies addressed the behavioural response of the widowed or unmanipulated parent: in five cases data on both behavioural responses and some measure of total care or brood success were presented, allowing us to make provisional conclusions about compensation. In two species of burying beetle (*Nicrophorus* spp.), females showed no change in care behaviour following male removal, whereas widowed males showed partial compensation (Rauter & Moore, 2004; Smiseth *et al.*, 2004). These results may be due to the females already working at maximum capacity, as males contributed relatively little to larval care in control pairs. Hunt & Simmons (2002) also report partial compensation by widowed female dung beetles (*Onthophagus taurus*). However, in a third *Nicrophorus* species, Suzuki & Nagano (2009) report partial compensation by males but not females in response to partner removal. These authors also provided the first investigation of responses to partner handicapping in insects: neither sex increased care when its partner reduced care behaviours as a result of weighting. In the one mammalian study that allowed us to make inferences about compensation, female California mice (*Peromyscus californicus*) did not compensate for mate removal, and so raised fewer pups than did pairs (Cantoni & Brown, 1997).

An increased focus on experimental manipulations of parental care responses in nonavian species would be valuable. Targeted experimental studies that report data on behavioural responses and total care received by the offspring – in such a manner as to allow the calculation of effect sizes – could in time allow a broader and more informative meta-analysis. This could be complemented by phylogenetic comparative studies that seek to determine the ecological or life-history correlates of changes in parental care types (for examples in birds, see Bennett & Owens, 2002; Olson *et al.*, 2008). Clades with significant variation in the relative contribution of the sexes to care,

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Supporting information

Additional supporting information may be found in the online version of this article:

Table S1 Data used in meta-analysis: (A) removal studies; (A) manipulation studies.

Appendix S1 Details the data set used in the meta-analysis, separated into mate (A) removal studies and (B) manipulation studies.

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