Negotiation over offspring care?—a positive response to partner-provisioning rate in great tits

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Game theoretical models of biparental care predict that a change in work rate by one parent should be met by incomplete compensation by its partner. However, in empirical studies on biparental birds, there has been some inconsistency in the direction and extent of the response, and the mechanism behind it has so far been unclear. Parents could be responding directly to partner work rate or indirectly via chick begging. In this study of great tits (*Parus major*), the work rate of one parent was increased experimentally by augmenting the begging of the chicks with playback of extra begging calls whenever the parent visited the nest. The playback had no effect on the chicks' begging behavior, so any change in the focal parent's behavior was a direct response to its partner's work rate over a short timescale. An experimental increase in care by either male or female parent led to an increase (to a lesser extent) in the work rate of its partner, which is counter to the decrease predicted by partial compensation models. This seemingly paradoxical result may reflect decisions made exclusively over a short timescale and is in keeping with new theoretical work, which takes into account the information content of partner work rates. *Key words:* begging, great tit, matching, parental care, partial compensation, playback, provisioning rate. *[Behav Ecol 17:6–12 (2006)]*

In species with biparental care, the amount of parental investment that each partner should provide is a major source of conflict between provisioning parents (Trivers, 1972). This sexual conflict arises because each parent will benefit from an investment in its offspring but pays a cost of providing that care in terms of reduced survival or fecundity (Clutton-Brock, 1991; Lessells, 1999; Maynard Smith, 1977). Thus, each parent will benefit if the other does more of the work (see Westneat and Sargent, 1996).

It might therefore benefit parents to adjust provisioning in relation to partner work rate, as well as to the hunger levels of their offspring (see Godfray, 1991; Kilner and Johnstone, 1997), and both theoretical and empirical work has investigated this. Houston and Davies (1985) developed a model by Chase (1980) and demonstrated that for biparental care to be stable, parents should partially compensate for a change in partner care. A parent should only partially redress a shortfall in care by its mate because compensating fully would leave it open to exploitation. Conversely, the model predicts that if one parent increases its work rate, the other should decrease by a lesser extent. In this model, each parent's optimal level of investment is fixed over evolutionary time and is now referred to as a "sealed bids" model because partners cannot respond directly to each other in real time. McNamara et al. (1999) took this further and produced a "negotiation model" which not only allows but predicts that it should be beneficial for each parent to adjust its care directly in response to its partner. Both types of model predict that there should be partial or incomplete compensation for a change in partner work rate.

The majority of experiments testing partial compensation models have used a variety of handicapping techniques to decrease the provisioning rate of one partner. Examples are feather cutting (Lifjeld and Slagsvold, 1990; Moreno et al., 1999; Sanz et al., 2000; Slagsvold, 1988; Slagsvold and Lifjeld, 1990; Whittingham et al., 1994), tail weighting (Lozano and Lemon, 1996; Markman et al., 1995; Schwagmeyer et al., 2002;

Wright and Cuthill, 1989, 1990a,b), or testosterone manipulations (Hegner and Wingfield, 1987; Hunt et al., 1999; Ketterson et al., 1992; Saino and Moller, 1995; Stoehr and Hill, 2000). Increased testosterone generally results in a decrease in male provisioning and full or over compensation by the female, presumably due to the increased attractiveness of her mate (e.g., Ketterson et al., 1992), and further discussion here will refer only to direct manipulation of partner care for example, handicapping experiments. Successful handicapping of one parent has resulted in no decrease in partner effort (Lifjeld and Slagsvold, 1990; Lozano and Lemon, 1996; Schwagmeyer et al., 2002; Slagsvold, 1988; Whittingham et al., 1994), partial compensation (as predicted) (Markman et al., 1995; Wright and Cuthill, 1989), or full compensation (Sanz et al., 2000; Wright and Cuthill, 1990a,b).

The discrepancy between tests of partial compensation models could be due to a variety of factors. The first is that in long-term manipulations (e.g., partner weighted a day or more before observations of response), the begging level of the chicks is very likely to increase, due to an increase in need, and parents are expected to increase their provisioning rate in response to this (Burford et al., 1998; Kilner et al., 1999; Ottoson et al., 1997). Begging has been proposed as the mechanism by which partial compensation takes place (Wright and Dingemanse, 1999), although how this works in practice is unclear. Nevertheless, a response to begging is likely to interact with other factors affecting negotiation.

The second is that all weighting and feather cutting experiments are likely to change the perception of partner quality. Differential allocation theory (Burley, 1988; Petrie et al., 1999; Sheldon, 2000) suggests that parents should invest less in the offspring of partners in poor condition, so parents are expected to compensate less for a shortfall in a handicapped partner's work rate than is normally expected. A study of yellow warblers (*Dendroica petechia*) showed that when males were handicapped with tail weights, they significantly decreased provisioning rates, but surprisingly there was a trend for their partners to also decrease provisioning levels (Lozano and Lemon, 1996). The lack of compensation in females could be due to the fact that, although the chicks must have been hungrier, perceived male quality could well have decreased, making the chicks appear less worthy of investment.

Thirdly, a recent model suggests that response to partner work rate may be more complex than previously thought (Johnstone and Hinde, in press). This model incorporates parental uncertainty regarding brood need or value. When each parent has only partial information regarding the need (e.g., long-term need) or quality (e.g., genetic quality perhaps inherited from a partner) of the young, a change in effort by one parent may serve as a signal of brood need or quality, which would predict that its partner should "match" this change by increasing or decreasing its provisioning rate in the same direction. At the same time, the impact that an increase in provisioning has on the marginal value of the brood (perhaps signalled via a decrease in begging over a longer timescale) favors a compensatory response. Parents are expected to integrate these signals, and the relative strength of these two effects will determine whether the outcome is matching (change in the same direction) or compensation (change in the opposite direction).

A possible example of this is a study using tail weights in house sparrows (*Passer domesticus*), which showed that when females were weighted, there was a nonsignificant trend for them initially to decrease their provisioning rate and then to increase it (Schwagmeyer et al., 2002). In response, males also significantly increased provisioning, a result which is intriguing and counter to previous predictions.

An example of how these manipulations could produce a variety of results is that a decrease in provisioning by the handicapped parent would lead to an increase in chick begging, so partner-provisioning rate is expected to increase. However, the extent of this increase or whether it happens at all will be offset by the fact that both the "information" model (Johnstone and Hinde, in press) and differential allocation theory predict a decrease. Indeed, both experiments that have been performed early in the breeding season (before egg laying) and have handicapped a parent via feather cutting (both factors which are likely to negatively affect perception of partner quality) resulted in no response by the unmanipulated partner (Slagsvold and Lifjeld 1988, 1990). Additionally, the majority of handicapping studies have found no response by the unmanipulated partner (see above), and this may be due to an increase in begging (which would favor an increase in provisioning) being offset by a decrease in perceived partner quality (due to handicapping—favoring a decrease in provisioning) as well as chick quality (information model—favoring a decrease in provisioning).

The current study investigates whether, when responding to partner work rate, parents integrate signals of partner quality and information independently to that of chick hunger. To test this in great tits (*Parus major*), I kept chick hunger and apparent long-term partner quality constant by performing a short-term experiment, which manipulated partner work rate alone.

Partner contribution was increased by playback of extra begging calls to either males or females only when they visited the nest because it is known that parent birds respond to begging vocalizations in determining their provisioning rate (Burford et al., 1998; Kilner et al., 1999; Ottoson et al., 1997). This is an unobtrusive approach that does not involve manipulating perceived levels of parental quality in the long term. These short-term playback experiments had no effect on chick begging during control treatments (no playback) versus partner playback treatments (playback to partner only). Therefore, any change in provisioning by the focal parent must be in response to the increase in provisioning by its partner alone, and not due to any changes in its perceived quality, or to any changes in chick begging, which would be altered if the manipulation was carried out over a longer time period.

This short-term manipulation of partner work rates independently of chick begging allowed the following questions to be asked:

1. Is a response to a change in partner effort mediated indirectly through begging levels or through direct observation of partner work rates?
2. In what direction do parents respond to a change in partner effort? When a parent increases its provisioning rate, partial compensation negotiation models predict that its partner should decrease by a lesser extent. An information model predicts that a partner could increase its provisioning rate in response to this.

METHODS

Study site

Experiments were carried out in April and May 2002 in Burnt Farm Plantation and Short Nursery Plantation (which are adjoined and have grid reference TL 395 606) and Madingley Wood (TL 402 596), Cambridgeshire, UK. These woodlands comprise two areas of similar habitat (mixed deciduous woodland) 1 mile apart, covering an area of 23 ha. A total of 142 "woodcrete" nest-boxes (Schwegler brand type 2M) attracted 61 breeding pairs of great tits.

Nest monitoring and brood size manipulation

Nest-boxes were checked every 2 days during laying to ascertain clutch size and the onset of incubation. Disturbance was kept to a minimum during incubation, but nests were checked daily from 2 days before the predicted hatch date to determine hatching (day 0). On day 2, I swapped nestlings between broods to give standard brood sizes of seven, which is close to the average of 6.8 in this population (personal observation 2000–2001). This is within the natural range of 5–15 reported by Lack (1966) and the range of 3–12 found in this population (personal observation 2000–2002). Nestlings were swapped between broods as in Brinkhof et al. (1999) so that each brood contained seven nestlings from two donor broods of the same age (three from one and four from the other) and none of their own chicks. A total of 17 manipulated nests were included in the experiment.

Playback experiment

I set up a portable hide approximately 12 m from the nest on day 8 of the nestling period at which time a dummy speaker, camera, and microphone were positioned in the nest-box. These were replaced with working equipment before the experiment on day 9. I concealed a miniature loud speaker (adapted from a small RS 250-687 speaker, as described by Davies et al., 1998) between the side of the nest and the inside wall of the nest-box, at the same height as the chicks. Additionally, a miniature camera (adapted from an infrared security camera with wide-angle lens, Maplins) and microphone (Sony Electret Condenser Microphone ECM-T6) were concealed inside the conical dome at the top of the nest-box (attached with magnets to a metal plate glued at the top of the nest-box) and pointed directly down into the nest. The cables ran down to the ground through a groove in the side of the box front and connected to a video recorder (Sony Handycam DCR-TRV310E) and tape recorder (Sony Professional Walkman WM-D6C) in the hide.

I made playback tapes by recording the calls of four chicks during three parental visits on day 9. These begging calls were recorded onto the computer and spliced together using the software package Canary version 1.2.1 (Charif et al., 1995) to

create 15 s of begging sound, which was recorded continuously onto audiotape. All recordings were made on day 9, most at nests not used in the experiment and the remainder after playback trials were completed. Tapes were not used at the nest at which they were made, and a different recording was used for each parent.

I began playback experiments 30–60 min after setting up the working equipment, when parents were visiting the nest regularly and showed no signs of hesitation or alarm. Parental-provisioning rates were manipulated by playing the begging calls of four extra chicks through the speaker in the nest to imitate the call rate of a large brood of 11. Each treatment lasted for 1 h, during which time I played back chick begging recordings to one partner only at each of its visits while the chicks in the nest were begging (observed via the nest camera), and there was a pause of at least half an hour between each one. Each pair received three experimental "playback" treatments: playback to female only, playback to male only, and no playback (control), the order of which was rotated between nests and time of day (morning or afternoon). This meant that for each focal bird, provisioning rate could be assessed during no playback, playback to its partner, and playback to the focal bird (itself).

Male and female great tits are easily distinguished because a male's breast stripe is wider than a female's and continues to the base of the tail. Before the hour-long playback treatments began, the partner designated to receive playback of the extra begging calls received playback over three successive visits. With all playbacks, care was taken to ensure that the undesignated bird did not hear the playback. Chick begging was only audible from very near the woodcrete nest-box. The begging calls were not played if the undesignated bird was inside or in the vicinity of the nest-box (approximately 5 m radius). This happened in less than 10% of visits because parents foraged in the canopy further away. The time of each nest visit was noted during the experiment.

Data collection from videotape

The videos allowed me to double-check parental-provisioning rates and the sex of the focal parent (male great tits have noticeably shinier crowns on black and white infrared video) for the 17 experimental nests during each of the three playback treatments. I also collected data on begging levels and prey size, which were available for all three playback treatments for 15 nests (views of chicks in two nests were obstructed by nest lining or adults). Six male and six female visits were selected from each treatment to be as evenly spaced over the hour as possible, and all begging and prey-size data were collected from these visits. These 12 visits per hour are almost half the average of 31 visits per hour during control treatments, so is a representative sample. Begging scores (gape, posture, call rate, and volume) for each nest were repeatable within a treatment. Repeatability was calculated as in Lessells and Boag (1987) and was between $F = r = .42$ and .79. All tapes were analyzed blind as to the treatment that had been received.

Sound analysis

Begging call rate and volume were recorded to check whether the begging levels each parent heard were similar during control treatments and playback to partner and higher when playback was directed at the focal bird. Recordings were made on audiotape during all three playback treatments for 13 nests for which audio recordings were available. After the experiment was completed, a "beeper" of a known standard volume (107.3 dB) was activated next to the chicks (19 cm from the

microphone) and recorded onto the audiotape. This allowed calibration of call volume during begging call analysis because all recordings used a standard recording level on each day.

For each of the three playback treatments, begging levels during the six evenly spaced parental visits that were selected for video analysis were transferred onto a computer (sample rate of 44,100 Hz, 16-bit precision) using Canary version 1.2.1 (Charif et al., 1995). The first 5 s of begging at any visit were analyzed because this is typical of the fastest nest visit (average nest visit, females = 9.7 SE ± 3.3 s, males = 8.8 SE ± 2.8 s). The recordings were all input at the same level of gain (1.3). The beeper that had been recorded after the observations at each nest enabled begging calls to be calibrated to a standard volume. A sonogram was generated for each begging bout to obtain a frequency profile of the vocalizations.

From the sonograms, the amplitude (dB) of begging calls was determined for each 5-s period. I also counted call rate, which was defined as the number of peaks visible in each period. Statistical tests were performed on the mean begging call rate and amplitude heard by each parent during each playback treatment.

Begging posture and number of gapes displayed

Begging posture was scored 0–3 for each chick during six male and six female visits per hour. Posture levels were recorded at the point at which the parent first leaned over the nest to feed a chick. Posture was defined as 0 = no gaping, 1 = gaping with neck bent, 2 = gaping with neck outstretched, and 3 = gaping with body raised. The total number of gapes on display was also counted at this time. Statistics were performed on the average posture and number of gapes seen by each parent during each hour-long experimental treatment.

Prey size

Prey size was scored for the same 12 visits for which begging posture and call were scored. The video was paused when the adult beak was approximately parallel to the plane of the camera lens (as seen from above), and the length and breadth of the prey item and the adult beak (width at widest point) were measured from the video in millimeters. Great tits almost always bring one item per visit, but on the rare occasion that more than one item was delivered, the total area of prey was measured. To control for varying distance to the camera, the area of the prey item (length × width) was expressed as a proportion of the adult beak area (1/2 base width × length). Due to the fact that females have slightly longer beaks than males (mean female beak length = 13.60 mm, mean male beak length = 13.36 mm, taken from 668 measurements in Wytham Wood, Oxford; Gosler, 1987), each measure of female beak length was multiplied by 13.36/13.60 before the proportional prey size was calculated. Statistics were performed on the average prey size proportional to beak size (from here on referred to as prey size) delivered by each parent during each hour-long experimental treatment.

Statistics

The effects of playback treatments on provisioning rate, begging levels, and prey size were analyzed in SPSS 11.0 using a repeated-measures ANOVA. Sex and playback treatment were within-subject factors for each nest. Provisioning rate was log transformed, and consequently all data met normality and equality of variances assumptions. Bonferroni post hoc comparisons were used to investigate differences between groups. An analysis of covariance (ANCOVA) was used to investigate whether focal birds increased their provisioning rate in

response to begging calls directed at their partners or their partners' increase in provisioning levels. The focal parent's increase in provisioning during playback to the partner (increase from control levels) was the dependent variable, and its partner's response to playback and the number of playbacks directed to its partner were the independent variables. Sex and nest were included as between-subject factors. In a similar way, the possibility for a change in begging within treatments was investigated using a repeated-measures ANCOVA, and an ANCOVA was used to test for an order effect of treatment as described in the text.

RESULTS

How does an increase in partner effort affect provisioning?

Provisioning adults responded significantly to both the playback of chick begging calls and the provisioning rate of the other parent. A repeated-measures ANOVA with provisioning rate for each playback treatment (control, playback to partner, playback to focal bird) as repeated measures within sex at each nest showed that playback treatment had a significant effect on provisioning rate (Table 1, Figure 1). Bonferroni post hoc tests revealed that parental-provisioning rate increased significantly between control treatments and playback to the focal bird ($p < .001$), which shows that parents responded positively to the playback of begging calls. Provisioning rate also increased between control treatments and playback to the partner ($p = .001$), which suggests that parents are responding positively to the increased work rate of their partners. Additionally, provisioning rates were significantly greater when playback was directed to the focal parent than when it was directed to its partner ($p = .039$, Figure 1). Figure 2 shows the increase in provisioning rate during playback and playback to partner for males and females separately, although

Table 1
Repeated-measures ANOVA showing the effect of within-subject (per nest) factors sex and playback treatment on provisioning rate

Provisioning rate	df	F	p
Playback treatment	2	22.34	<.001
Sex	1	2.78	.11
Sex × playback treatment	2	0.19	.83

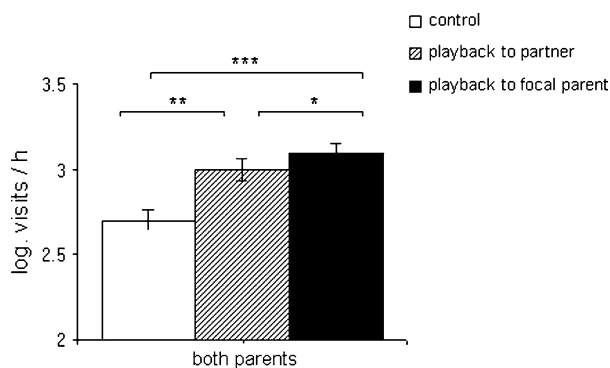$N = 102$ (34 adults at 17 nests, with three playback treatments at each nest).

Figure 1
Provisioning rate of parents during control, playback to partner, and playback to focal parent. ***$p < .001$, **$p < .01$, *$p < .05$. $N = 34$ adults at 17 nests, with three playback treatments at each nest. Error bars represent SEs of the mean.
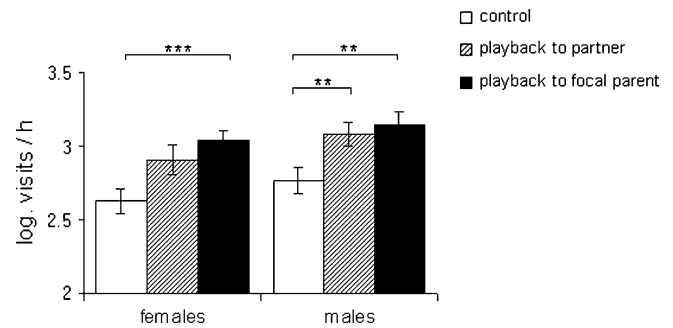

Figure 2
Provisioning rate of female and male adults during control, playback to partner, and playback to focal parent. There was no significant difference between male and female provisioning rates or response to treatments. ***$p < .001$, **$p < .01$, *$p < .05$. $N = 34$ adults at 17 nests, with three playback treatments at each nest. Error bars represent SEs of the mean.

the nonsignificant interaction between sex and playback treatment shows that males and females did not respond significantly differently (Table 1).

Response to change in partner-provisioning rate during playback to partner

The above analysis shows the difference between the overall levels of male and female provisioning rates among the three experimental treatments. A further analysis (ANCOVA, Table 2) showed that the observed response of focal birds (increase from control levels) was related to their partners' (who were exposed to playback) change in provisioning levels as intended, independently of the unlikely possibility that begging calls were overheard by the partners of birds receiving playback treatment.

The increase from control levels of the focal bird during playback to its partner was positively related to the increase in provisioning rate by its partner (relative to control levels), suggesting that focal parents increase their provisioning rate in response to a short-term increase by their partners. Focal birds appear not to be responding to the number of playbacks directed to their partners (similar to partners' total provisioning rate), although there was a nonsignificant trend for a positive effect. If this were significant, it would suggest that focal birds could hear the playback directed to their partners, but

Table 2
ANCOVA with response during playback to partner as the dependent variable (difference between provisioning rate during control and partner playback treatments)

Response during partner playback	df	F	p
Constant	1	4.69	.04
Partner's response to playback	1	13.63	.001
Number of playbacks to partner	1	2.47	.13
Sex	1	0.71	.41
Nest	16	0.73	.73
Partner's response to playback × number of playbacks to partner		1.61	.21

Independent variables are the partner's response to playback (difference between partners' provisioning rates during control and playback treatments) and the number of playbacks directed to the partner. Sex and nest were between-subject factors.
$N = 34$ adults at 17 nests.

Table 3

Repeated-measures ANOVA with playback treatment and sex as within-subjects factors

	Playback treatment						Sex		Playback treatment	
	Males			Females						
	Control	Playback to partner	Playback to focal parent	Control	Playback to partner	Playback to focal parent	F	p	F	p
(a) Call rate per 5 s	131.49 ± 10.53	137.82 ± 11.77	164.89 ± 13.25	136.88 ± 10.92	138.18 ± 10.32	166.95 ± 15.17	2.42	.15	33.76	<.001
(b) Amplitude (dB)	102.81 ± 1.04	102.28 ± 1.06	102.55 ± 0.99	102.48 ± 1.00	102.66 ± 0.90	102.70 ± 0.92	0.07	.79	0.21	.81
(c) Number of gapes	4.91 ± 0.26	4.67 ± 0.26	4.71 ± 0.25	4.76 ± 0.34	4.58 ± 0.31	4.81 ± 0.24	0.18	.68	0.62	.54
(d) Posture score	1.60 ± 0.18	1.50 ± 0.15	1.40 ± 0.18	1.52 ± 0.19	1.36 ± 0.18	1.55 ± 0.16	0.29	.60	1.41	.26
(e) Prey size	2.92 ± 0.28	2.44 ± 0.30	2.65 ± 0.27	2.16 ± 0.16	2.41 ± 0.18	2.40 ± 0.23	6.50	.03	0.13	.88

±SE values are shown.

a and b, $n = 13$ nests, and c–e, $n = 15$ nests, with three playback treatments at each nest.

even if this were the case the independent effect of a response to partner provisioning is what is of interest here.

Colinearity diagnostics suggest that although the independent variables in this analysis are correlated (Pearson's $r = .52$, $p = .004$), this is not sufficient to bias the results (tolerance = 0.73, variance inflation factor = 1.37) (Field, 2000).

Effect of playback on begging and prey size delivered

Between treatments
Begging call rate and volume were analyzed to check whether the begging levels that the parents heard were the same during control and playback to partners and higher during focal parent treatments (due to additional begging calls from the playback tape). Playback treatment (no playback [control], playback to partner, focal parent playback) significantly affected call rate (Table 3) because as intended, call rate increased between control and focal parent treatments (Bonferroni post hoc analysis, $p < .001$). Additionally, as intended there was a significant difference between partner playback and focal parent playback treatments ($p < .001$) because call rate was faster during focal parent treatments. Importantly, call rate did not change between control and partner playback treatments ($p = 1.00$). Confidence intervals were generated for the difference in call rate between these treatments in order to investigate the robustness of this null result (95% confidence interval = −15.02, 7.38, mean call rate = 136.09, mean effect size = −3.82). It is difficult to prove the null hypothesis because the confidence intervals are fairly large with respect to the mean call rate (Colegrave and Ruxton, 2003). However, accepting the null hypothesis would always be problematic when there is so much between-nest variations in call rate.

As intended, playback treatment did not significantly affect the average begging call amplitude, the number of gapes on display, the average posture level of the brood, or the average prey size delivered (Table 3). Chicks did not posture or gape to males and females differently, although males brought significantly larger prey than did females.

Within treatments
Chick begging levels did not change over time during any of the treatments. It was important to check for this because if the experiment had been conducted over a longer time period, chicks could have eventually become satiated during either playback treatment or alternatively sibling competition could have escalated begging during partner playback treatments. I therefore compared the average of the first and last

three begging scores for gape (Figure 3a) or posture (Figure 3b) variables. A repeated-measures ANOVA with playback treatment and time during hour (start or end) as within-subject factors showed that there was no difference in gaping ($F_{2,14} = 2.04$, $p = .17$) or posturing ($F_{2,14} = 0.28$, $p = .61$) between the average of the first and last three visits within each hour. Interestingly, there was a trend for a decrease in both variables, especially gaping, over the hour during partner playback treatment, which could be due to chicks getting slightly satiated during playback treatments. Even if this had affected the results, it would be expected to result in
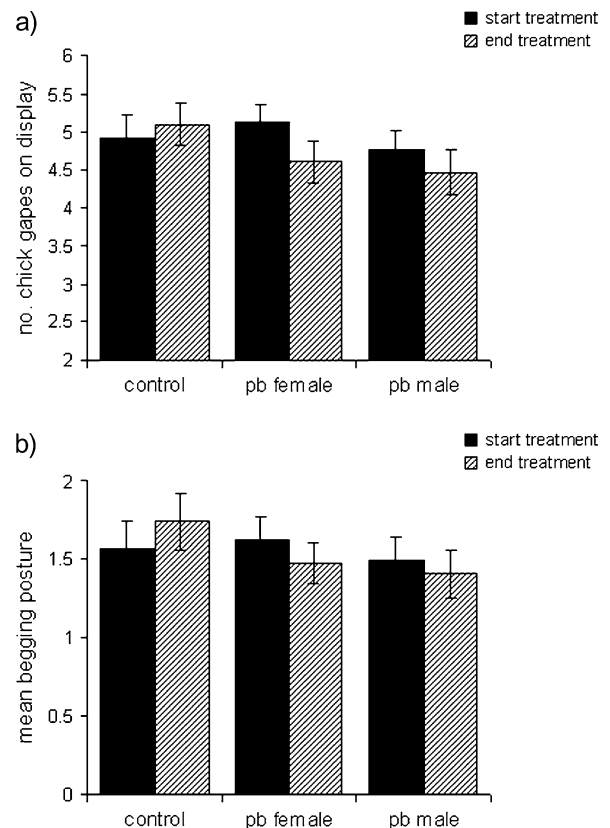

Figure 3
Mean ± SE values for the first and last three measures of number of (a) gapes on display and (b) begging posture in each hour. $N = 17$ nests.

a reduction in response to the increase in partner work rate rather than the observed increase.

Order of playback treatments

A final analysis showed that there was no order effect of experimental treatment on parental-provisioning rate. An order effect was unlikely, because order of the playback treatments was rotated, there was a period of at least half an hour between playback treatments, and there was no difference in begging levels between or within treatments. However, it is important to check for this because it is possible that provisioning rates could be lower in control treatments recorded after a playback treatment in which the chicks were satiated. I entered the order of playback treatments (coded 1–6) or the position of control treatment in that order (coded 1–3) as a between-subjects factor into the analysis reported in Table 1. When entered separately as factors, there was no main effect of order ($F_{5,11} = 0.54$, $p = .75$) or the position of control treatment in the order of treatments ($F_{2,14} = 2.43$, $p = .13$). Importantly, neither variable affected the significance levels of the main or post hoc analyses. There were also no interactions between either order variable and sex or playback ($p > .29$).

DISCUSSION

Both male and female parents increased provisioning significantly during begging playback, and there was no significant difference in the magnitude of their response (Table 1, Figure 2). Contrary to the predictions of partial compensation models, both sexes increased provisioning significantly when their partners increased provisioning in response to playback (Figures 1 and 2). This positive increase in provisioning rate during playback to the partner was not due to any detectable changes in chick begging levels between control and partner playback treatments (Table 3). Furthermore, the response to partner work rate was shown statistically to be due to the effect one parent had on the other as intended and not to begging calls being overheard by the partners of birds receiving playback treatment (Table 2). Provisioning great tits therefore appear to respond to partner work rates directly rather than through the begging display. The fact that parents responded positively to an increase in partner provisioning will be referred to as "matching" changes in partner work rate.

Differences between the current study and previous experiments

Other studies of biparental birds which have decreased partner-provisioning rate have reported results ranging from no response to full compensation, but none have found a matching result as does the present study. This could be due to three main ways in which differences in experimental design could affect the outcome. The first is that partner-provisioning rate was increased rather than decreased in the present study. This is not expected to influence whether compensation or matching occurs because compensation models predict that a decrease in effort by one partner should be met by an increase by the other and vice versa.

The second difference is that all handicapping experiments have been performed over a long timescale (days to weeks), so a change in provisioning would have been likely to affect begging levels. Begging is expected to have increased as provisioning decreased, and indeed this has been proposed as the mechanism by which partial compensation operates (Wright and Dingemanse, 1999). This is an important process but may not be the only one operating and could mask other short-term responses. The present study is performed over a short

timescale to observe responses to partner-provisioning rate independently of changes in chick begging. There is no prediction in the literature as to the timescale parents should use when responding to a change in partner work rate. However, there is no reason why it should not be instantaneous because adults appear to always be aware of each others' whereabouts—sometimes they forage together, sometimes calling to each other from near the box, and always coordinating their visits in such a way that they never collide—even when entering the box at great speed, up to 40 times each in an hour.

A third factor, which may differ between the present and previous studies, is perceived partner quality. If a parent appears to be in bad condition due to the manipulation (e.g., cut feathers) or the result of it (lower provisioning rate), both differential allocation theory and the information model (Johnstone and Hinde, in press; see Introduction) predict that its partner would be less likely to compensate for a shortfall in provisioning. This could explain why many studies have found no response to a decrease in partner care despite the probable increase in begging levels (see Introduction) or why parents may be likely to match a change in their partners' provisioning level.

Why do parents match their provisioning behavior?

Benefits of short-term coordination

Matching of parental nest-provisioning rates could have occurred because there is a benefit to partners coordinating in the short term. For example, the risk of predation to adults while foraging may make it beneficial for foraging adults to be in close proximity to each other. Additionally, parents could match partner provisioning because a consistent, alternating pattern of attendance benefits chicks—either because it increases potential nest defense or because of some benefit of regular food delivery (Montgomerie and Weatherhead, 1988; Redondo, 1989). Although very few studies have investigated specific patterns of food delivery (but see Rands et al., 2003), coordination between parents has been found in some studies of seabirds, for example little shearwaters (*Puffinus assimilis*), which often have very long feeding trips (Booth et al., 2000). Therefore, matching partner-provisioning levels could have been due to partners tending to forage together or alternate their feeding patterns rather than an increase in response to a partner's increase being adaptive in itself. If this is the case, the way in which parents work together and the strategies they use (i.e., coordination of provisioning) are interesting and understudied factors, which may well contribute to reproductive success.

Adaptive benefits of assessing partner care

A solution as to why parents may exhibit matching behavior is outlined in a game theoretical model (see Introduction), which incorporates parental uncertainty regarding brood need or value (Johnstone and Hinde, in press). Each parent has only partial information regarding these qualities, and a greater investment by one could serve as a signal of brood need or inherent quality to the other, which predicts a matching response. These predictions are in agreement with the experimental evidence presented here because the independent effects of begging calls and partner work rate on provisioning levels were demonstrated. Indeed, matching may only be observed over a short timescale as seen here because changes in begging over a longer timescale are expected to mask such a response.

To sum up, this study suggests that great tits respond to an increase in partner provisioning directly, independently of chick begging. Parents responded to increased partner provisioning by increasing their provisioning rate, even though no difference in chick begging levels could be detected. These

results are not anticipated by models of partial compensation but are consistent with a more recent model that incorporates a benefit to responding to partner information of brood need or value (Johnstone and Hinde, in press). This could be due to an adaptive response to partner work rates due to uncertainty regarding brood need or quality. The challenge for future work will be to investigate how these seemingly contrary predictions can be integrated and whether this can account for the variation found both within and between species.

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