Original Article

Reciprocity and conditional cooperation between great tit parents

Rufus A. Johnstone,[a] Andrea Manica,[a] Annette L. Fayet,[a] Mary Caswell Stoddard,[a] Miguel A. Rodriguez-Gironés,[b] and Camilla A. Hinde[a]

[a]Department of Zoology, University of Cambridge, Downing Street, Cambridge CB2 3EJ, UK and [b]Estación Experimental de Zonas Áridas, CSIC, Ctra. de Sacramento S/N, La Cañada de San Urbano, 04120 Almeria, Spain

When individuals invest in a common good, an efficient outcome is hard to achieve, because each can free ride on others' efforts. This problem can lead parents that raise their young together to reduce their investment in care, with negative consequences for offspring. Here, we present a mathematical model to show that a strategy of conditional cooperation, in which parents take turns feeding their young, can help to resolve this problem. To test this idea, we studied the behavior of great tit parents raising chicks together. We found that parents alternated visits to the nest more than would be expected by chance, speeding up their feeding rate after their partner had visited the chicks, but slowing down again once they had visited in turn. This effect was not mediated by visit-to-visit changes in offspring begging intensity, although females (but not males) were influenced by mean begging levels across broods. We conclude that conflict over parental investment in this species is partly ameliorated by a simple form of reciprocity.

Key words: **cooperation, family conflict, negotiation, parental care, reciprocity.**

INTRODUCTION

Joint investment in a common good is hard to maintain, because one individual can free ride on others' efforts (Hardin 1968; Rankin et al. 2007). Parents rearing young together, for instance, face an evolutionary conflict of interest, because each benefits from joint investment in the offspring, but pays a cost of providing that care in terms of reduced survival or fecundity (Trivers 1972; Lessells 1999). Because each parent stands to gain if the other does more of the work, models predict that they should reduce their effort below the most efficient level that would maximize their total fitness payoff (Houston and Davies 1985; Westneat and Sargent 1996; McNamara et al. 1999, 2003; Houston et al. 2005; Lessells and McNamara 2012). Experimental studies have confirmed this

prediction, showing that offspring raised by 2 adults together can suffer as a result of conflict between their parents (Royle et al. 2002, 2004, 2006).

The classical model of conflict over biparental care, developed by Houston and Davies (1985), assumed that levels of investment by males and females were genetically determined and changed only over an evolutionary timescale (a "sealed bid" analysis). More recent models have allowed for the fact that parents can adjust their own levels of investment in response to their partner's on a behavioral timescale (McNamara et al. 1999, 2003; Johnstone and Hinde 2006; Johnstone 2011; Lessells 2012; Lessells and McNamara 2012). Such flexibility can modify the precise outcome of parental interaction but, in existing analyses, does not seem to alter the conclusion that conflict leads to a reduction of investment below the most efficient level (McNamara et al. 1999, 2003; Johnstone and Hinde 2006; Johnstone 2011; Lessells 2012; Lessells and McNamara 2012). However, behavioral negotiation over investment opens up the possibility of conditional strategies that might serve to promote a more efficient outcome. When humans contribute to public goods, for instance, experimental studies have found that conditional cooperation—a tendency to contribute more when others do so too—can help to support more efficient levels of investment (Keser and van Winden 2000; Fischbacher et al. 2001; Frey and Meier 2004; Gächter 2007). Although evidence for similar forms of reciprocity in animals is sparse, perhaps due

to cognitive limitations such as temporal discounting and limited memory (Wilkinson 1984; Stevens and Hauser 2004; Stevens et al. 2005; West et al. 2007; Krams et al. 2008; Clutton-Brock 2009; Schino and Aureli 2009; Cheney et al. 2010), our goal in this article is to argue that a simple form of conditional cooperation may play a role in ameliorating the conflict between mates over parental investment.

Below, we first extend Houston and Davies classical model to allow for turn taking by parents feeding their young and show that this simple form of reciprocity can in principle maintain efficient investment levels. We then attempt to test this idea using data on pairs of great tits raising young together. The purpose of the great tit analysis is 2-fold—both to provide some empirical support for the possibility of alternation and to demonstrate the utility of continuous time Markov models as a means of detecting and quantifying imperfect turn taking (see also Harcourt et al. 2010).

A Simple Model of Conditional Care

In Houston and Davies' (1985) influential model of biparental care, 2 parents each decide, independently and in ignorance of the other's behavior, how much effort they will invest in offspring care. Fitness gained through the current brood of young increases with total investment, but with diminishing returns, whereas future fitness for each parent decreases with its own level of investment, with accelerating costs. Formally, the fitness payoff to a parent (of either sex) who invests x, paired with a partner who invests x', is given by

$$w(x, x') = f(x + x') + g(x)$$

where $f' > 0$ and f'', g', $g'' < 0$; the evolutionarily stable level of investment x^* (which we assume is >0) satisfies the condition

$$\left.\frac{\partial w(x, x')}{\partial x}\right|_{x = x' = x^*} = f'(2x^*) + g'(x^*) = 0$$

This stable level of investment x^* is less than the mutually most profitable level of investment $\hat{x}$ that maximizes the total fitness payoff to both parents. The latter satisfies the condition

$$\left.\frac{\partial w(x, x)}{\partial x}\right|_{x = \hat{x}} = 2f'(2\hat{x}) + g'(\hat{x}) = 0$$

whereas we can see that

$$\left.\frac{\partial w(x, x)}{\partial x}\right|_{x = x^*} = 2f'(2x^*) + g'(x^*) >$$
$$\left.\frac{\partial w(x, x')}{\partial x}\right|_{x = x' = x^*} = f'(2x^*) + g'(x^*) = 0$$

implying that if both parents were simultaneously to increase their level of investment above the evolutionarily stable value, they would both enjoy greater payoffs.

Suppose, however, that investment in care takes the form of repeated visits to the nest to feed the young and that each parent can monitor the other's behavior. If a parent visits randomly at rate λ when its partner was the last to visit the young, and at rate μ when it was itself the last to visit the young, what are the evolutionarily stable values of λ and μ? If we assume that individual investment in the young reflects a parent's own mean visit rate, whereas total parental investment reflects the mean combined visit rate of both parents, then the fitness payoff to an individual who adopts the rule (λ, μ), paired with a partner who adopts the rule (λ', μ'), is given by

$$w(\lambda, \mu, \lambda', \mu') = f\left(\frac{\lambda\mu + 2\lambda\lambda' + \lambda'\mu'}{\lambda + \lambda'}\right) + g\left(\frac{\lambda(\mu + \lambda')}{\lambda + \lambda'}\right)$$

The proportion of time during which the focal individual was the last to visit is equal to $\lambda/(\lambda + \lambda')$, during which time the focal visits at rate μ; the rest of the time, the focal visits at rate λ, giving an average visit rate for the focal equal to the argument of $g()$. An analogous expression can be derived for the average visit rate of the partner simply by exchanging primes, and the sum of these expressions, that is, the total visit rate by both parents, gives the argument of $f()$.

For simplicity, we restrict our attention to rules for which $\lambda > 0$, because those for which $\lambda = 0$ lead to the breakdown of biparental care, with a visit to the young by one parent triggering complete cessation of provisioning by the other. Any evolutionarily stable rule (λ^*, μ^*) must satisfy the condition

$$w(\lambda^*, \mu^*, \lambda^*, \mu^*) \geq w(\lambda, \mu, \lambda^*, \mu^*) \text{ for all } \lambda, \mu \geq 0,$$

implying that it represents a best response to an opponent playing that same rule (i.e., it must be a Nash equilibrium of the care game). This yields 2 possible solutions for which $\lambda > 0$ (see Supplementary Material): first, a rule that leads parents to ignore one another's behavior and invest the same level of effort as in the original Houston–Davies model, so that $\lambda = \mu = x^*$; second, an "alternating" rule, for which $\lambda > 0$ and $\mu = 0$, implying that after feeding the young once, a parent will not do so again until its partner has visited the nest, which leads to alternating visits. The first rule is, however, evolutionarily unstable. Moreover, under a simple adaptive dynamic in which the rate of evolutionary change in either parameter of the feeding rule is proportional to the slope of mutant fitness with respect to that parameter (evaluated at the population value), the first rule is also convergently unstable, whereas the alternating rule is both evolutionarily and convergently stable (see Supplementary Material).

Focusing on the alternating outcome, the stable rule $(\lambda^*, 0)$ must satisfy

$$\left.\frac{\partial w(\lambda^m, 0, \lambda^*, 0)}{\partial \lambda^m}\right|_{\lambda^m = \lambda^*} = \frac{1}{4}(2f'(\lambda^*) + g'(\lambda^*/2)) = 0$$

and leads to an outcome at which each parent works at a rate $x = \lambda^*/2$. From this, it follows that

$$2f'(2x) + g'(x) = 0$$

and hence that $x = \hat{x}$. Alternation thus supports an efficient outcome at which the parents both work at the optimal rate that maximizes their total joint fitness payoff, by contrast with the inefficient outcome of the original Houston–Davies model. Intuitively, turn taking promotes greater investment because it ensures that an increase in one parent's visit rate leads to a concomitant increase in the other's visit rate, providing greater incentives to work harder.

EXPERIMENTAL METHODS

To test the idea that alternation might help to ameliorate conflict between parents over care, we observed pairs of great tits provisioning their young during May 2009 in Madingley Woodlands, Cambridgeshire. Data were collected at 21 nests from a nest-box population at Burnt Farm Plantation and the adjoining Short Nursery

Plantation (latitude = 52.23°, longitude = 0.04°), and Madingley Wood (latitude = 52.22°, longitude = 0.05°), Cambridgeshire. Nests were visited every 2 days until incubation commenced, in order to determine clutch size, and were visited daily from the day before hatching was predicted, in order to determine hatching date. As part of another experiment, chicks were swapped between nests on day 1 (hatching = day 0) of chick rearing so that nests contained chicks from 2 other nests and none of their own. Experimental brood size (BS) was unrelated to original clutch size (CS) (linear regression, CS = 8.10, ±SE = 0.28, BS = 7.71, ±SE = 0.25, $F = 0.004$, $P = 0.95$). Observations were made via a nest-box camera with infrared illumination that was positioned inside the nest-box the day before recording took place. Recordings were made for 2.5 h on both day 9 and day 10 of chick rearing with an Archos AV500 portable hard drive recorder. Only the last 2 h of each recording period was used to minimize the effects of human disturbance on behavior. Male and female visit times were determined from nest recordings. Begging posture was also scored from recordings on a 4-point scale for each chick at the moment when provisioning took place, yielding a mean intensity for the brood (Hinde 2006).

RESULTS

Parents showed a significant tendency to take turns visiting the nest. Using a runs test to detect alternation, 20 out of 21 pairs had a positive score, 14 of which were significant (binomial test against the expectation of false positives at a rate of 0.05: $P < 0.001$), although they did not maintain strict alternation (proportion of alternated visits 71.8 ± 1.2%; see Figure 1A). Males and females visited at similar rates (14.9 ± 1.1 vs. 15.8 ± 1.7 visits per hour, paired $t_{20} = -0.61$, $P = 0.546$; see Figure 1A) and also showed similar tendencies to alternate (proportion of alternated visits 71.6 ± 1.6% vs. 72.1 ± 1.8%; paired t on arcsine square-root transformed data: $t_{20} = -0.22$, $P = 0.825$; see Figure 1B).

To better study how parents respond to each other, we modeled feeding visits as a continuous time Markov process (see Supplementary Material). A parental pair was characterized as switching between 2 possible states, distinguished by which parent had last visited the nest. Female parents were assumed to visit randomly at rate λ_f when their partner was the last to visit the young and at rate μ_f when they themselves were the last to visit the young,

with the corresponding rate parameters for males denoted λ_m and μ_m. The maximum likelihood estimates of these rate parameters can thus provide a precise description of the typical behavior of both sexes and the way in which they respond to one another's movements (Harcourt et al. 2009, 2010). We also considered covariates that might influence visit rates, including brood size and mean begging intensity of the young at a parent's most recent visit to the nest.

There was no difference between the sexes in their baseline visit rates, yielding a best-fit model in which $\lambda_f = \lambda_m = \lambda$ and $\mu_f = \mu_m = \mu$ (comparing with a model in which $\lambda_f \neq \lambda_m$, and $\mu_f \neq \mu_m$, $\chi_2^2 = 3.6$, $P = 0.166$; see Figure 2A). However, both sexes showed a significant tendency to speed up their rate of return to the nest after a visit by their partner (best estimate and 95% confidence interval [CI] from 1000 bootstraps of $\lambda/\mu = 1.34$ [1.24–1.46]; comparing a model in which $\lambda = \mu$, with a model in which $\lambda \neq \mu$, $\chi_1^2 = 46.7$, $P < 0.001$; see Figure 2A), explaining the tendency to alternate described above.

The Markov model assumes that visits occur randomly in any given state; that this represents a reasonable approximation is confirmed by comparison of the mean and standard deviation (SD) of intervisit intervals, which yields a ratio that does not deviate from the value of one expected under a random model, in which intervals follow an exponential distribution (median and interquartile range of mean/SD across pair states = 1.01 [0.87–1.24]; H_0: median = 1; Wilcoxon $V = 2086$; $P = 0.120$). However, inspection of the distribution of intervisit intervals for individual parents (see Supplementary Figure S2) reveals that the frequency of intervals does drop off rapidly below about 40 s, presumably because parents cannot return to the nest immediately after visiting, but must take some time to locate another food item first. Such a refractory period would tend to promote some degree of alternation, even if parents did not respond to one another's visits. However, a randomization test confirms that this effect is much too weak to account for the alternation we observe.

For each pair during each 2-h observation period, we randomized the sequence of intervisit intervals of each parent and then combined the 2 time series to generate a new data set of visits by both parents. In this way, we preserve the observed distribution of intervals (including the refractory period) while removing any coordination between parents. We repeated the randomization
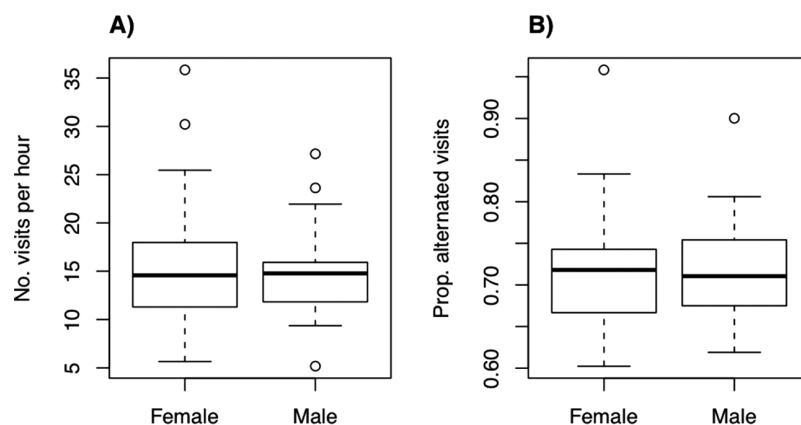

Figure 1
Parental feeding rates. (A) Number of visits to the nest per hour to feed the young by female and by male parents. (B) Proportion of visits to the nest by female and by male parents that follow a visit by the focal parent's partner.
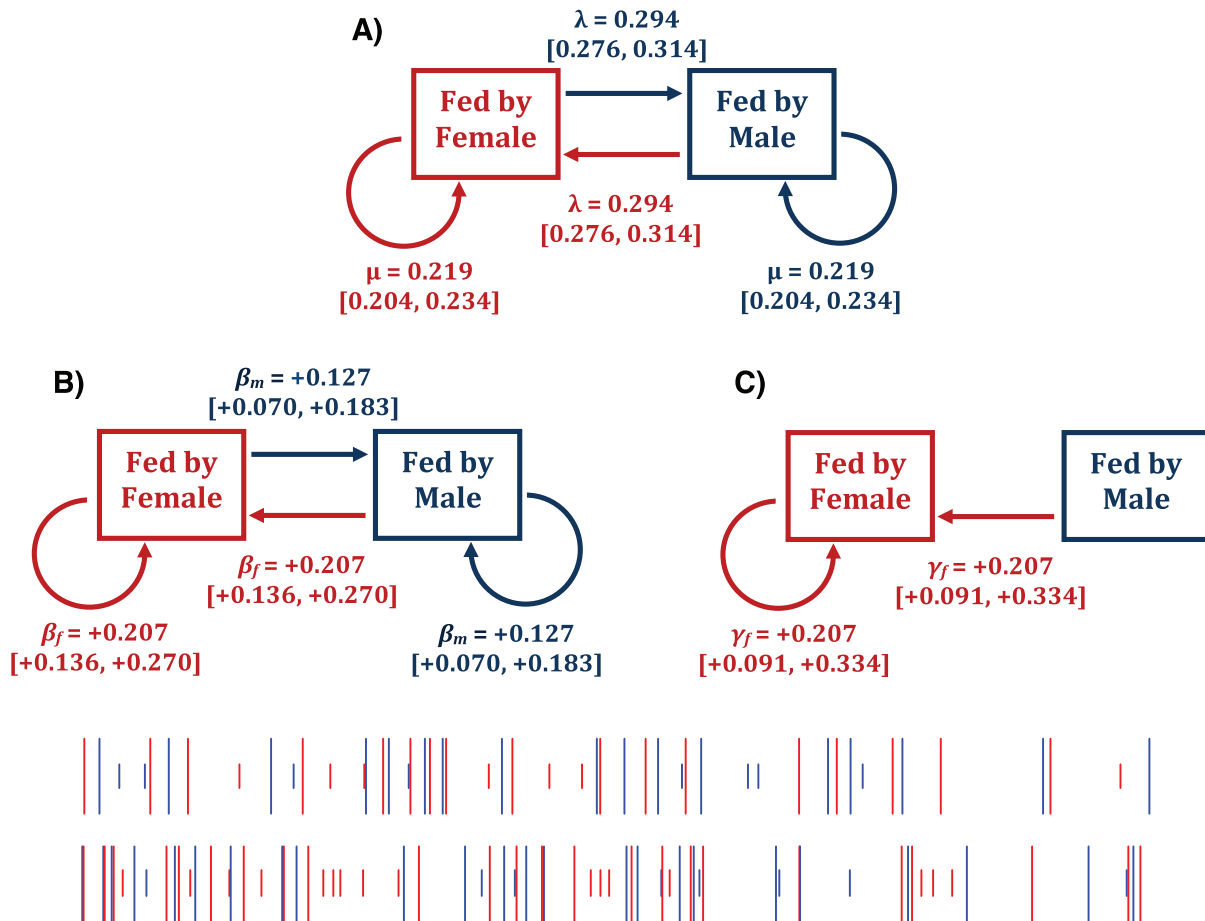
Figure 2
Parental feeding rules. We modeled feeding visits as a continuous time Markov process. A parental pair was characterized as switching between 2 possible states, distinguished by which parent had last visited the nest. Female parents were assumed to visit randomly at rate λ_f when their partner was the last to visit the young and at rate μ_f when they themselves were the last to visit the young, with the corresponding rate parameters for males denoted λ_m and μ_m. We also considered covariates that might influence visit rates, including brood size and mean begging intensity of the young at a parent's most recent visit to the nest. (A) Maximum likelihood estimates (and 95% CI) for the visit rate parameters; note that the best-fit model features no difference in baseline visit rates between the sexes, so that $\lambda_f = \lambda_m = \lambda$ and $\mu_f = \mu_m = \mu$. (B) Best estimates (and 95% CI) for effects of brood size on all visit rate parameters; note that effects in the best-fit model are independent of which parent visited last, but differ between the sexes, and are denoted β_f for females and β_m for males. (C) Best estimate (and 95% CI) for effects of begging intensity on female visit rate parameters; these are once again independent of which parent visited last and are denoted by γ_f (the nonsignificant effects of begging intensity on male visit rate parameters are not shown). Illustrative time series of parental feeding visits for 2 different pairs are shown below the Markov models; time runs from left to right and each vertical bar represents a feeding visit, with female visits colored red and male visits blue, and alternated (as opposed to repeat visits) represented by longer (as opposed to shorter) bars.

1000 times and fitted a Markov Chain model to each. In these randomized data sets, we failed to find any significant difference in visit rate depending on which parent visited the offspring last (mean of $\lambda/\mu = 1.06$, 95% CI = 0.99–1.13), with even the most extreme randomized data set still giving a λ/μ ratio (1.19) well below the value observed in the original data set (1.34); similarly, in the randomized data sets, both parents' tendencies to alternate were no greater than expected by chance, by contrast with the significantly higher levels observed in the original data set (proportion of alternated visits for females: 49.6%, CI = 48.8–51.3%, in the randomized data sets, vs. observed 71.6%; for males, 53.2%, CI = 51.4–55.0%, in the randomized data sets, vs. observed 72.1%; see Figure 3). We thus conclude that parents show a tendency to alternate that is significantly greater than expected by chance and that cannot be attributed merely to the constraints on very short intervisit intervals, implying that they actively track and respond to one another's visits.

Brood size was the most important covariate ($\chi_2^2 = 76.9$, $P < 0.001$) in the Markov model and had a positive effect on all rate parameters; in other words, parents with larger broods returned to the nest faster than parents with smaller broods (see Figure 2B). This effect was independent of which parent was the last to visit the young (no difference between the effect on repeat vs. alternated visits: $\chi_2^2 = 4.3$, $P = 0.115$), but females responded more strongly than males ($\chi_1^2 = 4.1$, $P = 0.043$).

Females also responded to more intense begging by increasing their visit rates ($\chi_1^2 = 12.3$, $P < 0.001$; see Figure 2C), with no significant difference in this effect depending on which parent last visited ($\chi_1^2 = < 0.1$, $P = 0.858$), but males showed no detectable response to begging ($\chi_2^2 = 3.2$, $P = 0.207$). It should be noted that mean begging intensity of a brood varied relatively little from visit to visit, with 97% of variance in begging intensity being explained
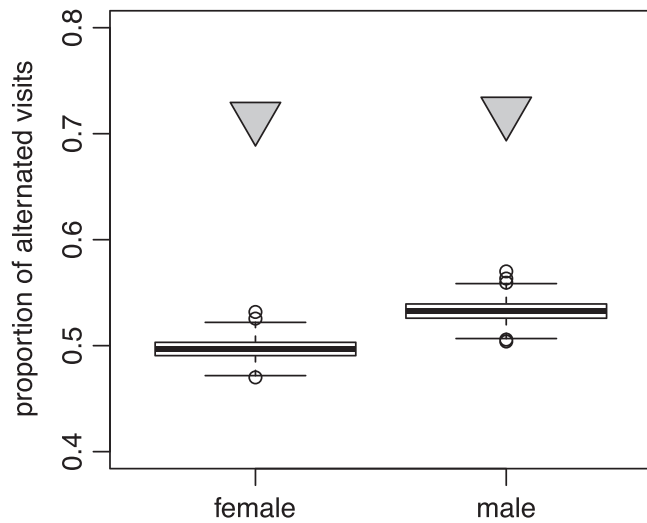
Figure 3

Comparison of the observed proportion of alternated visits with the level expected due to chance. The frequency of intervisit intervals drops off rapidly below about 40 s, and this refractory period would tend to promote some degree of alternation, even if parents did not respond to one another's visits. The graph shows the results of a randomization test confirming that this effect is much too weak to explain the alternation we see. Triangles represent the observed proportion of alternated visits, and boxplots represent the distribution of proportions of alternated visits from 1000 randomizations in which we preserved the observed distribution of intervals (including the refractory period) while removing any coordination between parents (see text for details).

by differences between nests rather than between visits within the same nest. Indeed, if we split begging intensity at each visit into 2 components—1) the overall mean for a given nest and 2) the deviation from the nest mean at that particular visit—and then substitute these 2 components into the model, we recover an effect of begging on female visit rates from the nest means ($\chi^2_1 = 6.6$, $P = 0.010$) but not from the deviations ($\chi^2_2 = 0.9$, $P = 0.646$). It thus appears that the tendency to alternate is not mediated by short-term changes in chick begging. In addition, although parents kept track of who made the last visit to the young, there was no evidence that their memory extended to earlier visits; a model with 4 states, distinguished by which parent attended the young at the previous visit, and at the visit before that, gave no improvement in fit over the simpler 2-state model ($\chi^2_2 = 2.4$, $P = 0.124$).

DISCUSSION

Existing models of behavioral negotiation over parental investment have adopted 1 of 2 approaches. First, McNamara et al. (1999) developed a modeling framework in which parents take turns choosing their levels of investment each in response to the other's most recent choice, with payoffs dependent only on the stable outcome to which this process eventually settles down. This approach allows one to predict not only equilibrium levels of investment but also how responsive individual parents (and possibly other helpers) should be to variation in the costs and benefits of care and to the behavior of others (see also McNamara et al. 2003; Johnstone and Hinde 2006; Johnstone 2011). However, it does not explicitly predict the dynamics of investment over an extended period of care.

More recently, Lessells and McNamara (2012) have developed a dynamic model of biparental investment over a finite period of care, in which parents choose their levels of investment in each of a series of time steps in response to the current state of the offspring, which reflects the history of investment by both parents until that point. Despite the difference in approach, both types of model predict that negotiation leads to a less efficient outcome than would be obtained in a sealed bid game. By contrast, our theoretical analysis above suggests that negotiation can lead to a more efficient, alternating outcome, ameliorating rather than exacerbating the costs of sexual conflict. Why do we obtain such contrasting results?

First, we allow for more complex strategies than did previous models. In particular, we allow (as previous models have not) for strategies that respond to relative levels of past investment by the focal parent and its partner, which facilitates turn-taking equilibria. Second, we assume that parents adjust their level of investment in care by changing their rate of return to the nest. This leads to an efficient outcome at a turn-taking equilibrium because strict alternation of visits ensures that any change in one parent's visit rate entails an equal change in the other's visit rate. We expand on both of these points below.

In the negotiation models deriving from McNamara et al. (1999), and in our analysis, parental strategies take the form of a rule specifying some choice of investment level (amount of food delivered, or rate of return to the nest) as a function of immediately preceding choices. A key difference between the two, however, lies in the information on which parents can base their decision. In McNamara et al. (1999), investment levels are chosen depending on the other parent's last choice. In our analysis, by contrast, visit rates are chosen depending on which parent last visited the young, an outcome that reflects both its partner's and its own previous choice of visit rate. This facilitates alternation because a strategy may specify a higher level of investment when the partner appears to have invested more than the focal individual in the previous step (i.e., when the partner returned sooner) and a lower level of investment when the partner appears to have invested less than the focal individual (i.e., when the focal returned sooner). By contrast, in McNamara et al. (1999), a parent can respond only to its partner's last choice and must ignore its own previous level of investment. If parents in the negotiation game could respond to both their partner's and their own previous choice, this would permit a rule that specified high investment when the focal parent invested less in the last round, and low investment when the focal parent invested more, giving rise to alternation. Such strategies are ruled out, however, by the limitation that parents must ignore their own previous behavior.

The model of Lessells and McNamara (2012), while introducing greater realism in the form of explicit dynamics of investment, also rules out turn taking of the kind we consider because it assumes that parents base their choices on the current state of the young. This reflects the total level of previous investment by both parents, but not their relative contributions. Once again, therefore, parents in this model cannot choose to invest more if they previously invested less than their partner, or less if they previously invested more, as they do in our alternating equilibrium. We suggest, therefore, that our model predicts a more efficient outcome of negotiation than did previous analyses in part because it allows for more complex strategies that respond to relative levels of past investment by the focal parent and its partner. Whether such complex strategies are, in fact, plausible is a point to which we return below.

The second feature that distinguishes our analysis from previous models of negotiation is our assumption that parents adjust their level of investment in care by changing their rate of return to the nest. At an equilibrium that features strict turn taking, the average visit rates of both parents are perforce identical. Consequently, any change in the visit rate of one parent (when it is the focal's turn to feed the young) entails an equal change in the visit rate of its partner. This is why selection favors efficient levels of investment at our alternating equilibrium—because there is no opportunity for one parent to unilaterally reduce its own visit rate and free ride on the other's efforts. Alternation can be seen as a form of reciprocity or "tit for tat" in which, having fed the offspring once, a parent "refuses" to feed again until its partner has done so, thus enforcing equal work rates. If, by contrast, parents were able to adjust their level of investment by changing the amount of food delivered at each visit, alternation would not necessarily ensure a perfectly efficient outcome. Even if parents take turns visiting the young, one individual could unilaterally reduce the amount of food given to the offspring at each of its own visits, without necessarily inducing any change in the other's rate of food delivery. In reality, there is likely to be variation in both visit rates and load size (Royama 1966; Kacelnik 1984; Wright et al. 1998), so we might expect turn taking to eliminate some but not all of the costs of parental conflict.

What of our empirical results? Previous studies have shown that parents of many bird species respond to more prolonged changes in partner work rate with a compensatory (Wright and Cuthill 1989; Harrison et al. 2009) or, more rarely, a matching change (Hinde 2006) in their own visit rate. In addition, begging has been shown to influence the visit rates of both females and males, although in several cases, females are the more responsive sex (Kölliker et al. 2000; Kilner 2002). On a shorter timescale, there is evidence in some cases of synchronized nest visits (Raihani et al. 2010; Mariette and Griffith 2012). Relatively little attention, however, has been devoted to the possibility of reciprocity and conditional cooperation at the level of alternating visits, which is compatible with both compensatory and matching responses to longer term changes in partner work rate (though see Hunt and Simmons 2002 for a nonavian example). Our data suggest, however, that great tit parents do attend to one another's visits and do display a significant tendency to take turns feeding their young. This pattern cannot simply be attributed to parents' inability to return to the nest with food twice in quick succession, because a randomization test shows that the effect of this refractory period is much too weak to explain the frequency of alternation we observe. Moreover, the turn taking does not seem to be mediated by parental responses to offspring begging, because the begging intensity of broods varies very little from visit to visit within the same nest, and what little variation there is does not help to predict visit rates.

Although we did observe a significant tendency for parents to take turns, we did not see the strict alternation predicted by our theoretical model. At a strict turn-taking equilibrium, the parent who last fed the young should cease further feeding until its partner has taken a turn. The great tit parents in our study, by contrast, merely reduced their rate of visiting the nest by approximately 25% while waiting for their partner to take a turn. This led to a frequency of alternation (approximately 72%) that was greater than one would otherwise expect by chance, but less than 100%. How can we account for the discrepancy between our theoretical predictions and the data? One likely explanation is that parents cannot monitor each other's behavior with complete reliability, as we assumed in our theoretical model. When there is a chance that parents may overlook one another's visits, they cannot afford to cease feeding completely while waiting for their partner to take a turn. If one parent has not noticed the other's visit, both will be left expecting their partner to provide the next feed, and a strict turn-taking strategy would lead to the chicks starving. Incorporating a possibility of error into the model may lead to a more plausible equilibrium, similar to the observed behavior of the great tits, at which parents reduce their visit rate when it is not their turn, but do not cease feeding entirely. Allowing for error, we would not expect the perfectly efficient outcome predicted by our error-free model. Rather, imperfect turn taking may be expected to reduce, but not entirely to eliminate, the costs of conflict between parents.

Regardless of the evolutionary explanation for the behavior we observe, our results highlight the value of continuous time Markov models such as we have used to analyze feeding behavior. If turn taking is not strict, but involves more subtle changes in feeding rate in response to visits by a focal parent and its partner, discrete Markov models that focus only on the sequence of visits rather than their timing have much less power to detect such effects (as they make use of less information). In our case, the changes in feeding rate were sufficiently great to yield a significant level of alternation even in a simple runs test, but the continuous time analysis is capable of identifying a significant (though weak) tendency to alternate even when this is not the case.

Although reciprocity is common in humans, evidence for it in animals is sparse and in some cases contentious (Wilkinson 1984; Stevens and Hauser 2004; Stevens et al. 2005; West et al. 2007; Krams et al. 2008; Clutton-Brock 2009; Schino and Aureli 2009; Cheney et al. 2010). One possible explanation is that it poses substantial cognitive challenges, including the problem of remembering past interactions with multiple partners, the difficulty of quantifying benefits offered and received, and the propensity in animals to discount delayed rewards (Stephens et al. 2002, 2005; West et al. 2007). In the case of biparental care, however, individuals need only attend to the behavior of a single partner. Moreover, to adopt a simple turn-taking strategy of the kind we have considered, they need only track who made the last visit to the young, and they need only retain this information for the typically short interval between visits. Our empirical results imply that this is not beyond the capacity of great tit parents and suggest that biparental care in birds may provide a good context in which to look for simple forms of reciprocity.

SUPPLEMENTARY MATERIAL

Supplementary material can be found at http://www.beheco.oxfordjournals.org/

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