

Evidence for conditional cooperation in biparental care systems? A comment on Johnstone et al.

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Introduction

In species with biparental care, the joint benefit from care provided by each parent makes it possible to free ride on the partner's investment, introducing parental conflict over care. How this conflict is evolutionarily resolved (and by which behavioral mechanism) has been subject of much research, both theoretically and empirically. In a recent paper, Johnstone et al. (2014, hereafter J&al) propose a novel solution to this conflict: "conditional cooperation", a strategy where individuals reduce their feeding rate when they were the last parent to feed and increase their feeding rate following a feed by their partner. Based on a game theoretic model, J&al argue that such a strategy generates an efficient solution of the conflict over care, which is immune to exploitation, because it enforces reciprocal adjustment of feeding behavior between partners.

To put their model to an empirical test J&al analyze parental nest visit data from a great tit (*Parus major*) population. They implement a continuous-time Markov model (CTMM) and deduce that a conditional cooperation strategy occurs in this species. Here, we argue that fundamental assumptions of their model are violated in many biologically relevant settings. We suggest that alternative processes should be considered, and illustrate a mechanism that can explain the visit patterns without implying conditional cooperation.

The CTMM used by J&al assumes that at any instant, the feeding dynamics are determined by parental visit rates that can only change when a feeding event occurs and remain otherwise constant, unaffected by additional factors (Figure 1a). This assumption is violated (1) when the likelihood that an individual returns to the nest depends on the time it has been away from the nest (non-constant return rates), and (2) when confounding factors introduce additional dependencies in sequences of nest visits.

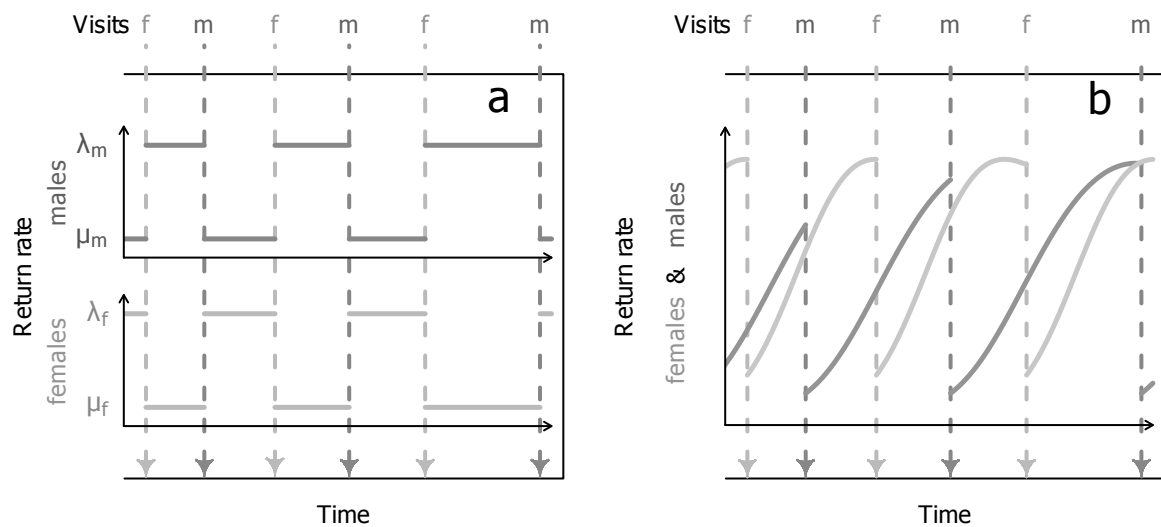


Figure 1: (a) Schematic diagram illustrating the process underlying the continuous-time Markov model. The return rate can only take on two values (λ or μ). It remains constant between visits, but switches between the two values, whenever one parent visits. The parent visiting last always exhibits its return rate λ , the other its return rate μ . Therefore the current return rate is conditional only on the identity of the parent visiting last and it does not depend on additional factors, such as weather. (b) Schematic diagram illustrating how non-constant return rates can introduce alternation. Because of its shorter absence duration the return rate of the parent visiting last has not yet increased, while the other parent already has a higher return rate. In both panels females (f) are shown in light gray, males (m) in dark gray.

Violations of the Markov Property 1: Non-Constant Return rates

Using the CTMM J&aI demonstrate that return rates show a higher value, λ , when the partner was last to visit and a lower value, μ , when the bird itself was last at the nest ($\mu < \lambda$). While this supports the conditional cooperation hypothesis in the framework of the CTMM where feeding effort is constant between visits (Figure 1a), the finding of lower return rates after an own visit than after the partner's visit can also arise in a range of other biologically realistic scenarios. J&aI acknowledge this by considering a "refractory period", because parents cannot (or do not) feed immediately after a visit (Figure S2 in J&aI). Then, the individual who has been away from the nest longest is more likely to return next (Figure 1b). Indeed, the great tit data show that – for both parents – the probability to return after a visit initially increases rapidly over time (Figure 2). Even in the absence of conditional cooperation, this will introduce some degree of alternation (Figure 1b) and the question is how that affects the result of $\mu < \lambda$ from the CTMM.

J&al address this issue by utilizing a randomization procedure. If the refractory period governs the visit patterns, the return rate depends only on the individual's identity and the time since its last visit, but not on the partner's behavior. Shuffling the inter-visit times of each individual should therefore not affect the underlying distribution. In their randomization, J&al inspect whether this is the case; individual inter-visit intervals are drawn at random from their original sequence – independently for the male and the female – to form a randomized sequence. Generating 1000 such sequences reveals that this model does not typically produce a difference between λ and μ comparable to that observed in the real data. Shuffling inter-visit times changes the statistical results significantly. Hence, the refractory period or, more generally, non-constant return rates, cannot drive the observed visit patterns. Having ruled out this possibility, J&al now conclude that conditional cooperation must indeed occur, even under divergence from the Markov property introduced by the duration of absence (for example the refractory period). We agree that this analysis excludes that visit patterns arise from a mechanism based solely on non-constant return rates. However, we argue that there are additional processes that, in combination with non-constant return rates, can lead to visit patterns that are not distinguishable from those that would arise under conditional cooperation. We show below how a biologically plausible modification of J&al's randomization procedure can produce values of λ/μ that are similar to those observed in the great tit data.

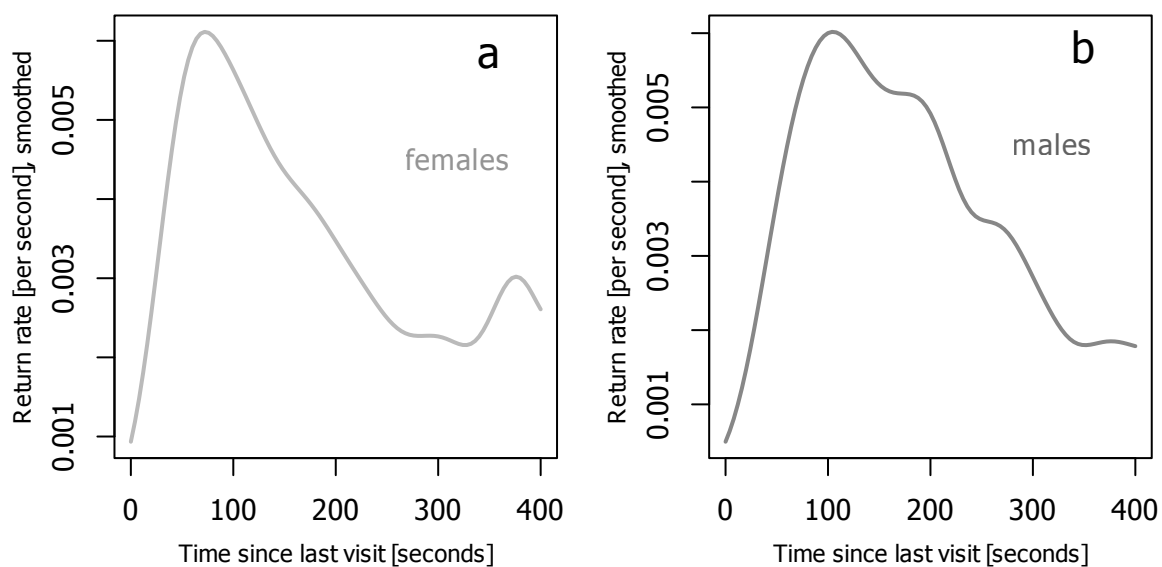


Figure 2: The relationship between the return rate and the time passed since the last visit for (a) female and (b) male great tits (see Supplementary Text S1 for details of the calculation). In violation

of the Markov property, the rate is clearly not constant. The peak at approximately 90 s suggests that birds have a tendency to return after a fixed time interval (which is much longer than the refractory period of approximately 40 s represented in Figure S2, J&al). This will always introduce some degree of alternation (see Figure 1b). We argue that J&al's treatment of this issue does not exclude the possibility that the observed alternation arises from non-constant return rates in combination with additional processes.

Violations of the Markov Property 2: Additional Dependencies

In the CTMM the current return rate depends only on the identity of the individual visiting last and is unrelated to the return rate from previous visits. In the framework of the CTMM, it is then correct to treat all visits in a sequence and all sequences identically. Accordingly, J&al's estimates for the return rates λ and μ are average values obtained by pooling events from all sequences. However, there are factors such as brood size, begging intensity, or weather conditions that influence multiple visit rates in a sequence. This introduces additional dependencies among visits, which, unless explicitly modeled, the CTMM cannot explain. J&al take into account two of these factors by including them as covariates: brood size and begging intensity. Assuming these are the only additional dependencies, this permits them to maintain the pooling approach. However, weather conditions, predator presence, and many other factors can also strongly influence multiple visit rates in a sequence. Whenever such additional dependencies among visits exist, the calculation based on average values no longer accurately reflects the feeding dynamics.

Alternative Randomizations

To verify that the divergence from the Markov property does not affect the result of the CTMM, J&al use a randomization procedure, in which individual inter-visit intervals are assembled at random (see above). This not only removes effects of conditional cooperation, but also potential effects of the additional dependencies discussed above. For example, inter-visit intervals typically become longer when weather conditions become less favorable. A complete randomization of the order of intervals removes this structure by making consecutive intervals less similar in length, thus reducing alternation (Figure 1b). In essence, J&al rule out one specific alternative process where an individual's identity and the duration of absence are the sole determinants of return rates. However, it is difficult to prove one process (conditional cooperation) by exclusion of alternatives. As soon as the assumption of the Markov property is relaxed, the influence of many biological processes may lead to the same relation of λ and μ as observed in the actual data. Here, we stay within the framework of J&al's randomization procedure, and demonstrate that making this procedure slightly more realistic affects the conclusions.

We modified the randomization procedure of J&al to allow for one additional dependency. We consider a situation where all parents show a tendency to increase the length of their inter-visit intervals over the course of a sequence (that is over a duration of on average 84 minutes, range: 5-118 minutes, see J&al supplementary data). Note that the same reasoning applies when all parents tend to increase their return rates or when some pairs show an increase while others show a decrease. To simulate this situation, we introduce a parameter p into the randomization procedure presented by J&al that allows us to control the tendency of shorter inter-visit intervals to appear before longer inter-visit intervals. p does not relate to any biological property, but is simply a means to obtain sequences sorted to varying degree. Specifically, p is the expected proportion of cases in which a shorter inter-visit interval appears after a longer one (considering all pairs of inter-visit intervals for a given individual) and varies from 0 (fully sorted) to 0.5 (completely random, equivalent to the randomization performed by J&al) to 1 (reverse order). To implement this, we reorder the fully sorted sequence ($p = 0$) according to permutations drawn from a distribution with the desired statistical properties (Supplementary Text S2). We repeat this 1000 times to estimate λ/μ . By varying p we can evaluate how the tendency for increased absence durations affects λ/μ (Figure 3). This shows that even when the tendency that individuals increase their time of absence is relatively weak ($p = 0.25$), the return rate after the partner's visit relative to the return rate after an own visit is still as high as observed by J&al. For a typical sequence of 20 visits, for example, a value of $p = 0.25$ means that the second of two consecutive inter-visit intervals will still be shorter than the first one in 44% of the cases (compared to 50% in the completely random situation, cf. Remark (1) in Supplementary Text S2). Such a scenario represents an alternative mechanism to explain the observed visit patterns in the great tit data, without conditional cooperation. Thus, the introduction of one simple and biologically reasonable process (tendency to increase or decrease return rates over a relatively short time period, e.g. due to changing weather conditions, presence of a predator close to the nest, temporal changes in food availability) can substantially bias return rates towards a pattern that resembles conditional cooperation.

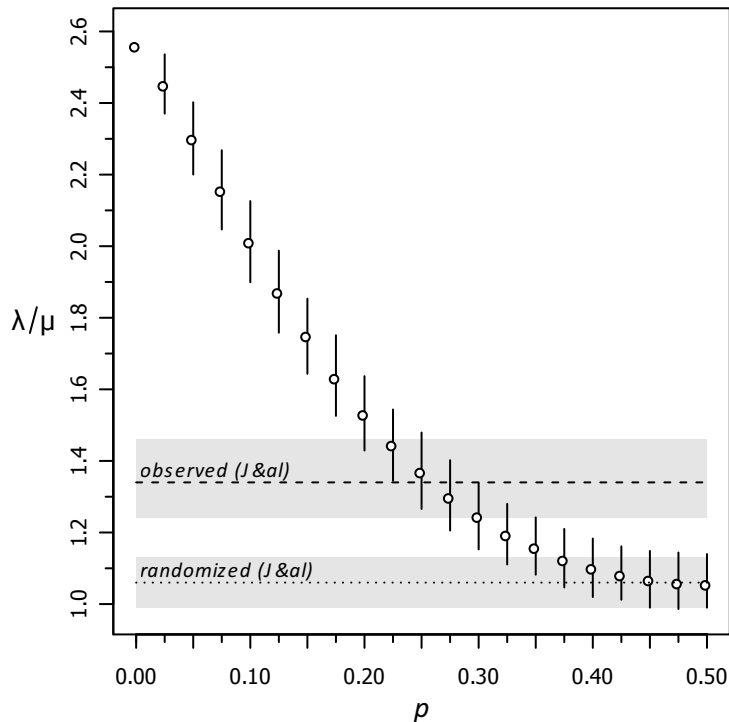


Figure 3: Influence of changing return rates over time on λ/μ . The parameter p controls the tendency for an increase in inter-visit intervals in a sequence of visits (strictly ordered: $p = 0$, completely random: $p = 0.5$; see Supplementary Text S2 for details). Points and bars show the mean and 95% prediction intervals obtained for λ/μ based on quotients of rate estimates in 1000 simulation runs. The dashed and dotted lines show the estimates calculated by J&aI for the original sequence observed in the great tits and for the randomized sequence, respectively. Gray shaded areas represent the 95% prediction intervals for these estimates. A value of λ/μ similar to that calculated by J&aI for the observed data ($\lambda/\mu = 1.34$, 95% CI: 1.24–1.46) can be obtained with $p = 0.25$ ($\eta = -0.243$), i.e. when the additional dependencies are already relatively weak.

Conclusions

J&aI have introduced an intriguing, new hypothesis of ‘conditional cooperation’ in the study of parental care. Using the continuous-time Markov approach, they achieve a neat mathematical structure that rests well in existing theory and show that the observed pattern of great tit nest visits is consistent with predictions of the conditional cooperation hypothesis. There is a clear merit to their analysis. Models in mathematical biology are often developed and presented in a purely theoretical setting, but J&aI go a step further and include an analysis of empirical data. However, by drawing heavily on the Markov property, their model is probably not valid in many biologically relevant settings. We have shown how an alternative randomization procedure that simulates non-independence of events and a non-constant return rate can easily lead to a visit pattern that

resembles conditional cooperation. Therefore, whilst the current analysis does not refute conditional cooperation, neither does it provide compelling evidence for its actual occurrence in nature. J&al's conclusion 'that conflict over parental investment in this species is partly ameliorated by a simple form of reciprocity' is overstating the results. J&al's paper is cited as demonstrating that conditional cooperation occurs in nature (Carter 2014; Savage 2014; Bebbington and Hatchwell 2015; Iserbyt et al. 2015; Mariette and Griffith 2015), an interpretation which we believe is unwarranted.

Given the variety of mechanisms that can cause individuals to have a higher return rate following a visit by their partner, it is necessary to consider many factors when testing observational data for the presence of conditional cooperation. This indeed makes it a very difficult task. We therefore advocate the implementation of experiments designed to test whether parents adjust their provisioning behavior to the provisioning behavior of their partner (e.g. Iserbyt et al. 2015). One possibility is to manipulate one parent to return faster to the nest (e.g. by playing back begging calls at a single visit, or by selectively providing food) and then examine whether the partner reduces its inter-visit interval. Meanwhile, we believe that statements about the occurrence of conditional cooperation in nature are premature.

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Supplementary Material

Text S1: Derivation of calculations used in Figure 1.

Text S2: Derivation of calculations used for randomization procedure as illustrated in Figure 2.

SUPPLEMENTARY MATERIAL

Supplementary Text S1: Derivation of Calculations used in Figure 1

The assumption in the Markov process studied by J&al is that the visit rates of an individual only change when a visit occurs and do not depend on the time that has passed since the individual was at the nest. To verify this, it is interesting to inspect the course of visit rates over time. We focus here on the time intervals starting at the last visit of the individual and ending at the consecutive visit (of the individual or its partner). These intervals are free of relationships with the current visit behavior of the partner.

We here consider male rates, the argument for female rates being the same. The rate for a male visit at time t is

$$\lim_{\Delta t \downarrow 0} \frac{1}{\Delta t} \Pr(\text{male visit in } [t, t + \Delta t) \mid \text{past in } [0, t)),$$

which can generally depend on the entire dynamics in the past before time t . The assumption by J&al is that this rate depends only on which parent visited last. In particular, the *average* rate for a male visit at t time units after a preceding male visit, assuming there were no intervening visits, should not depend on t .

The latter can be estimated from the data as

$$\lim_{\Delta t \downarrow 0} \frac{1}{\Delta t} \frac{\text{number of male visits followed by a male visit after a time in } [t, t + \Delta t)}{\text{number of male visits followed by a (male or female) visit after a time } \geq t}.$$

There are two mathematical difficulties, essentially due to the discrete nature of the data. First, there can be ties. These are resolved most easily by artificially imposing some temporal ordering, recognizing that the values are rounded anyway. Second, the limit above is always zero or infinity. In order to avoid a full mathematical treatment, we introduce a left-continuous weight function $\varphi(s)$ and consider an integrated (or smoothed) form of the expression above:

$$\begin{aligned} & \lim_{\Delta t \downarrow 0} \int_{-\infty}^{\infty} \frac{1}{\Delta t} \frac{\text{number of male visits followed by a male visit after a time in } [t+s, t+s+\Delta t)}{\text{number of male visits followed by a visit after a time } \geq t+s} \varphi(s) ds \\ &= \lim_{\Delta t \downarrow 0} \sum_{j=1}^k \frac{1}{\Delta t} \int_{t_j - t - \Delta t}^{t_j - t} \frac{\varphi(s)}{\text{number of male visits followed by a visit after a time } \geq t+s} ds \\ &= \sum_{j=1}^k \frac{\varphi(t_j - t)}{\text{number of male visits followed by a visit after a time } \geq t_j}, \end{aligned}$$

where t_1, \dots, t_k are the waiting times between successive male visits (with no intervening visits). The curve presented in Fig. 2b results when $\varphi(s)$ is chosen as a normal density for a mean of 0s and a standard deviation of 25s.

Supplementary Text S2: Derivation of Alternative Process and Calculations used in Figure 2

We reorder the fully sorted sequence of n inter-visit intervals of a parent according to permutations $x = (x_1, \dots, x_n)$ of $(1, \dots, n)$ that are drawn from a probability distribution for which the expected value of the number $T(x)$ of pairs $i < j$ with $x_i > x_j$ has the desired value $p \frac{n(n-1)}{2}$ with $0 < p < 1$. (Here $\frac{n(n-1)}{2}$ is the total number of pairs $i < j$.)

For the specific choice of this probability distribution, we follow a maximum entropy approach and choose the distribution that minimizes, among all probability distributions that satisfy the constraint given by p , the relative entropy (Kullback–Leibler information) with respect to the uniform distribution (for which each permutation has probability $1/n!$). It is well known from the theory of Gibbs measures and information theory (see, for example, Georgii 2003, Proposition 3.13) that probability distributions from an exponential family with a density (probability mass function) of the form $f(x) \propto e^{\eta T(x)}$, where η is a real number, are unique solutions of this minimization problem among all distributions with the same expected value $p \frac{n(n-1)}{2}$ of $T(x)$. Explicitly, writing $f(x) = \frac{1}{Z} e^{\eta T(x)}$, the relative entropy for a distribution with density $g(x)$ and $\sum_x g(x) T(x) = p \frac{n(n-1)}{2}$ is

$$\begin{aligned} \sum_x g(x) \ln \frac{g(x)}{1/n!} &= \sum_x f(x) \frac{g(x)}{f(x)} \left(\ln \frac{g(x)}{f(x)} - 1 \right) + \sum_x g(x) \left(\eta T(x) + \ln \frac{1}{Z/n!} + 1 \right) \\ &= \sum_x f(x) \int_1^{g(x)/f(x)} \ln s \, ds - 1 + \eta p \frac{n(n-1)}{2} + \ln \frac{1}{Z/n!} + 1, \end{aligned}$$

which is minimal if the integral is minimal for all x , that is, if we choose $g(x) = f(x)$ for all x .

A permutation x of $(1, \dots, n)$ can be generated by first generating a permutation y of the numbers $(1, \dots, n-1)$ and then inserting n at one of the possible positions $j = 1, \dots, n$ in this sequence, i. e. setting $x = (y_1, \dots, y_{j-1}, n, y_j, \dots, y_{n-1})$. Note that $T(x) = T(y) + n - j$, so the permutation is from the distribution with density $f(x) \propto e^{\eta T(x)} \propto e^{\eta T(y)} e^{-\eta j}$ if y and j are chosen independently according to densities proportional to $e^{-\eta T(y)}$ and $e^{-\eta j}$. In particular, the reduction to a shorter permutation allows for a simple iterative implementation of the simulation procedure. Moreover, since the expected value of $n - j$ is then $n - \sum_{j=1}^n j e^{-\eta j} / (e^{-\eta} + \dots + e^{-\eta n})$, we obtain, by iteration, for the expected value of $T(x)$ the expression

$$\sum_{i=1}^n i - \frac{e^{-\eta} + \dots + i e^{-\eta i}}{e^{-\eta} + \dots + e^{-\eta i}},$$

from which we can numerically determine η for any desired value of p . Note that this expression can be simplified to

$$\frac{n(n-1)}{2} + \frac{n}{1-e^\eta} - \frac{1}{1-e^\eta} \dots - \frac{n}{1-e^{\eta n}}$$

unless $\eta = 0$, as can be seen by using the equalities $(1 - e^\eta)(e^{-\eta} + \dots + e^{-\eta i}) = e^{-\eta i} - 1$ and $(1 - e^\eta)(e^{-\eta} + \dots + i e^{-\eta i}) = e^{-\eta i} - 1 - e^{-\eta} \dots - e^{-\eta i} + i e^{-\eta i}$.

Remarks. (1) The choice of the density implies that the probabilities for permutations with $x_i > x_{i+1}$ and for permutations with $x_i < x_{i+1}$ have a ratio of e^η for each $i = 1, \dots, n-1$. (2) $1 - 2p$ is the expected value of Kendall's τ statistic for the fully sorted and the permuted sequence.

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