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Response

Evidence for conditional cooperation: a response to Schlicht et al.

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Schlicht et al. (2016) question whether our study (Johnstone et al. 2014) provides compelling evidence for conditional cooperation between great tit parents, on the grounds that other processes might explain the alternating visit patterns we observed. Specifically, they consider a process in which both members of a pair tend to increase their visit rates over the course of a sequence (or, equivalently, in which both tend to decrease their visit rates). Schlicht et al. (2016) show that if this tendency is strong enough, it can lead to values of λ/μ that are similar to those observed in the great tit data, and thus account for the observed visit pattern without conditional cooperation. However, they do not consider whether the parental pairs in our study actually display correlated, directional trends in visit rate of this strength. Here, we show that they do not.

Schlicht et al. (2016) measure the tendency for visit rates to increase or decrease over a sequence using a "p-score," the proportion of all pairs of intervisit intervals for a given individual in which a shorter interval appears after a longer one. Using this approach, $p = 0.5$ represents no tendency for directional change, whereas $p = 0$ implies that successive intervisit intervals are strictly increasing in length, and $p = 1$ that they are strictly decreasing. To quantify the absolute strength of directional tendency in an individual's visit rate, regardless of the direction of the trend, we therefore calculate a modified value p' equal to $\mathrm{Min}\{p, 1 - p\}$; $p' = 0.5$ still corresponds to no directional change, but any tendency for intervisit intervals either to increase or to decrease now corresponds to a value of $p' < 0.5$ regardless of the direction of change. The distribution of these p' values for all birds across all sequences are plotted in Figure 1 (NB we exclude the 6 sequences out of a total of 51 that feature 3 or fewer intervisit intervals for a parent because very small sequences inevitably yield extreme p-scores). In their comment, Schlicht et al. (2016) invoke a value of $p = 0.25$ as sufficient to account for our results; but although

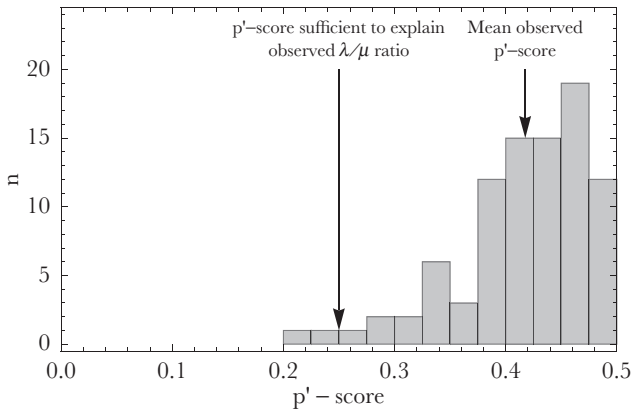

Figure 1
Distribution of observed p'-scores in our great tit data set ($p' = 0$ implies strictly increasing or strictly decreasing intervisit intervals; $p' = 0.5$ implies no directional trend). We highlight the disparity between the observed mean p'-score, and the value of 0.25 that Schlicht et al. (2016) invoke as sufficient to produce a mean λ/μ ratio equal to that observed.

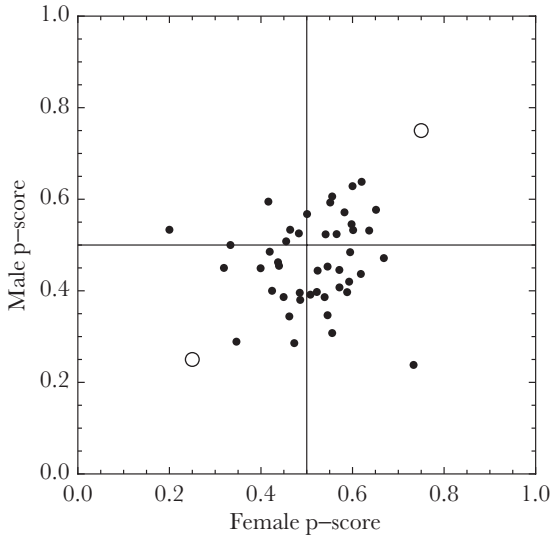

Figure 2
There is no correlation between the p-scores of mates in our great tit data set (where $p = 0$ implies strictly increasing intervisit intervals, $p = 0.5$ implies no directional trend, and $p = 1$ implies strictly decreasing intervals). Each dot corresponds to one observed sequence of visits by a single pair. Unfilled circles correspond to the p-scores invoked by Schlicht et al. (2016) as sufficient to produce a mean λ/μ ratio equal to that observed (with the intervisit intervals of both birds either increasing or decreasing).

they characterize this as a "relatively weak" directional trend, Figure 2 reveals that it actually represents a stronger tendency than is shown by either parent in 43 out of 45 sequences. The observed mean value of p' is equal to 0.418 (median 0.429), and examining Figure 3 of Schlicht et al. (2016), their results suggest that a directional tendency of this strength produces λ/μ ratios virtually indistinguishable from the simple randomization process we employed. It thus appears that the birds in our study did not display strong enough directional changes in visit rate to account for the observed pattern of visits.

In addition, although Schlicht et al. (2016) do not require that different pairs should all exhibit change in the same direction, they do assume in their modified randomization procedure that the 2 members of each pair both show the same directional trend. However, plotting male against female p-scores for the sequences of visits in our data in Figure 2 (so that each point represents a single observed sequence of visits by one pair), we see that pairs in our study did not show correlated changes in visit rate ($r_{43} = 0.065$, $p = 0.673$).

To conclude, we consider the possibility suggested by Schlicht et al. (2016) interesting and well-worth testing. Parents might, in some cases, display correlated, directional changes in visit rate due to weather, predators, etc., and Schlicht et al. (2016) have shown that this could in principle produce results similar to the effects of conditional cooperation. But in the case of our great tit dataset, parents do not in fact show such directional change, and the process that Schlicht et al. (2016) propose cannot therefore account for the alternating pattern of visits we observed. Consequently, although we welcome the possibility of further, experimental tests, we feel that conditional cooperation currently offers a more convincing explanation for our results.

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