



Male parental investment reflects the level of partner contributions and brood value in tree swallows

Ádám Z. Lendvai^{1,2,3} · Çağlar Akçay^{1,4} · Mark Stanback⁵ · Mark F. Haussmann⁶ · Ignacio T. Moore¹ · Frances Bonier^{1,7}

Received: 28 May 2018 / Revised: 19 October 2018 / Accepted: 22 October 2018
© Springer-Verlag GmbH Germany, part of Springer Nature 2018

Abstract

Biparental care presents an interesting case of cooperation and conflict between unrelated individuals. Several models have been proposed to explain how parents should respond to changes in each other's parental care to maximize their own fitness, predicting no change, partial compensation, or matching effort as a response. Here, we present an experiment in tree swallows (*Tachycineta bicolor*) in which we increased the offspring provisioning of females by presenting them, but not their mates, with additional nestling begging calls using automated playbacks. We performed this experiment in two populations differing in future breeding opportunities. We found that in response to a temporary increase in female parental effort, males in the northern population (with lower future breeding opportunities and thus higher brood value) matched the increased effort, whereas males in the southern population did not. We also found that increases in parental care during playbacks were driven by the females (i.e., females initiated the increased effort and their mates followed them) in the northern population but not the southern population. These results support the idea that with incomplete information about the brood value and need, cues or signals from the partner might become important in coordinating parental care.

Significance statement

Male tree swallows increase parental effort when their mates need to work harder. Using an automated system, we broadcast playback of hungry nestling calls only when the female parent was visiting the nest. In a population where the value of the current brood was high, males significantly increased their provisioning rate, much more than their partners did. Since only the females could hear the playbacks, and the begging of the nestlings did not change in response to the treatment, we suggest that either the males used their partner's feeding rate as a cue or the females may have communicated to their mates that they should work harder. These results suggest that cues or signals from the partner may be important in coordinating parental care.

Keywords Biparental care · Parental effort · Negotiation · Sexual conflict · Tree swallow

Ádám Z. Lendvai and Çağlar Akçay contributed equally to this work.

Communicated by M. Leonard

Electronic supplementary material The online version of this article (<https://doi.org/10.1007/s00265-018-2594-3>) contains supplementary material, which is available to authorized users.

✉ Ádám Z. Lendvai
az.lendvai@gmail.com

✉ Çağlar Akçay
akcay.caglar@gmail.com

¹ Department of Biological Sciences, Virginia Tech, Blacksburg, VA, USA

² Department of Evolutionary Zoology and Human Biology, University of Debrecen, Egyetem tér 1, Debrecen 4032, Hungary

³ Department of Geology, Babeş-Bolyai University, Cluj-Napoca, Romania

⁴ Department of Psychology, Koç University, Rumelifeneri Yolu, Sariyer, 34450 İstanbul, Turkey

⁵ Department of Biology, Davidson College, Davidson, NC, USA

⁶ Department of Biology, Bucknell University, Lewisburg, PA, USA

⁷ Department of Biology, Queen's University, Kingston, ON, Canada

Introduction

In many animal species, parents provide some form of parental care before offspring become independent (Clutton-Brock 1991). Although in many species parental care is only provided by a single parent, biparental care is especially common among birds (Cockburn 2006). Biparental care provides an interesting case study in cooperation between unrelated individuals as well as conflict between sexes (Royle et al. 2002; Johnstone and Hinde 2006; Harrison et al. 2009), given parental care is often costly and reduces the chances of future breeding (Trivers 1972). Although both parents gain a fitness benefit from increased parental care via increased survival of the offspring, each parent is better off if the other parent supplies the majority of the care, thus creating sexual conflict over parental care (Trivers 1972; Houston and Davies 1985; Houston et al. 2005).

Several models have been proposed to predict how conflict over parental care may be resolved. These models differ in the assumptions they make regarding information about the brood value and need as well as behavioral strategies available to parents and consequently the predictions they offer when a parent increases or decreases parental care. The first type of model is the “sealed-bid model” (Houston and Davies 1985) which assumes that parents will be behaviorally insensitive to changes in each other’s reproductive effort, instead engaging in a fixed level of parental effort (Houston and Davies 1985; Schwagmeyer et al. 2002). In this model, changes in parental effort of one of the sexes only occur through evolutionary change. An alternative prediction comes from “negotiation models” that assume that parents are able to respond to changes in partner investment. In these models, parents are viewed as being in partial conflict over the amount of parental care they provide, with each parent preferring the other parent do more, and themselves do less. When one parent decreases their effort, the other parent is predicted to compensate by increasing their own effort, but this compensation has to be incomplete for this model to be evolutionarily stable (Chase 1980; McNamara et al. 1999, 2003; Hinde and Kilner 2007; Lendvai et al. 2009). The logical extension of these models is that when a parent increases parental effort, the other parent should compensate by decreasing their own parental effort (Kosztolányi et al. 2009). A third model, the “information model” (Johnstone and Hinde 2006; Meade et al. 2011), was built upon the negotiation models by assuming that when parents have only incomplete information about the brood value and need, they use their mate’s parental effort as a cue in determining the level of parental care needed to optimize reproductive success. Under this model, if the information available to parents about brood need is different, they are expected to match an increase in the other parent’s effort with an increase in their own effort. Finally, in the “perfect family” model (Akçay and Roughgarden 2009), parents are assumed

to be able to communicate directly to coordinate their parental efforts. This model also predicts a matching response when one parent increases their parental effort.

Several studies have tested how the change in one parents’ provisioning behavior affects the parental behavior of its partner. In a meta-analysis, the general pattern across these studies was partial compensation, consistent with the predictions of the negotiation models and the information model when information about brood value is complete and symmetrical (Harrison et al. 2009). However, most of the experimental tests used handicapping, i.e., an experimentally induced decrease in one parent’s parental effort (e.g., by feather clipping, weight addition, or hormonal manipulation) or mate removal (Harrison et al. 2009). Both handicapping and mate removal may have limitations in addressing models to explain parental care. Handicapping alters not only the focal parent’s contribution to offspring care but also potentially its physical appearance and/or attractiveness, which may confound how its partner will perceive the treatment (Griggio et al. 2005). Mate removal simulates the desertion or death of one parent, and the response of the remaining parent may be contingent on the complete absence of the partner, instead of representative of responses to changes in ongoing biparental care (Whittingham et al. 1994; McNamara et al. 2003; Harrison et al. 2009; Lendvai et al. 2009). Only a few studies have sought to experimentally increase the parental effort of one parent. Three of these studies (Hinde 2006; Hinde and Kilner 2007; Meade et al. 2011) found evidence for matching of partner effort while one (Kosztolányi et al. 2009) found partial compensation (i.e., a decrease of own effort in response to an increase in partner effort).

In this study, we used playbacks of recordings of nestling begging calls as an experimental treatment to stimulate an increase in parental care (nestling provisioning) in female tree swallows (*Tachycineta bicolor*) and then measured the response of their mates. Previous studies that used begging calls used short-term modification of parental behavior (usually a 1 h-playback session) (Hinde 2006; Meade et al. 2011). We designed an automated broadcasting and recording system (Lendvai et al. 2015b) that allowed us to deliver the experimental stimulus only to focal females and the treatment lasted up to 6 h during the day of the study. We have previously shown that this experimental manipulation temporarily increased the females’ feeding rate (Akçay et al. 2016). Here, we investigated how their partners reacted to the manipulation and tested predictions from the hypotheses presented above. The sealed-bid model predicts that males will not be responsive to short-term changes in female provisioning behavior. The negotiation models predict that when females increase their provisioning rate, the males should decrease their own effort. Finally, the information and perfect family models predict that males should match the female response to the playback, thus increasing their own parental effort.

We also tested the hypothesis that behavioral responses to changes in partner's parental care may depend on the value of the current reproduction. Brood value (not equivalent to reproductive value) is a simple concept that summarizes the value of the current brood relative to the potential for future reproduction and is defined as $\log\{1/[(\text{broods per year}) \times (\text{reproductive lifespan})]\}$ (Bókony et al. 2009; Sol et al. 2012). In populations with lower potential for future reproduction (due to a shorter breeding season, higher adult mortality rates, etc.), the current brood is more valuable compared to a brood in a population where the probability of future reproduction is higher. Brood value may affect negotiation rules that parents use in determining their response to changes in partner behavior. We examined the role of brood value by carrying out the experiment in two populations of tree swallows that differ in brood value. One population, in Ontario, Canada, has lower annual survival rates, a shorter breeding season, and thus higher brood value (Cox et al. 2018). The other population, in North Carolina, USA, has higher annual survival rates and a longer breeding season. Preliminary evidence suggests that some birds may successfully nest twice in 1 year, and thus, the longer reproductive lifespan and the possibility for multiple broods in a season lower the current brood value in that population (Akçay et al. 2016). Because of these differences in brood value, we predicted that male tree swallows in the Ontario population would be more likely to match their partner's increased parental effort than the males in North Carolina.

Methods

Study site and species

In 2014, we studied tree swallows at two field sites where they breed in artificial nest boxes: Queen's University Biological Station, Ontario, Canada (N 44° 34' 2", W 76° 19' 26", 121 m elevation) and Davidson College, Davidson, North Carolina, USA (N 34° 31' 32", W 80° 52' 40", 240 m elevation). These two sites differ in the length of the breeding season, with longer seasons in North Carolina. For example, in 2014, the time between the laying date of the first and the last clutch in the season was 60 days in North Carolina, whereas it was only 43 days in Ontario. Annual survival rates are also higher in North Carolina. Tree swallows have high breeding site fidelity, and so return to the breeding population is often used as a proxy of annual survival (Winkler et al. 2004). In our North Carolina study site, return rates are around 50% (51% for females and 49% for males in 2015) which is higher than in the Ontario study site (average 22% between 1978 and 2012, range 13–43%). Return rates were calculated as the proportion of adults banded that were recaptured in later years. Note that return rates are the product of true survival, site fidelity, site

propensity, and detection probability. Because of this, return rates are expected to be lower than survival probability and can be considered as a minimum estimate of true survival (Sandercock 2003). Similar findings have been reported in other studies comparing southern and northern populations of tree swallows (Ardia 2005), although we note that some other northern populations have higher survival rates than our Ontario population (Clark et al. 2018; Cox et al. 2018).

Subjects

We captured birds using traps at their nest box or placing our hands over the nest entrance. We caught females on day 10 of the incubation period and males on day 2 or 3 post-hatching. We recorded body measurements (tarsus, wing chord, weight, skull size) and marked birds with a numbered metal leg band (US Fish and Wildlife Service or Canadian Wildlife Service) and a unique passive integrated transponder (PIT) tag that was integrated into a colored (red for females, blue for males) plastic leg band (EM4102 tags from IB Technology, UK). More details on the field methods can be found in Akçay et al. (2016).

Playback experiment

Nestling begging calls were recorded as described in Akçay et al. (2016). Briefly, we recorded the calls from 10 nests on day 6 post-hatching by tapping at the nest entrance to simulate the sound of an arriving parent and pointing a directional microphone (Sennheiser ME66/K6 directional microphone connected to a Marantz PMD 660 solid-state recorder) into the nest. We used the software Syrinx (John Burt, Seattle, WA; www.syrinxpc.com) to create 30-s stimulus files from the recordings thus obtained, as described in (Akçay et al. 2016). The initial calling rate was ~14 begs/s (consisting of overlapping calls by multiple nestlings) that gradually decreased to a constant ~4 begs/s (see supplementary material for an example stimulus). The 10 stimulus files were randomly allocated to the treatment nests. Parent tree swallows cannot distinguish the calls of their own young from calls of unrelated nestlings (Leonard et al. 1997); therefore, the stimulus files were expected to stimulate increased provisioning of the focal parents.

Playback setup

We used a radio frequency identification (RFID) reader attached to a micro-computer (Raspberry PI) to carry out the playbacks automatically (Lendvai et al. 2015b). The computer was programmed to carry out playbacks every time the female was perched at the nest entrance (where the RFID antenna was attached). The playback was not initiated if the male's tag was detected. Each playback lasted 30 s after the RFID reader

detected the female's PIT tag, and there was a refractory period of 2 min from the start of each playback (to avoid situations where the playback would be triggered by the female leaving the nest soon after she had entered). We used earbud headphones (Sony MDRE9LP, Sony Inc.) secured with tape at the back of the nest box as speakers (see for picture: Lendvai et al. 2015b), playing calls at approximately 55 dB (measured from approximately 10 cm), which is comparable to call amplitudes of tree swallow nestlings at that age (Leonard and Horn 2006). The playback apparatus was also installed in control nests, but no sound was played. Treatments were allocated to the nests using a randomized block design, to control for seasonal differences. The playback may possibly stimulate the focal nestlings to beg more, which would directly affect the males' behavior. To control for this effect, we also recorded nestling begging calls in nine nests in Ontario following the methods described in Dakin et al. (2016).

We set up the playback systems at around 7 am on day 6 post-hatching and playbacks stopped approximately 6 h later, after which we captured the females to obtain a blood sample for hormone analysis (Akçay et al. 2016). We had 20 control and 16 playback nests in NC and 12 control and 12 playback nests in Ontario.

Quantifying parental effort

We quantified rates of parental visits to the nest, used here as the measure of parental effort. Visit rates are an excellent measure of feeding rates in the tree swallows, as 95–98% of nest visits are for feeding (McCarty 2002). We measured feeding rate on day 5 and day 6 (the day before and the day of the treatments). Day 5 feeding rates served as a “baseline” measurement for each nest, where feeding rates were measured without any disturbance to the nest and therefore were useful to see if there were any pre-treatment differences between the populations and treatment groups. Feeding rate was then also measured on day 6 (in the same timeframe as on the previous day) during the treatments. We quantified feeding rates in two ways: (1) using 1-h direct observations and (2) using RFID records. For the behavioral observations, an observer (blind to the type of the treatment to minimize observer bias) sat ~ 30 m from the nest and noted every visit of the male and female using a spotting scope and a voice recorder. For 15 observations, simultaneous video recording was also made, and by watching these recordings, we could not detect any behavior of the parents that would have suggested that they were startled or in other ways disturbed by the playbacks (e.g., hovering in front of the entrance or hesitating before entering). We also quantified visit rates from the RFID records as described in detail in Lendvai et al. (2015a). We checked the visit rates from 1-h nest watches against the visit rates calculated from RFID logs of the same time periods. There was a high correspondence between the two measures (Lendvai et al. 2015a).

Because the RFID observations spanned the entire duration of the experiment, we used these data as the primary measure of parental visit rates.

Statistical analyses

We used generalized linear mixed models (GLMM) to assess the effects of treatment and population on male behavior. For all models, we first fitted a fully parameterized model with all interactions included and then used a model selection based on the Akaike information criterion (AICc). We performed model averaging of the best models (within 2 AICc units compared with the model with the lowest AICc value) and report the model-averaged coefficients. The conclusions drawn from this model selection procedure were consistent with an alternative approach using stepwise model selection to achieve a single, minimal adequate model. We analyzed the feeding rates derived from RFID recordings with GLMMs using the fixed factors treatment (playback vs. control), population (Ontario vs. North Carolina), time period and all their two-way interactions and the three-way interaction. We performed these analyses separately for males and females. For the time period factor, initially, we used four levels: pre-treatment (day 5) feeding rates (6 h during the same time of day as the experimental period on the next day) and feeding rates from the period while the playback or control treatment was in effect in day 6, which we further divided into three 2-h periods to assess any temporal changes in effects of playback on female behavior. These periods separate the experimental period into equal durations of reasonable length, but the choice of the cutoff point is unavoidably arbitrary; therefore, we later analyzed these data using time series analyses (see below). We included playback stimulus recording and bird ID as random factors and also included an offset variable for log of duration of playback to control for variation in how long the birds were exposed to the playbacks (mean = 6.24 ± 0.05 SE hours).

In a next step, we analyzed the *change* in male visit rate from the pre-treatment period (day 5) to the experimental period (day 6) as a function of the treatment, population, and the change in provisioning behavior of females over the same time period. The change in visit rate was calculated as the difference in the number of feeding visits per time between day 5 and day 6, where time was the total 6 h of experimental period on day 6, and the same time frame on day 5. Because in this case, we only had one male and one female change in visit rate value per nest, this was analyzed by a GLM with male change in visit rate as the response variable and with female change in visit rate, treatment, and population as explanatory variables. The initial model contained all possible interactions.

Finally, we analyzed the relationship between male and female feeding rate over a more continuous scale using time series analyses. To do that, the event recordings from the RFID logs were transformed into time series using moving

averages (calculating the average feeding rate over a frame of 60 min and in 20 min steps, i.e., lags). We tested various combinations of these parameters, and they gave qualitatively similar results (i.e., they did not change our conclusions). During the time series analyses, first we tested if the male and the female time series are significantly related to each other using cross correlation analyses within ± 80 min (that corresponds to lag = 4). In those pairs where we found a significant relationship between the time series, we determined the peak of the cross-correlation distribution, and the lag that corresponded to it. Finally, we repeated these analyses using only the experimental period to test how the experimentally induced change in female behavior may affect their partners' parental contributions.

Data availability All data generated or analyzed during this study are included in this published article and its supplementary information files.

Results

Feeding rates

Before the treatments, feeding rates did not differ between control and playback nests or between the two populations either in females (Table 1) or in males (Table 2). The playback had a transient (first 2 h) and positive effect on the feeding rate of females in both populations (Table 1). We tested how males reacted to the change in behavior of their mates during the

Table 1 Model-averaged parameter estimates of a general linear mixed effects model (Poisson error and log-link) on the effects of playback on female feeding rate. The intercept corresponds to the baseline level (pre-treatment, day 5), North Carolina, and control treatment. Statistically significant effects are in italics

Term	Estimate	SE	<i>t</i>	<i>p</i>
(Intercept)	<i>2.14</i>	<i>0.10</i>	<i>22.20</i>	<i>< 0.001</i>
Population (Ontario)	-0.14	0.14	0.99	0.320
Treatment (playback)	-0.08	0.13	0.63	0.530
Playback \times Ontario	0.17	0.24	0.70	0.480
During 1st 2 h	0.03	0.05	0.46	0.640
During 2nd 2 h	<0.01	0.06	0.01	0.990
During last 2 h	0.05	0.05	1.14	0.250
During 1st 2 h \times Ontario	-0.12	0.07	1.63	0.100
During 2nd 2 h \times Ontario	0.13	0.07	1.74	0.080
During last 2 h \times Ontario	0.06	0.07	0.95	0.340
During 1st 2 h \times playback	<i>0.25</i>	<i>0.07</i>	<i>3.53</i>	<i>< 0.001</i>
During 2nd 2 h \times playback	0.10	0.07	1.35	0.180
During last 2 h \times playback	0.04	0.06	0.55	0.580

Table 2 Model-averaged parameter estimates of a general linear mixed effects model (Poisson error and log-link) on the effects of playback on male feeding rate. The intercept corresponds to the baseline level (pre-treatment, day 5), North Carolina, and control treatment. Statistically significant effects are in italics

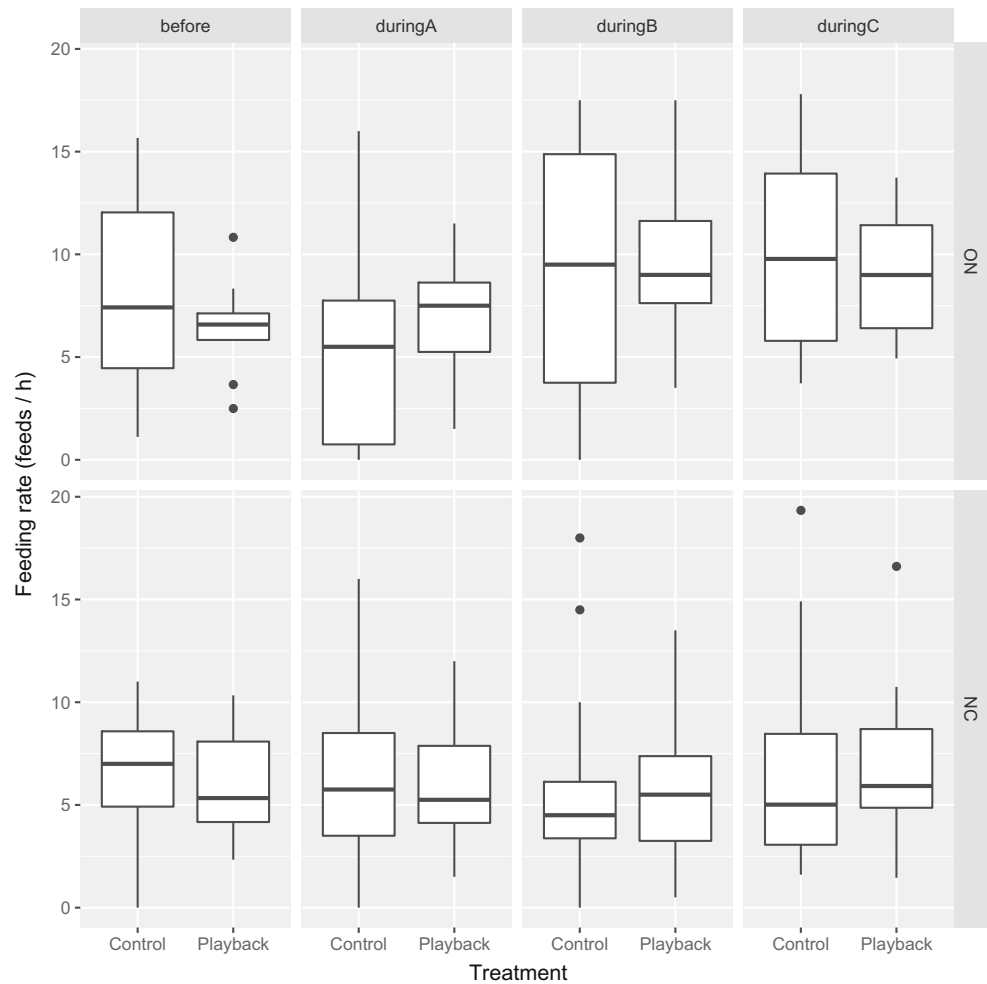
Term	Estimate	SE	<i>t</i>	<i>p</i>
(Intercept)	<i>1.75</i>	<i>0.10</i>	<i>16.94</i>	<i>< 0.001</i>
Population (Ontario)	0.24	0.15	1.60	0.110
Treatment (playback)	-0.08	0.14	0.57	0.570
Playback \times Ontario	-0.17	0.26	0.66	0.510
During 1st 2 h	-0.10	0.08	1.27	0.200
During 2nd 2 h	-0.14	0.08	1.88	0.060
During last 2 h	<-0.01	0.06	0.04	0.960
During 1st 2 h \times Ontario	-0.24	0.13	1.84	0.070
During 2nd 2 h \times Ontario	<i>0.24</i>	<i>0.11</i>	<i>2.14</i>	<i>0.030</i>
During last 2 h \times Ontario	0.14	0.08	1.70	0.090
During 1st 2 h \times playback	0.19	0.12	1.56	0.120
During 2nd 2 h \times playback	0.15	0.11	1.32	0.190
During last 2 h \times playback	0.14	0.08	1.74	0.080
During 1st 2 h \times playback \times Ontario	<i>0.40</i>	<i>0.17</i>	<i>2.29</i>	<i>0.020</i>
During 2nd 2 h \times playback \times Ontario	0.31	0.16	1.91	0.060
During last 2 h \times playback \times Ontario	0.10	0.14	0.66	0.510

same periods, and we found a significant 3-way interaction (treatment \times population \times time period), indicating that the males' behavior was affected by the playbacks broadcast to their partner, and this response was different between the two populations (Table 2). Specifically, this model showed that in control nests, during the first 2 h of treatment, males tended to decrease their feeding rate compared to day 5, but this effect was more pronounced in Ontario. The decrease in parental care in the first 2 h of controls disappeared by the second hour of playback and resulted in higher feeding rates in Ontario than in North Carolina. However, in playback nests, this initial decrease was not seen in Ontario; on the contrary, during the first 2 h of the playback, males increased their feeding rate and increased it further in the second 2-h period (Fig. 1).

Change in feeding rates

Analyzing the change in feeding rate from the baseline (day 5) to the entire experimental period (day 6) revealed that the most important predictor of how males changed their behavior was the change of their partners' provisioning rate (Fig. 2; Table 3). In control nests, most pairs' behavior followed the predictions of the matching hypothesis, i.e., an increase or a reduction in female feeding rate was mirrored by a similar change in the male's behavior. This pattern remained the most common one in response to the playback as well. Interestingly, males in Ontario showed a stronger response to the playback treatment than

Fig. 1 Nestling provisioning behavior in male tree swallows in two populations (NC North Carolina, USA, ON Ontario, Canada) before (day 5) and during broadcasting experimental nestling begging stimuli for female parents (day 6). The experimental period was divided into three 2 h subsets (A, B, C). The boxplots represent the median (middle line), 25% and 75% percentiles (the lower and upper boundaries of the boxes, respectively), the 1.5 interquartile range (whiskers), and points outside this range, i.e., outliers (dots)



their mates (even though playback was only broadcast to females): despite the modest increase in female feeding rate during the playback period, all but one male in Ontario increased their feeding rate compared to the baseline (Fig. 2b) resulting in a significant increase in that population (Fig. 2d).

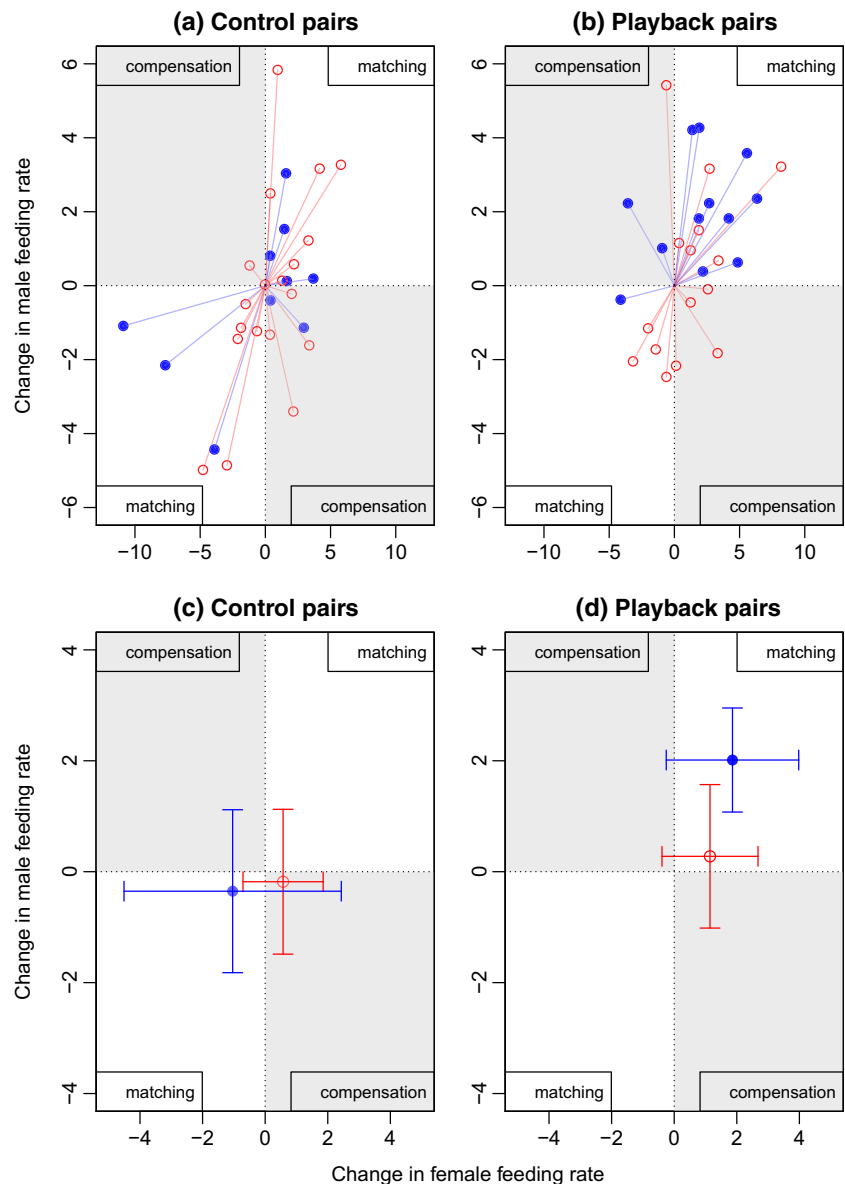
Pair coordination

In many pairs the two parents follow each other's behavior closely (Fig. S2). In both populations, most pairs show a matching pattern (i.e., the cross-correlation coefficient before the treatment was significantly positive in 27 out of 36 nests in North Carolina and 19 out of 24 nests in Ontario; Fig. S3). This pattern was unaffected by the treatment or the experimental period (day 5 vs. day 6). As a result, the analyses of the cross-correlation coefficients showed that the best model was the null-model (ΔAICc from the next model was >4), where only the intercept was significantly positive confirming the positive relationship between the parents' provisioning efforts (Fig. 3; Table 4). Thus, increases or decreases in one

parent's provisioning effort tended to be matched by the other parent's provisioning effort in the same direction irrespective of the treatment and experimental period.

However, treatment had a modest effect on who was leading the changes in provisioning behavior (as measured by the lag at which the cross-correlation coefficients were maximal with positive lags indicating female-led changes and negative lags indicating male-led changes; Fig. S3), but only in the Ontario population, resulting in a marginally non-significant three-way interaction (Table 5). While changes in provisioning behavior were highly synchronous among pair members in NC during the pre-manipulation period (day 5) (the lag corresponding to the peak cross-correlation was close to zero), in Ontario, females tended to follow changes in their partners' behavior before the experimental treatment. This pattern changed in the Ontario population in response to the treatment: in the playback group variation in the feeding rates became female-driven in most nests with males following the change in female provisioning, i.e., the lags became positive (Fig. 4; Table 5). The control group, by contrast, became more synchronous (with the lag becoming near zero).

Fig. 2 Relationship between changes in feeding rates from pre-treatment (day 5) to the experimental periods (day 6) within tree swallow pairs. **a, b** The individual data points. **c, d** The means and 95% confidence intervals. Red color and open circles indicate North Carolina; blue color and filled circles denote Ontario



Discussion

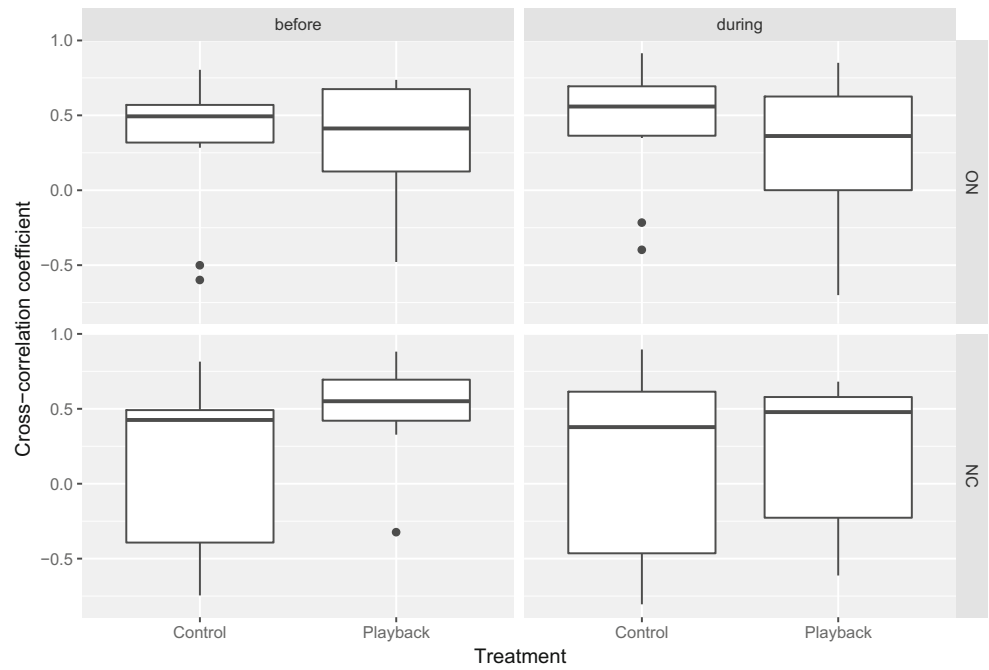
We found that when experimental nestling begging calls were broadcast to female tree swallows, in two different populations with differing brood value, their males showed marked

Table 3 Model-averaged parameter estimates for the model analyzing change in male feeding rate from the baseline (day 5) to the experimental period (day 6). Statistically significant effects are in *italics*

Term	Estimate	SE	<i>t</i>	<i>p</i>
(Intercept)	-0.46	0.43	1.05	0.294
Change in female feeding rate	<i>0.41</i>	<i>0.13</i>	<i>3.10</i>	<i>0.002</i>
Treatment (playback)	0.74	0.56	1.29	0.197
Population (Ontario)	1.06	0.57	1.80	0.072
Change in female feeding rate × Ontario	-0.24	0.17	1.37	0.169

differences in their reaction. In Ontario (population with high brood value), males in the playback and control groups behaved differently during the treatment. While control males fed their chicks at the same rate as they did the day before, males whose partners received the playbacks significantly increased their feeding rates compared to the previous day. In contrast, males in North Carolina (lower brood value) did not increase their feeding rates in response to the playbacks, even though females in both populations showed a transient increase in their feeding rates (Akçay et al. 2016). Because the females' reaction to the playback was similar in the two populations, and only females received the playbacks, our results suggest that males in the population where brood value was high reacted more strongly to an increase in demand perceived by their mates than males in a population where brood value is lower. The finding that males in the high brood value

Fig. 3 Parental coordination (cross-correlation coefficients) for tree swallow pairs in two populations (ON Ontario, NC North Carolina). Positive values indicate a matching response (an increase in provisioning in one sex results in an increase of its partner), while negative values indicate a compensation response. The boxplots represent the median (middle line), 25% and 75% percentiles (the lower and upper boundaries of the boxes, respectively), the 1.5 interquartile range (whiskers), and points outside this range, i.e., outliers (dots)



population responded with an increase in feeding rates is consistent with the predictions of the information model (Johnstone and Hinde 2006) and the perfect family model of biparental care (Akçay and Roughgarden 2009). We discuss below possible mechanisms that may explain the male parents’ response to playbacks that females received.

The effect of begging playbacks on male feeding rates suggests that males matched increases in female feeding rates, at least in the Ontario population. Interestingly, although the direction of the males’ response matched that of their mates, males increased their feeding rate more than their partners did. Time series analysis also showed that, at least in some pairs, males substantially increased their feeding rate during the playback period before the increase of their mates’ contribution was apparent.

The mechanism by which male parents match females is currently unknown, but there are several plausible explanations, which are not mutually exclusive. First, males may have been simply responding directly to offspring begging call playbacks they overheard. This could occur if they were perched at the nest box entrance or on the box at

the time of a playback. We designed the playback system to minimize this possibility: after the initial playback that was played upon the arrival of the female, there was a refractory period of 2 min, so during most feeding visits, when females left the nest after entering to feed, a playback was not played. We also verified with the RFID data that it was very rare for males to be perched at the box entrance while the playback was active and the female was inside the box (see [Supplementary Information](#)). Additionally, behavioral observations suggest that males were rarely present on the box when females triggered playbacks and the latter measure did not differ between treatment groups or experimental periods (day 5 vs. day 6—see [Supplementary Information](#)). Thus, it is unlikely that males directly overheard the playbacks.

A second possibility is that the playbacks may alter nestling begging behavior during male visits. In particular, nestlings may anticipate higher acoustic competition from

Table 4 Model-averaged parameter estimates for the model analyzing peak cross-correlation coefficients between male and female feeding rate. Statistically significant effects are in italics

Term	Estimate	SE	<i>t</i>	<i>p</i>
(Intercept)	<i>0.28</i>	<i>0.05</i>	<i>5.10</i>	<i>< 0.001</i>
Treatment (playback)	0.10	0.09	1.07	0.283
Population (Ontario)	0.10	0.09	1.04	0.297
Period (day 6—during playback)	-0.08	0.09	0.87	0.382

Table 5 Model-averaged parameter estimates for the model analyzing the temporal association between male and female feeding rates

Term	Estimate	SE	<i>t</i>	<i>p</i>
(Intercept)	0.02	0.37	0.06	0.955
Population (Ontario)	-0.53	0.76	0.68	0.494
Period (day 6—during playback)	0.14	0.69	0.20	0.839
Treatment (playback)	0.39	0.74	0.52	0.601
Ontario × day 6	0.32	1.36	0.24	0.814
Ontario × playback	-1.15	1.26	0.90	0.367
Playback × day 6	-1.47	1.13	1.29	0.195
Ontario × Playback × day 6	3.39	1.78	1.89	0.059

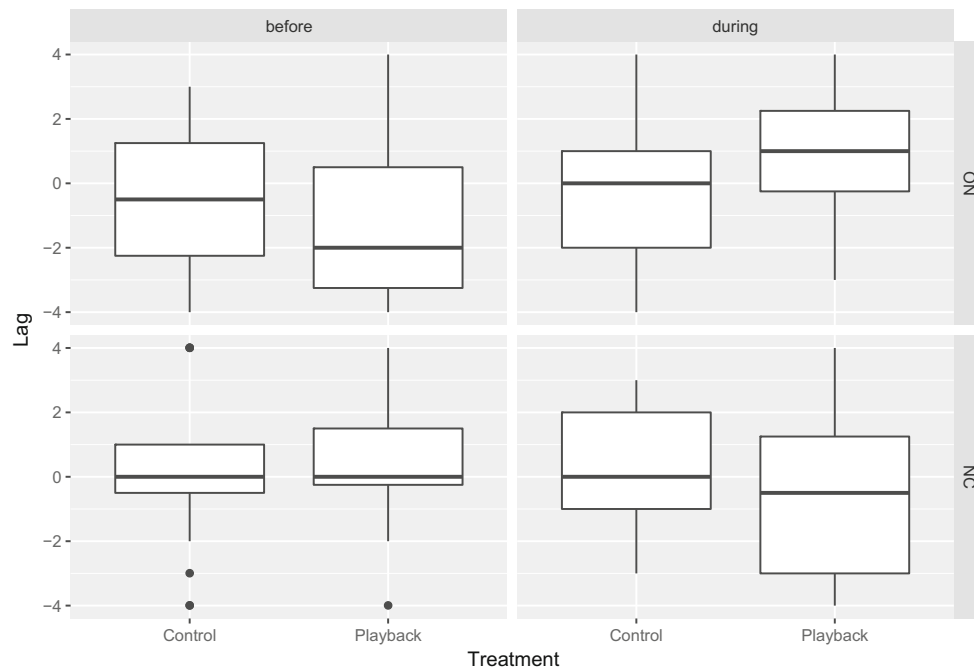


Fig. 4 Temporal association between provisioning behavior of tree swallow parents in two populations (Ontario: ON and North Carolina: NC) as shown by lags at which the cross-correlation is maximal between female and male feeding rate. The closer the lag is to zero, the more synchronous the parents are. Positive lags indicate that the male's parental

behavior follows the female's behavior; negative lags mean that female behavior follows the male's behavior. The boxplots represent the median (middle line), 25% and 75% percentiles (the lower and upper boundaries of the boxes, respectively), the 1.5 interquartile range (whiskers), and points outside this range, i.e., outliers (dots)

their real and simulated nest mates (Horn and Leonard 2008), and therefore increase their own begging rate, which can to influence parental feeding in this species (Leonard and Horn 2001). There is evidence that nestlings tend to beg more intensely in larger broods (Leonard et al. 2000), which suggests that acoustic competition could lead to higher calling rates, even when there is no playback (i.e., during the male's visit). We recorded nestling begging behavior in a subset of nests in Ontario, and the analysis of these audio recordings showed that while begging rates increased from day 5 to day 6, this increase was similar in control and playback nests (see [Supplementary Information](#)). An earlier study with great tits (*Parus major*) testing this hypothesis also found that begging behaviors did not significantly predict partner response in females and males (Hinde and Kilner 2007).

A third possibility is that males may match their feeding rate to that of the females using a tit-for-tat style alternation of provisioning where individuals time their feeding according to their partners' provisioning (Johnstone et al. 2014; Bebbington and Hatchwell 2016). Under this scenario, we would expect that because the treatment is targeted to females, they are the ones who initially start increasing their feeding rate and the males match their effort. This explanation is consistent with the results of the time series analysis, where we observed a change in the temporal association in the experimental group in Ontario. While the cross-correlation of the male and female feeding rates was significantly positive, and

did not change in response to the treatment, the lag in the playback group in the Ontario population shifted from slightly male-driven towards slightly female-driven. Note that if the parents are well coordinated, we do not expect a large change in time lags, because that would suggest that there is a considerable delay in how parents respond to the changes in their partner's behavior. A moderate shift towards a more female-driven cross-correlation is consistent with the explanation that males were responding to cues provided by the females.

Males may have adjusted their feeding effort as a result of communication with the female receiving the playbacks (Akçay and Roughgarden 2009; Elie et al. 2010; Boucaud et al. 2015). This explanation would be most consistent with the perfect family hypothesis wherein males adjust their parental effort based on cues or signals from their mates. It could also explain the result that in some pairs, the increase in male feeding rate precedes that of the females: if the females can communicate the need of a higher contribution towards their partner early during the experimental period, then some males may adjust their provisioning behavior sooner than their partner. This possibility is difficult to test, because parents often communicate while flying (personal observations).

While a matching response is consistent with both the perfect family and the information model, it is also important to note that the predictions of the information model depend on the exact cues available to the parents. This model, unlike the perfect family model, does not assume direct communication between the parents and only predicts a matching response if

the parents do not have symmetrical and complete information about the needs of the offspring, which might be the case in chick rearing. In this experiment, we deliberately created conflicting information available to the males. While cues coming from the nestlings did not convey the message of hungry chicks (nestling begging rate did not seem to be affected by the treatment; see [Supplementary Information](#)), the females may have communicated a need for higher levels of provisioning, creating a situation of potentially incomplete and asymmetrical information from the male parent's perspective. Our results suggest that in such a situation, the males use cues from their partners (either direct information through communication as the perfect family hypothesis suggests, or indirect cues, such as their feeding rate). The situation created in our experiment can be contrasted with another study that also set out to increase (rather than to decrease) one parent's effort. This study found the opposite result, i.e., that the predominant response of focal parent's mates was reversible compensation and not matching (Kosztolányi et al. 2009). An important difference in this study was that it was carried out during incubation, and both parents could easily detect the difference between optimal and actual egg temperature and use this as a direct cue in the decision about parental care (Kosztolányi et al. 2009). In this case, the information model does not predict matching.

Another interesting finding in our study was that, in contrast to the findings in Ontario, there was no effect of playback on male behavior in the North Carolina population. We interpret this result as consistent with the brood value hypothesis as the current brood in the Ontario population should be more valuable to the males compared to the broods in North Carolina, where adult survival is higher and the reproductive season is longer. Interestingly, however, we did not see a population difference in females in our earlier analyses (Akçay et al. 2016), so the brood value hypothesis only seems to hold for males but not females. This difference between the sexes could be due to the fact that brood values between the populations may vary less for females than for males. The brood value for males may vary depending on the extra-pair paternity (Dunn et al. 1994) or sex-specific differences in adult annual survival rates. It is currently not known how extra-pair paternity varies with latitude and life history in this species. In any case, whether brood values differ between sexes across populations warrant further research.

Taken together, our results are most consistent with the perfect family and the information model of biparental care and suggest that males may use cues from their partners to decide about their actual parental effort. The intriguing possibility that parents can directly convey such messages to their partners through communication supports the notion that animal communication signals may be much more complex than previously thought (Elie et al. 2010; Gill et al. 2015).

Acknowledgments We are grateful to Alice Domalik, Pria St. John (Queen's University), and Drew Gill and Spencer Gill (Davidson College) for excellent help in the field and for Fruzsina Demcsák (University of Debrecen) for analyzing the begging recordings. We thank Katharina Mahr, the associate editor Marty Leonard, and anonymous reviewers for comments on previous versions of the manuscript.

Author contributions ÇA and ÁZL designed and coordinated the study, collected field data, carried out data analysis, and drafted the manuscript; MS collected field data and helped draft the manuscript; MFH contributed to the design of the study and helped draft the manuscript; FB collected field data, contributed to the design of the study, and helped draft the manuscript; ITM contributed to the design of the study and helped draft the manuscript. All authors gave final approval for publication.

Funding This work was supported by a U.S. National Science Foundation (NSF) grant (FB, ITM and MFH; IOS-1145625) and by the Natural Sciences and Engineering Research Council of Canada Discovery Grant (FB). During the preparation of the manuscript, ÁZL was supported by grants from the National Research Development and Innovation Office (OTKA K113108 and TÉT_15-1-2016-0044) and by the Romanian Ministry of Education (PN-III-P4-ID-PCE-2016-0572).

Compliance with ethical standards

Ethical approval We confirm that the procedures used in the study followed the guidelines for animal care outlined by Animal Behaviour Society and Association for the Study of Animal Behaviour and were approved by approved by the Institutional Animal Care and Use Committee at Virginia Tech (#12-020) and Animal Care Committee of Queen's University (#2013-019) and the Canadian Wildlife Service (#CA0211). The field research was conducted with a permit from US Geological Survey Bird Banding Laboratory to MS (#22742) and Canadian Wildlife Service permit to FB (#10771).

Conflict of interest The authors declare that they have no competing interests.

References

- Akçay Ç, Lendvai ÁZ, Stanback MT, Haussmann MF, Moore IT, Bonier F (2016) Strategic adjustment of parental care in tree swallows: life-history trade-offs and the role of glucocorticoids. *R Soc Open Sci* 3: 160740. <https://doi.org/10.1098/rsos.160740>
- Akçay E, Roughgarden J (2009) The perfect family: decision making in biparental care. *PLoS One* 4:e7345. <https://doi.org/10.1371/journal.pone.0007345>
- Ardia DR (2005) Tree swallows trade off immune function and reproductive effort differently across their range. *Ecology* 86:2040–2046. <https://doi.org/10.1890/04-1619>
- Bebbington K, Hatchwell BJ (2016) Coordinated parental provisioning is related to feeding rate and reproductive success in a songbird. *Behav Ecol* 27:652–659. <https://doi.org/10.1093/beheco/arv198>
- Bókony V, Lendvai ÁZ, Liker A, Angelier F, Wingfield JC, Chastel O (2009) Stress response and the value of reproduction: are birds prudent parents? *Am Nat* 173:589–598. <https://doi.org/10.1086/597610>
- Boucaud IC, Mariette MM, Villain AS, Vignal C (2015) Vocal negotiation over parental care? Acoustic communication at the nest predicts partners' incubation share. *Biol J Linn Soc* 117:322–336. <https://doi.org/10.1111/bij.12705>
- Chase ID (1980) Cooperative and noncooperative behavior in animals. *Am Nat* 115:827–857. <https://doi.org/10.1086/283603>

- Clark RG, Winkler DW, Dawson RD, Shutler D, Hussell DJT, Lombardo MP, Thorpe PA, Dunn PO, Whittingham LA (2018) Geographic variation and environmental correlates of apparent survival rates in adult tree swallows *Tachycineta bicolor*. *J Avian Biol* 49:jav-012514. <https://doi.org/10.1111/jav.01659>
- Clutton-Brock TH (1991) The evolution of parental care. Princeton University Press, Princeton, NJ
- Cockburn A (2006) Prevalence of different modes of parental care in birds. *Proc R Soc B Biol Sci* 273:1375–1383. <https://doi.org/10.1098/rspb.2005.3458>
- Cox AR, Robertson RJ, Bradley FC, Wallace RB, Bonier F (2018) Demographic drivers of local population decline in Tree Swallows (*Tachycineta bicolor*) in Ontario, Canada. *Condor* (published online, doi: <https://doi.org/10.1650/CONDOR-18-42.1>)<https://doi.org/10.1650/CONDOR-18-42.1>
- Dakin R, Ouyang JQ, Lendvai ÁZ, Haussmann MF, Moore IT, Bonier F (2016) Weather matters: begging calls are temperature- and size-dependent signals of offspring state. *Behaviour* 153:871–896. <https://doi.org/10.1163/1568539X-00003370>
- Dunn PO, Robertson RJ, Michaud-Freeman D, Boag PT (1994) Extra-pair paternity in tree swallows: why do females mate with more than one male? *Behav Ecol Sociobiol* 35:273–281. <https://doi.org/10.1007/BF00170708>
- Elie JE, Mariette MM, Soula HA, Griffith SC, Mathevon N, Vignal C (2010) Vocal communication at the nest between mates in wild zebra finches: a private vocal duet? *Anim Behav* 80:597–605. <https://doi.org/10.1016/j.anbehav.2010.06.003>
- Gill LF, Goymann W, Ter Maat A, Gahr M (2015) Patterns of call communication between group-housed zebra finches change during the breeding cycle. *Elife* 4:e07770
- Griggio M, Matessi G, Pilastro A (2005) Should I stay or should I go? Female brood desertion and male counterstrategy in rock sparrows. *Behav Ecol* 16:435–441. <https://doi.org/10.1093/beheco/ari009>
- Harrison F, Barta Z, Cuthill I, Székely T (2009) How is sexual conflict over parental care resolved? A meta-analysis. *J Evol Biol* 22:1800–1812. <https://doi.org/10.1111/j.1420-9101.2009.01792.x>
- Hinde CA (2006) Negotiation over offspring care?—a positive response to partner-provisioning rate in great tits. *Behav Ecol* 17:6–12. <https://doi.org/10.1093/beheco/ari092>
- Hinde CA, Kilner RM (2007) Negotiations within the family over the supply of parental care. *Proc R Soc B Biol Sci* 274:53–60. <https://doi.org/10.1098/rspb.2006.3692>
- Horn AG, Leonard ML (2008) Acoustic interactions in broods of nestling birds (*Tachycineta bicolor*). *J Comp Psychol* 122:298–304. <https://doi.org/10.1037/0735-7036.122.3.298>
- Houston AI, Davies NB (1985) The evolution of co-operation and life history in the dunnock, *Prunella modularis*. In: Sibly RM, Smith RH (eds) Behavioural ecology: ecological consequences of adaptive behaviour. Blackwell, Oxford, pp 471–487
- Houston AI, Székely T, McNamara JM (2005) Conflict between parents over care. *Trends Ecol Evol* 20:33–38. <https://doi.org/10.1016/j.tree.2004.10.008>
- Johnstone RA, Hinde CA (2006) Negotiation over offspring care—how should parents respond to each other's efforts? *Behav Ecol* 17:818–827. <https://doi.org/10.1093/beheco/arl009>
- Johnstone RA, Manica A, Fayet AL, Stoddard MC, Rodríguez-Gironés MA, Hinde CA (2014) Reciprocity and conditional cooperation between great tit parents. *Behav Ecol* 25:216–222. <https://doi.org/10.1093/beheco/art109>
- Kosztolányi A, Cuthill IC, Székely T (2009) Negotiation between parents over care: reversible compensation during incubation. *Behav Ecol* 20:446–452. <https://doi.org/10.1093/beheco/am140>
- Lendvai ÁZ, Akçay Ç, Ouyang JQ, Dakin R, Domalik AD, St John PS, Stanback M, Moore IT, Bonier F (2015a) Analysis of the optimal duration of behavioral observations based on an automated continuous monitoring system in tree swallows (*Tachycineta bicolor*): is one hour good enough? *PLoS One* 10:e0141194. <https://doi.org/10.1371/journal.pone.0141194>
- Lendvai ÁZ, Akçay Ç, Weiss T, Haussmann MF, Moore IT, Bonier F (2015b) Low cost audiovisual playback and recording triggered by radio frequency identification using raspberry pi. *PeerJ* 3:e877. <https://doi.org/10.7717/peerj.877>
- Lendvai ÁZ, Barta Z, Chastel O (2009) Conflict over parental care in house sparrows: do females use a negotiation rule? *Behav Ecol* 20:651–656. <https://doi.org/10.1093/beheco/arp047>
- Leonard ML, Horn AG (2001) Begging calls and parental feeding decisions in tree swallows (*Tachycineta bicolor*). *Behav Ecol Sociobiol* 49:170–175. <https://doi.org/10.1007/s002650000290>
- Leonard ML, Horn AG (2006) Age-related changes in signalling of need by nestling tree swallows (*Tachycineta bicolor*). *Ethology* 112:1020–1026. <https://doi.org/10.1111/j.1439-0310.2006.01259.x>
- Leonard ML, Horn AG, Brown CR, Fernandez NJ (1997) Parent-offspring recognition in tree swallows, *Tachycineta bicolor*. *Anim Behav* 54:1107–1116. <https://doi.org/10.1006/anbe.1997.0559>
- Leonard ML, Horn AG, Gozna A, Ramen S (2000) Brood size and begging intensity in nestling birds. *Behav Ecol* 11:196–201. <https://doi.org/10.1093/beheco/11.2.196>
- McCarty JP (2002) The number of visits to the nest by parents is an accurate measure of food delivered to nestlings in tree swallows. *J Field Ornithol* 73:9–14. <https://doi.org/10.2307/4131060>
- McNamara JM, Gasson CE, Houston AI (1999) Incorporating rules for responding into evolutionary games. *Nature* 401:368–371. <https://doi.org/10.1038/43869>
- McNamara JM, Houston AI, Barta Z, Osorno J-L (2003) Should young ever be better off with one parent than with two? *Behav Ecol* 14:301–310. <https://doi.org/10.1093/beheco/14.3.301>
- Meade J, Nam K-B, Lee J-W, Hatchwell BJ (2011) An experimental test of the information model for negotiation of biparental care. *PLoS One* 6:e19684. <https://doi.org/10.1371/journal.pone.0019684>
- Royle NJ, Hartley IR, Parker GA (2002) Sexual conflict reduces offspring fitness in zebra finches. *Nature* 416:733–736. <https://doi.org/10.1038/416733a>
- Sandercock BK (2003) Estimation of survival rates for wader populations: a review of mark-recapture methods. *Wader Study Group Bull* 100:163–174
- Schwagmeyer P, Mock DW, Parker GA (2002) Biparental care in house sparrows: negotiation or sealed bid? *Behav Ecol* 13:713–721
- Sol D, Maspons J, Vall-Ilosera M, Bartomeus I, García-Peña GE, Piñol J, Freckleton RP (2012) Unraveling the life history of successful invaders. *Science* 337:580–583. <https://doi.org/10.1126/science.1221523>
- Trivers RL (1972) Parental investment and sexual selection. In: Campbell BG (ed) Sexual selection and the descent of man, 1871–1971. Aldine, Chicago, pp 136–179
- Whittingham LA, Dunn PO, Robertson RJ (1994) Female response to reduced male parental care in birds: an experiment in tree swallows. *Ethology* 96:260–269. <https://doi.org/10.1111/j.1439-0310.1994.tb01014.x>
- Winkler DW, Wrege PH, Allen PE, Kast TL, Senesac P, Wasson MF, Llambias PE, Ferretti V, Sullivan PJ (2004) Breeding dispersal and philopatry in the tree swallow. *Condor* 106:768–776