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2 **Strategic adjustment of parental care: life-history trade-offs and the role of glucocorticoids**

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21 **Strategic adjustment of parental care: life-history trade-offs and the role of glucocorticoids**

22 **Abstract**

23 Life history theory predicts that optimal strategies of parental investment will depend on
24 ecological and social factors such as current brood value and offspring need. Parental care strategies are
25 also likely to be mediated in part by the hypothalamic-pituitary-adrenal (HPA) axis and glucocorticoid
26 hormones. Here we present an experiment in tree swallows (*Tachycineta bicolor*), a biparental songbird
27 with wide geographic distribution, asking whether parental care is strategically adjusted in response to
28 signals of offspring need and brood value and whether glucocorticoids are involved in these
29 adjustments. Using an automated playback system, we carried out playbacks of nestling begging calls
30 specifically to females in two populations differing in their brood value: a northern population in
31 Ontario, Canada (relatively high brood value) and a southern population in North Carolina, USA (lower
32 brood value). We quantified female offspring provisioning rates before and during playbacks and plasma
33 corticosterone levels (cort) once during late incubation and once immediately after playbacks. Females
34 in both populations increased feeding rates temporarily during the first two hours of playback but the
35 increase was not sustained for the entire duration of playback (six hours). Cort levels from samples at
36 the end of the playback did not differ between control females and females that received playbacks.
37 However, females that had higher increases in cort between the incubation and nestling period had
38 greater fledging success. These results suggest that females are able to strategically respond to offspring
39 need, although the role of glucocorticoids in this strategic adjustment remains unclear.

40

41 **Keywords:** tree swallow, corticosterone, nestling begging, provisioning, brood value, latitude, fitness

42

43 **Introduction**

44 Parental investment comprises costly behaviors that can improve the survival of current
45 offspring at the expense of future reproduction (Trivers, 1972). Life history theory predicts that animals
46 will adopt strategies that optimize the level of parental investment in a given reproductive bout. To
47 determine the optimal level of investment, parents must incorporate several potential cues about the
48 value of both current and future reproductive activities (Stearns, 1992). For instance, parents may adjust
49 their investment in offspring in response to cues that indicate genetic quality or condition of their
50 partner (Burley, 1988; Dakin et al., 2016; Sheldon, 2000) or parental effort of their partner (Hinde, 2006;
51 Hinde and Kilner, 2007; Westneat et al., 2011). In addition, parents may also adjust investment based on
52 cues from their offspring such as the frequency and intensity of begging calls and begging displays
53 (Leonard and Horn, 2001; Mock et al., 2011; Ottosson et al., 1997).

54 Decisions about allocation of parental resources can also depend on life history strategy. In
55 particular, the likelihood of future reproduction is expected to affect the level of parental investment in
56 current reproduction. For instance, in bird populations breeding at more extreme latitudes, the
57 potential for future reproduction tends to be lower due to lower adult survival. Consequently, parents
58 invest more in current reproduction in higher latitudes compared to birds breeding in lower latitudes
59 (Ardia, 2005; Ghalambor and Martin, 2001; Martin et al., 2000).

60 Resource allocation decisions may be proximately regulated by the physiological state of an
61 individual (McNamara and Houston, 1996). For example, the hypothalamic-pituitary-adrenal (HPA) axis,
62 and glucocorticoid hormones in particular, can mediate the trade-off between resources allocated to
63 reproduction or self-maintenance (Bonier et al., 2009a; Wingfield and Sapolsky, 2003; Wingfield et al.,
64 1998). An acute increase in glucocorticoids might trigger allocation of energetic resources to self-
65 maintenance and survival at the expense of allocation to reproductive effort (Wingfield and Sapolsky,

66 2003; Wingfield et al., 1998). Conversely, experimental studies showed that individuals with high current
67 reproductive effort have a reduced glucocorticoid response to stressors (Lendvai and Chastel, 2008;
68 Lendvai et al., 2007). Finally, glucocorticoid levels often covary negatively with measures of individual
69 condition or habitat quality (Moore et al., 2000). Based on these lines of evidence, levels of
70 glucocorticoids are often expected to be negatively correlated with reproductive investment (Bonier et
71 al., 2009a).

72 More recently, evidence has started to accumulate that corticosterone (the main avian
73 glucocorticoid, henceforth referred to as “cort”) at baseline levels may support reproductive investment
74 such that cort levels actually increase with some metrics of reproduction (Bonier et al., 2009b; Bonier et
75 al., 2011; Crossin et al., 2012; Love et al., 2004; Moore and Jessop, 2003; Ouyang et al., 2013). This
76 hypothesis, termed the Cort-Adaptation Hypothesis, suggests that increased baseline cort levels can
77 induce increased foraging and offspring provisioning behavior and decreased sensitivity to acute stress,
78 which in turn leads to higher reproductive effort and fitness (Angelier and Chastel, 2009; Angelier et al.,
79 2007; Bonier et al., 2009a). Consistent with this hypothesis, brood value and baseline cort are positively
80 correlated across species (Bokony et al., 2009), implying that baseline cort reflects high investment in
81 current reproduction.

82 Evidence for the Cort-Adaptation hypothesis also comes from studies of variation in parental
83 investment and cort within species. For instance in a recent study of tree swallows (*Tachycineta bicolor*),
84 females with higher baseline cort during the offspring provisioning stage fledged more young than
85 females with lower cort (Bonier et al., 2009b). Female swallows also increased baseline cort levels when
86 they were caring for an experimentally enlarged brood, as compared to females caring for
87 experimentally reduced broods (Bonier et al., 2011). Similarly in house sparrows (*Passer domesticus*),
88 the number of fledglings a female was able to raise was positively correlated with the change in the

89 females' baseline cort levels from pre-laying to the nestling feeding period (Ouyang et al., 2011). In
90 another study on macaroni penguins (*Eudyptes chrysolophus*), experimentally increased cort levels
91 within the normal range of baseline caused increased foraging activity of females who subsequently
92 raised heavier chicks than control implanted females (Crossin et al. (2012).

93 Here, we ask two related questions regarding the strategic adjustment of parental care in
94 response to offspring signals in two box-nesting populations of tree swallows in Ontario, Canada and
95 North Carolina, USA. We manipulated offspring demand perceived by females through the use of an
96 automated playback system (Lendvai et al., 2015b) where nestling begging calls were directed
97 specifically to females for six hours when nestlings were six days of age. In addition, we measured
98 baseline cort levels in the same females once during the incubation period and once immediately after
99 the playback period (9-13 days after the first sample, depending on the hatch date).

100 Tree swallows in our southern population in North Carolina have higher annual return rates – a
101 robust proxy for annual survival in this highly philopatric species (Winkler et al., 2004) – and a longer
102 breeding season that in some instances even allows birds to raise a second brood (MS & ÇA,
103 unpublished data). In contrast, tree swallows in Ontario have lower annual return rates and a shorter
104 breeding season, with only one brood raised per pair each year. Greater annual survival in the North
105 Carolina population means that, on average, these birds have more opportunities for future
106 reproduction than birds in Ontario. Higher potential for future reproduction will tend to decrease the
107 value of the current brood (Ardia, 2005), such that current brood value will be lower for NC tree
108 swallows compared to Ontario tree swallows. Thus, the use of these two populations allows us to
109 compare responsiveness of parental investment to cues of offspring demand across populations with
110 different brood values (Bokony et al., 2009; Silverin et al., 1997; Sol et al., 2012).

111 The first question we ask is whether adjustment of parental care effort to offspring begging calls
112 differs between the two populations. This question relates to the Brood Value Hypothesis which predicts
113 that adjustment of parental investment in response to cues from offspring will depend on the value of
114 current reproduction vs. future reproduction (Silverin et al., 1997). Thus, this hypothesis predicts that
115 females should increase parental care in response to experimentally increased offspring demand more
116 (or only) in the northern population with higher brood value compared to the southern population.

117 The second question relates to the role of cort in mediating strategic adjustments in parental
118 effort. The Cort-Adaptation Hypothesis predicts that increases in parental investment should be
119 positively correlated with increases in cort levels (Bonier et al., 2009a). As such, females that received
120 playbacks should show greater increases cort levels than control females, which did not receive
121 playbacks. We also test the prediction from the Cort-Adaptation hypothesis that higher increases in cort
122 during nestling period will predict higher fledging success.

123 **Material and Methods**

124 *Study site and species*

125 The tree swallow is a widespread secondary cavity nesting species that breeds across a wide
126 range of latitudes from Alaska and Northern Canada to the southern USA. We studied tree swallows at
127 two field sites where they nest in artificial nest boxes: Queens's University Biological Station, Ontario,
128 Canada (N44°34'2.02", W76°19'26.036", 121 m elevation) and near Davidson College, Davidson, North
129 Carolina (NC), USA (N34°31' 32.34", W80°52'40", 240 m elevation). These two sites differ in the length
130 of the breeding season (May to July in Ontario and March to July in NC). Tree swallows have high
131 breeding site fidelity, and so return to the breeding population is often used as a proxy of annual
132 survival (Winkler et al., 2004). In our NC population, return rates are around 50% for females (51% in
133 2015), higher than the Ontario population (average 22% between 1975-2012, range 10-45%), as has

134 been found in other studies comparing southern and northern populations of tree swallows (Ardia,
135 2005). The procedures used in the study followed the guidelines for animal care outlined by Animal
136 Behavior Society and Association for the Study of Animal Behavior, and were approved by approved by
137 the Institutional Animal Care and Use Committee at Virginia Tech (#12-020) and the Canadian Wildlife
138 Service (#10771).

139 *Nest monitoring*

140 We monitored the nests by visiting each nest box weekly until the parents started nest
141 construction, after which point we visited the nest box every three days until an egg was detected. We
142 checked the nest box every day until no new eggs were laid for two days in a row, which indicated that
143 incubation had started. Female tree swallows typically lay 1 egg per day, and begin incubation on the
144 day of laying of the last egg (Winkler et al., 2011). The date of laying of the last egg was considered day 0
145 of the incubation period. The incubation period typically lasts 14 days, so we checked each incubating
146 nest daily starting from day 12 of the incubation period until all chicks hatched to determine the date of
147 hatching, which was defined as the day when the first chick hatched. Day of hatching was considered
148 day 0 of the nestling period. Throughout the nestling period, we checked the nest at least every 3 days
149 until day 16, at which point we stopped disturbing the nest until day 22 to determine fledging success.

150 *Banding parents and nestlings*

151 We captured females using box traps at their nest on day 10 of the incubation period to record
152 body measurements (tarsus, wing chord, weight, skull size), collect a blood sample for cort analysis
153 (within 3 minutes of capture), and mark birds with a numbered metal band and a unique passive
154 integrated transponder (PIT) tag that was integrated into a plastic colored leg band (EM4102 tags from
155 IB Technology, UK). Each female was tagged with a red color band/PIT tag. We captured the males at
156 their nest box on day 2 or 3 of the nestling period. We took the same measurements from the males,

157 except that we did not collect blood samples to minimize handling time and capture stress for males.
158 Males were also tagged with a numbered metal band and a blue PIT tag. We report a detailed analysis of
159 male parental behavior as a function of treatment and female behavior elsewhere. We measured tarsus
160 length and weighed nestlings on the afternoon of day 6 and again on day 12 when each nestling
161 received a numbered metal band.

162 *Playback experiment*

163 We recorded begging calls from 10 nests on the afternoon of day 6 by pointing a Sennheiser
164 ME66/K6 directional microphone attached to a Marantz PMD 660 Solid State recorder into the nest. To
165 initiate nestling begging, we tapped at the nest entrance, which is a similar sound to what the parents
166 make as they land on the nest box. We used the software Syrinx (John Burt, Seattle, WA;
167 www.syrinxpc.com) to create 30 second stimulus files from the recorded begging calls, with a standard
168 call rate that initially was 14 begs/sec that gradually decreased to a constant 4 begs/sec, simulating a
169 natural pattern of begging in which the nestlings beg vigorously immediately upon arrival of the parent
170 and then tail off gradually. The 10 stimulus files were randomly allocated to the treatment nests. We
171 used a radio-frequency identification (RFID) reader (an upgrade of the model described in Bridge and
172 Bonter, 2011), that was obtained from Cellular Tracking Technology, PA, USA) attached to a micro-
173 computer (Raspberry PI) to carry out the playbacks automatically every time the female (but not the
174 male) perched at the nest box entrance. The playback set-up is described in detail elsewhere (Lendvai et
175 al., 2015b). Briefly, we attached an antenna around the entrance hole of the nest box that was
176 connected to an RFID reader. The RFID reader in turn was connected to a Raspberry PI computer which
177 was running a Python script that played back the begging calls for 30 seconds every time the RFID reader
178 detected the female's PIT tag, with the exception of a refractory period of 2 minutes from the start of
179 each playback (to avoid situations where the playback would be triggered when the female left the

180 nest). The playback apparatus was also installed for control nests, but no sound was played. Treatments
181 were allocated to the nests using a randomized block design, to control for seasonal differences.

182 The playback system was set up in the morning around 7am on day 6 post hatching and stopped
183 approximately 6 hours later when we captured the females in their nest box and obtained a second
184 blood sample for cort analysis. We had 21 control and 15 playback nests in NC and 19 control and 18
185 playback nests in Ontario. In NC, three of the nests that were intended to be playback nests never
186 received any playbacks due to the failure of the system, and as such they were included in the analysis
187 as control nests, which caused the uneven sample sizes. One additional nest in NC was excluded from
188 analyses because it only received 2.7 hr of playback due to equipment failure halfway through the
189 experiment, making it intermediate to control and playback conditions.

190 *Blood sampling and hormone assay*

191 We obtained blood samples (approximately 120 μ l) by puncturing the brachial vein within 3
192 minutes of capturing the females to minimize the influence of the stress of capture on measured cort
193 levels (Romero and Reed, 2005). Blood was stored on ice in the field, and centrifuged in the laboratory
194 within 6 hours to separate the plasma. The plasma was then stored at -20°C until taken to Virginia Tech
195 for hormone assay.

196 Total cort in plasma was determined by direct radioimmunoassay following an extraction with
197 dichloromethane (Bonier et al., 2009a; Wingfield et al., 1992). Mean extraction efficiency of a known
198 quantity of radiolabeled hormone was 83%, and we corrected for the individual extraction efficiencies in
199 calculating final concentrations. Briefly, we incubated the extracts overnight at 4°C with 10K cpm of 3H-
200 Cort (Perkin Elmer, Product number: NET399250UC) and antiserum (Esoterix Endocrinology, Calabasas
201 Hills, CA 91301, Product number: B3-163). We then added dextran-coated charcoal to separate cort
202 bound to antibodies. Intra-assay variation of known concentration standards was 3.93%.

203 *Quantifying parental effort*

204 We quantified parental visit rates in two ways: first, we carried out 1-hour feeding watches on
205 day 5 and day 6 (the day before and the day of the treatments) where an observer sat 30 m from the
206 nest and noted every visit of the male and female using a spotting scope and a voice recorder. We also
207 quantified visit rates from the RFID records as described in detail in Lendvai et al. (2015a). We checked
208 the visit rates from 1-hour nest watches against the visit rates calculated from RFID logs of the same
209 time periods. There was a high correspondence between the two ($r=0.68$, $p=0.2 \times 10^{-7}$, for females and
210 $r=0.67$, $p=0.4 \times 10^{-7}$ for males, $n=43$). Because the RFID observations spanned the entire duration of the
211 experiment we used these as the main measure of parental visit rates. Visit rates are an excellent
212 measure of the feeding rates in the tree swallows, as most visits are for feeding (McCarty, 2002).

213 *Data analyses*

214 We used generalized linear mixed models (GLMM) to assess the effects of treatment and
215 population on cort and behavioral data. We entered the cort data into a GLMM with time period
216 (incubation or nestling), treatment (playback vs. control), and population (Ontario vs. NC) as fixed
217 factors. Playback stimulus and bird ID were included as random factors.

218 We analyzed the female feeding rates derived from RFID recordings with GLMMs using the fixed
219 factors treatment (playback vs. control), population (Ontario vs. NC), and time period. For the latter
220 factor, we used four levels: pre-treatment (day 5) feeding rates (6 hrs during the same time of day as the
221 experimental period on the next day) and feeding rates from the period while the playback or control
222 treatment was in effect in day 6, which we further divided into three two-hour periods to assess any
223 temporal changes in effects of playback on female behavior. We included playback stimulus and bird ID
224 as random factors and also included an offset variable for log of duration of playback to control for the
225 variation in how long the birds were exposed to the playbacks (mean= 6.24 ± 0.05 SE hours). Because of

226 the large number of predictor variables (3 fixed factors and their interactions) in these mixed models,
227 we used a model averaging approach. We first ran a model with all predictor variables and their
228 interactions and subsequently used model averaging with R-package MuMIn (Bartoń, 2013). In the
229 averaged models, we included all models within 2 AICc of the best model (i.e. the model with the lowest
230 AICc).

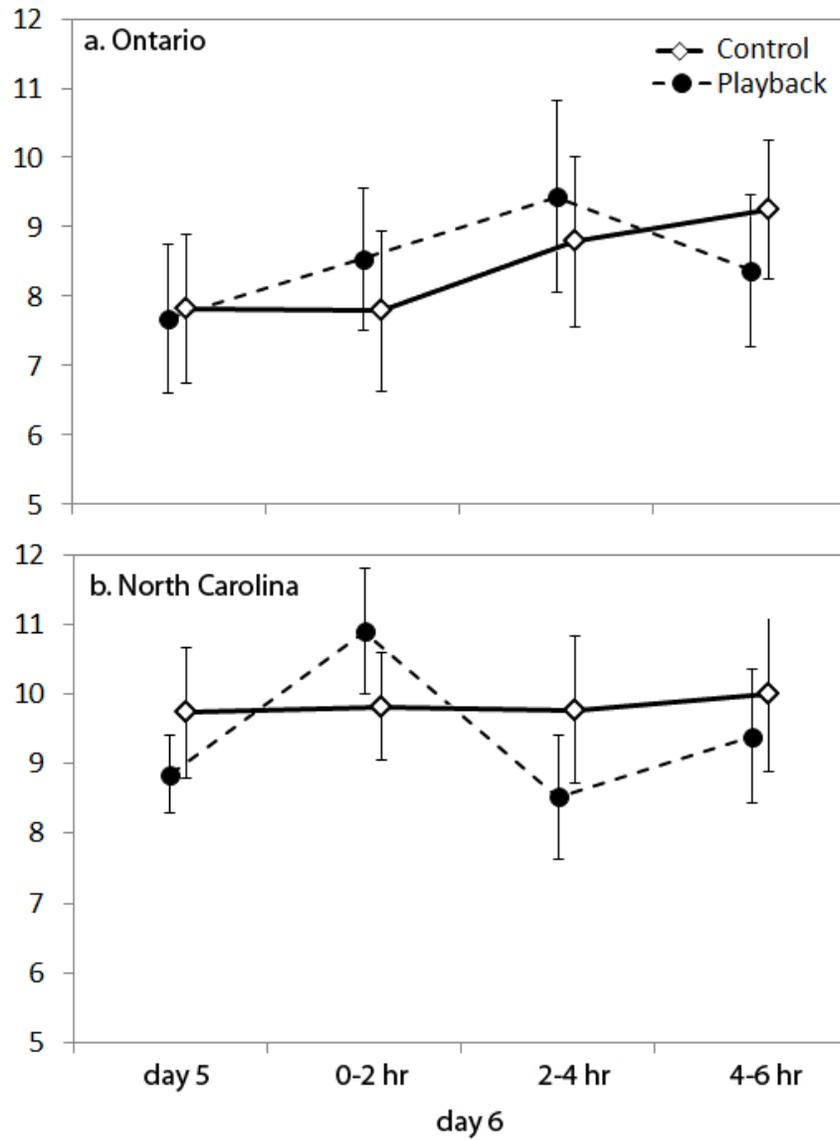
231 We also examined whether change in cort (base-10 logarithm of ratio of post-treatment cort to
232 pre-treatment cort) between incubation and nestling periods predicted number of chicks fledged using a
233 generalized linear model with Poisson distribution and log link (Bonier et al., 2011). For this analysis we
234 included change in cort, treatment, population and their interactions as predictor variables and again
235 used model averaging as above.

236 Finally, we analyzed nestling growth (nestling mass on day 6 and day 12) as well as fledging
237 success using GLMMs. In these models, we examined the fixed factors population, treatment, and their
238 interactions and included relative lay date (number of days from the first egg of the respective
239 population) as a random factor as it has a strong effect on clutch size with later clutches containing
240 fewer eggs in both populations.

241 **Results**

242 *Female feeding rates:* Nestling playbacks had a transient effect on female feeding rates. Females
243 that received playbacks of nestling begging calls increased their feeding rates in the first two hours of
244 the playbacks on day 6, compared to their average feeding rates the previous day. No such increase was
245 observed in the control females (Figure 1, see model results in Table 1). No other main or interaction
246 effects were significant (Table 1).

247



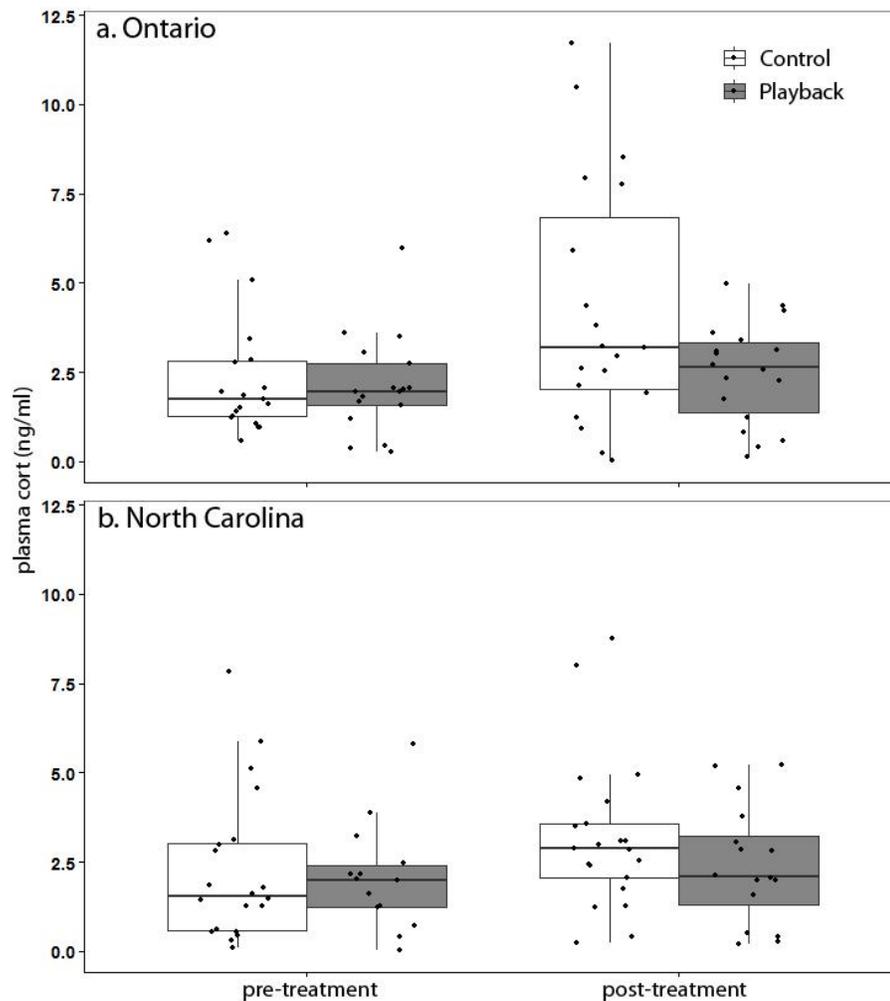
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249 Figure 1. Average feeding rates of females on the day before treatment (day 5) and during the treatment
250 (day 6), the latter in 3 two-hour increments. The feeding rates were estimated from RFID logs. The error bars
251 denote ± 1 standard error.

252

253

254 *Corticosterone*: In the averaged model, the only significant coefficient was nesting stage:
255 females had significantly higher cort levels during the nestling period compared to the incubation period
256 (Figure 2). Treatment did not have a main effect or enter into an interaction with stage.

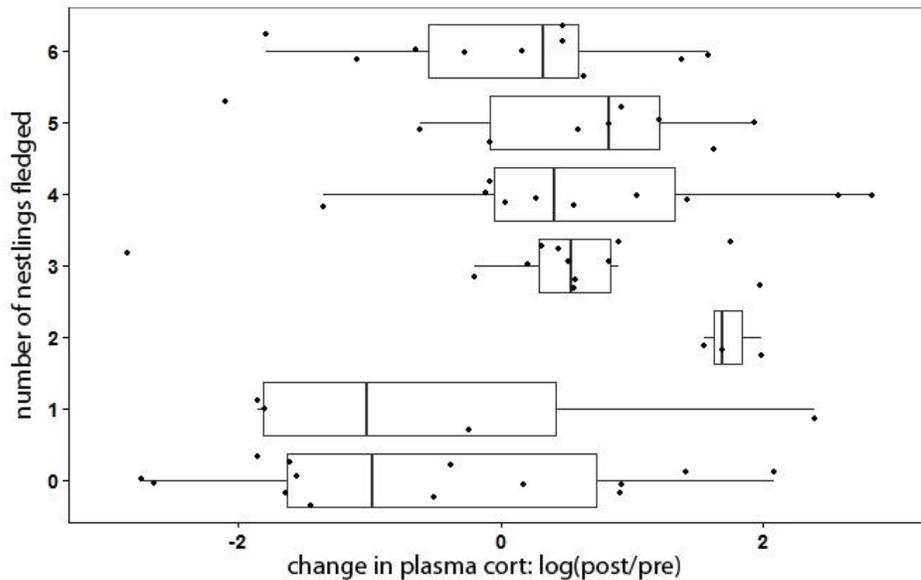


257
258 Figure 2. Circulating plasma cort (baseline) levels of females pre-treatment (late incubation stage) and post-
259 treatment (immediately after the playbacks during the nestling stage). The boxplots represent the median (middle
260 line), 25% and 75% percentiles (the lower and upper boundaries of the boxes respectively), and the 1.5
261 interquartile range (whiskers). Individual data points are also shown.

262

263

264 There was a positive correlation between female change in cort (ratio of post- to pre-treatment
265 cort) and fledging success. In the averaged model, females with greater increases in cort from the
266 incubation to the nestling stage fledged more offspring (Figure 3, see Table 4 for the averaged model).
267 The effects of treatment and population were not significant.



268

269 Figure 3. Fledging success as a function of change in baseline plasma cort levels of females from incubation to the
270 nestling period. Change in plasma cort is depicted as the logarithm (base 10) of the ratio of plasma cort during
271 nestling period to plasma cort during incubation. Thus, zero equals no change in plasma cort from incubation to
272 nestling period. The boxplots show the change in cort for each number of fledging category, and the dots are
273 individual data points.

274 *Mass:* There was a significant effect of nesting stage on body mass: almost all females lost
275 weight from the first to second capture (see Table 5 for the best model). The main effects of population
276 and treatment were also significant. The main effects were modified by two significant interactions:
277 treatment by population (females in the playback treatment were lighter than the control females in the
278 NC but not in Ontario population), and population by stage (females in NC lost more weight between
279 the incubation and nestling periods as compared to females in Ontario). Finally, there was an effect of
280 relative laying date with females starting to lay eggs later in the season being lighter.

281 *Clutch size, nestling mass, and fledging success*: There were no significant effects of treatment
282 on clutch size, nestling mass at day 6 and day 12, or fledging success. Nestlings in Ontario were on
283 average significantly heavier at both day 6 and day 12 (Tables S6 and S7, Figures S2, S3), but clutch size
284 and number of nestlings fledged did not differ between the populations. There were no significant
285 interactions of population and treatment in any of the models (see supplementary information).

286 **Discussion**

287 Our aim was to manipulate nestling begging calls to study (1) whether a perceived increase in
288 offspring demand induces a change in parental effort of females in two different populations of tree
289 swallows with distinct brood values. If there was a change in parental effort, we further asked whether it
290 led to (2) an increase in baseline cort as predicted by the Cort-Adaptation Hypothesis and whether the
291 changes in baseline cort from incubation to nestling period was predictive of fledging success. We found
292 that (1) females increased parental effort in response to offspring begging call playback in both
293 populations, but the increase was transient and confined to the early hours of the playback treatment.
294 Consequently, (2) baseline cort levels obtained from blood samples at the end of the 6 hour period did
295 not differ between the control and playback groups. However, change in baseline cort from incubation
296 to nestling period did predict how many nestlings females fledged (with higher increases in cort
297 associated with greater fledgling success).

298 *Change in parental care and baseline cort*

299 Prior experiments on tree swallows and other species showed that glucocorticoids vary with
300 parental effort (Bonier et al., 2009a; Bonier et al., 2009b; Bonier et al., 2011). These studies generally
301 looked at changes in parental care over a longer period (e.g. through brood enlargement or reduction
302 throughout the nestling period). Our aim here was to extend these findings by asking whether cort
303 would dynamically co-vary with changes in cues of offspring demand in the short term. Our failure to

304 detect a difference in cort between females in the playback and control groups does not support this
305 hypothesis. Given our relatively large sample size ($n = 73$ nests) we do not believe the absence of a
306 treatment effect is due to lack of power. We do however offer another caveat in that the effect of the
307 nestling playbacks on female parental behavior was transient and confined to the first few hours of the
308 playbacks whereas we obtained blood samples at about 6 hours after the start of the playback, and
309 compared cort in those samples to cort measured 9-10 days prior to the playback. By the time the post-
310 experimental blood samples were collected, female nest visit rates had returned to baseline levels, and
311 were not significantly different between the playback and control group. Our experimental approach
312 may have therefore lacked the precision to detect a transient increase in cort corresponding to the
313 transient increase in female feeding rates.

314 The fact that playbacks had only a transient effect on female feeding behavior is somewhat
315 surprising given that previous studies manipulating female feeding behavior through automated or
316 manual playbacks of nestling begging calls used durations from 1 hour (in great tits, *Parus major*; Hinde,
317 2006; and in blue tits; Lucass et al., 2016) or several days (in pied flycatchers, *Ficedula hypoleuca*;
318 Ottosson et al., 1997), and in both cases found an effect of the playbacks on behavior. This could reflect
319 habituation to the stimulus, and/or an inability of the females to maintain a high rate of feeding,
320 although the latter possibility seems less plausible given the above studies found persistent effects in
321 different species. Whatever the cause, the transient effect of the playbacks means that any effect on
322 cort may also have been transient and therefore would only have been detected if we had captured the
323 females when the playbacks had their maximal behavioral effect.

324 The Cort-Adaption Hypothesis predicts that increases in baseline cort during the period of
325 parental care should increase fledging success. We found support for this prediction: females with the
326 greatest increases in cort from incubation to nestling period fledged more offspring. This finding is

327 consistent with an earlier study in the Ontario population, in which experimentally increased broods
328 induced greater increases in cort through the breeding season, and changes in cort within females were
329 positively correlated with fledging success across both experimental and control groups (Bonier et al.,
330 2011). The current results extend the previous findings by showing that the positive link between small
331 increases in baseline cort and fledging success can be detected in natural brood sizes.

332 The finding that females in both populations adjusted parental care in response to begging calls
333 is in contrast to an earlier study in this species that found effects of brood size manipulation on females
334 consistent with the brood value hypothesis (Ardia, 2005). In that study, broods were either enlarged or
335 reduced by 50% in two populations of tree swallows in Alaska and Tennessee. Females in Alaska
336 increased their nest visit rate in the enlarged condition to maintain the same level of nestling condition,
337 whereas females in Tennessee did not increase their visit rate and, subsequently, nestlings in enlarged
338 broods were of lower condition. These results were consistent with the life-history theory and the
339 brood-value hypothesis (Ghalambor and Martin, 2001; Martin et al., 2000). However, the present result
340 may suggest that females in southern populations are able to increase their parental effort in the short-
341 term similar to their northern counterparts (the finding in the present study) but may be limited in the
342 long term due to lower food availability in the southern populations (the situation faced by females due
343 to permanent addition of extra nestlings in the study by Ardia, 2005). Indeed, Ardia (2005) found that
344 insect availability was lower in the southern population, making a chronic increase in offspring demand
345 harder to meet for the southern parents.

346 In summary, our results suggest that females are able to flexibly adjust their feeding rates in
347 response to simulated increased demand from their nestlings. Additionally, increases in baseline cort
348 levels of females from incubation to nestling period predicted fledging success across broods. Therefore,
349 although it is unclear whether glucocorticoids are involved in short-term strategic adjustment of

350 parental care, the data suggest that longer-term changes in baseline cort levels are positively correlated
351 with fitness. We believe the data warrant further research into hormonal changes that may occur at
352 shorter time scales and that glucocorticoids may play a casual role in short-term adjustment of parental
353 effort.

354 **Acknowledgements**

355 We are grateful to Alice Domalik, and Pria St John (Queen's University), Drew Gill and Spencer Gill

356 (Davidson College) for the excellent help in the field.

357 Funding: This work was supported by a U.S. National Science Foundation (NSF) grant (FB, ITM, and MFH;

358 IOS-1145625), and by the Natural Sciences and Engineering Research Council of Canada Banting

359 Postdoctoral Fellowship (FB). During the preparation of the manuscript, ÁZL was supported by a grant

360 from the Hungarian Research Fund (OTKA K 113108).

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- 454

455 Table 1. Model averaged coefficients of predictors of female feeding rates. The comparison for the
 456 period, population, and treatment is pre-treatment (day 5), NC, and control, respectively. See
 457 text for details and supplementary materials for the specific models in the averaged model.

	coefficient	Estimate	Std. Error	P value	# of models
Period	during 1 st 2 hrs	0.10	0.06	0.090	4
	during 2 nd 2 hrs	0.03	0.05	0.568	
	during last 2 hrs	0.06	0.04	0.146	
Population	Ontario	-0.18	0.12	0.126	3
Period*population	during 1 st 2 hrs*Ontario	-0.12	0.07	0.084	2
	during 2 nd 2 hrs*Ontario	0.11	0.07	0.102	
	during last 2 hrs*Ontario	0.03	0.06	0.616	
Treatment	Playback	-0.05	0.12	0.661	1
Period*Treatment	during 1st 2 hrs* playback	0.18	0.07	0.005	1
	during 2 nd 2 hrs* playback	0.03	0.07	0.625	
	during last 2 hrs* playback	0.01	0.06	0.886	

458

459 Table 2. Model averaged coefficients of predictors of male feeding rates. The comparison for the period,
 460 population, and treatment is pre-treatment (day 5), NC, and control, respectively. See text for details
 461 and supplementary materials for the specific models in the averaged model.

	coefficient	Estimate	Std. Error	p-value	# of models
Period	during 1 st 2 hrs	-0.07	0.08	0.369	4
	during 2 nd 2 hrs	-0.13	0.08	0.093	
	during last 2 hrs	0.00	0.06	0.941	
Population	Ontario	0.23	0.15	0.142	4
Treatment	Playback	-0.09	0.15	0.542	3
Period*Population	during 1 st 2 hrs*Ontario	-0.20	0.13	0.131	4
	during 2nd 2 hrs*Ontario	0.26	0.11	0.013	
	during last 2 hrs*Ontario	0.15	0.08	0.075	
Period*Treatment	during 1 st 2 hrs* playback	0.10	0.13	0.421	3
	during 2 nd 2 hrs* playback	0.14	0.11	0.184	
	during last 2 hrs* playback	0.14	0.08	0.094	
Population*Treatment	Ontario*Playback	-0.23	0.25	0.349	2
Period*Population*	during 1st 2 hrs* Ontario* playback	0.43	0.17	0.010	1
Treatment	during 2 nd 2 hrs* Ontario* playback	0.28	0.15	0.073	
	during last 2 hrs* Ontario* playback	0.15	0.14	0.282	

462

463

464 Table 3. Averaged GLM model from 4 best models (within 2 Δ AICc of best) of predictors of female CORT.
 465 The following factor levels were used as baseline for the intercept: incubation (Stage), control
 466 (Treatment), and NC (Population). Female baseline corticosterone (cort) levels significantly increased
 467 from incubation to nestling period.

	model averaged coefficients	standard error	p-value	# of models
Stage	1.15	0.48	0.017	4
Treatment	-0.51	0.51	0.33	4
Stage*Treatment	-1.09	0.69	0.12	2
Population	0.37	0.34	0.29	2

468

469 Table 4. Averaged model (from 3 best models) examining predictors of the number of fledglings. For the
 470 treatment and population, control and NC were used as baseline, respectively. Change in corticosterone
 471 (cort) was positively correlated with number of nestlings fledged.

	model averaged coefficients	standard error	p-value	# of models
Change in cort	0.10	0.047	0.029	3
Treatment	0.14	0.15	0.35	1
Population	-0.08	0.15	0.61	1

472

473 Table 5. The best GLM model on female body mass. The model selection table revealed that the Δ AICc
 474 between the best model and the second best was 2.32. The following factor levels were used as
 475 baseline for the intercept: incubation (Stage), control (Treatment), and NC (Population).

	Coefficient	Std Error	p-value
Treatment	-0.83	0.37	0.03
Population	-0.89	0.43	0.04
Stage	-4.30	0.31	<0.0001
Relative Lay Date	-0.06	0.02	0.0001
Treatment*Population	1.43	0.53	0.002
Population*Stage	1.38	0.42	0.007

476