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1 **Sex-specific negotiation rules in a costly conflict over parental care**

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18

19 **Abstract**

20 Sexual conflict theory predicts a trade-off in individual parental care allocated to either
21 current or future reproduction. The optimal amount of current parental effort is expected to
22 differ between adult males and females, with a conflict resolution being reached by
23 negotiation depending on multiple family cues. Currently, a debate exists on how negotiation
24 takes place, along with its potential costs or benefits for all family members. In particular, the
25 specific negotiation rules that male and female parents apply often remain obscure, which in
26 part results from a shortage of empirical studies. We used captive canaries, *Serinus canaria*,
27 to evaluate consequences of sexual conflict for the offspring by comparing uniparental
28 (female cared for a half clutch) and biparental (both parents cared for a full clutch) families.
29 Our results suggest overall less parental effort in biparental families and offspring were
30 observed to beg harder for parental resources, weigh less as fledglings and tended to grow
31 slower compared to uniparental families. To further increase our understanding of parental
32 negotiation rules, we manipulated the degree of partner visibility and thus information about
33 partner effort by temporarily splitting biparental families. Male and female provisioning
34 strategies depended on both partner visibility and brood demand. An increase in male
35 provisioning was observed after mate removal, whereas the opposite pattern was observed in
36 females. Females, however, increased provisioning in response to offspring begging. We
37 conclude that (1) sexual conflict over parental care is costly for the offspring, (2) sex-specific
38 negotiation rules exist and probably relate to an asymmetry in gathered information and (3)
39 changes in parental feeding strategies trigger a feedback mechanism via brood demand,
40 highlighting the need to consider all family members in order to understand family conflicts
41 and their potential resolution.

42 **Key words:** negotiation, offspring begging, parental care, parental provisioning, sexual
43 conflict

44 **Introduction**

45 Sexual conflict is expected to arise when males and females have different fitness optima for
46 a given trait and do not reach these optima simultaneously (Arnqvist & Rowe 2005). Previous
47 studies on sexual conflict, along with its causes, consequences and role in speciation (Parker
48 & Partridge 1998; Arnqvist et al. 2000), have mainly focused on a battle prior to zygote
49 formation (Parker 2006). However, sexual conflict after zygote formation is receiving
50 increased research interest (reviewed in Royle et al. 2012). In particular, the role of
51 negotiation between parents in how conflict over the amount of parental care provided for the
52 offspring can be resolved (Lessells 2012) has been the focus of attention since Trivers (1972)
53 started the evolutionary discussion on the limited harmonization that exists between parents.
54 The essence of sexual conflict over parental care is captured in a trade-off between current
55 and future reproduction for each parent (Houston et al. 2005). Care results in a clear benefit
56 for the offspring and inherently increases the fitness of both parents, but each parent only has
57 to pay the cost of its own contribution (Royle et al. 2012). In most cases, it is therefore in
58 each parent's interest to limit its own effort and leave the highest workload for its mate. None
59 the less, biparental care is observed in a taxonomically diverse range of species (Royle et al.
60 2012), with an overall increased number of offspring reared being the main benefit over
61 uniparental care (Smith & Härdling 2000; Royle et al. 2006). Indeed, once biparental care has
62 evolved, subsequent coevolution of male and female parental behaviour may result in one
63 parent becoming unable to care for the entire brood alone (Houston & Davies 1985; Lessells
64 2012). How sexual conflict is resolved and to what extent each parent should provide care
65 have been central themes of numerous mathematical models (Lessells 2012) and empirical
66 studies (reviewed by Harrison et al. 2009).

67 The classic 'sealed bid' game-theoretical approach of Houston & Davies (1985) suggested
68 that each parent benefits by exploiting its partner's effort until an evolutionarily stable level

69 of care is established. This model assumed fixed levels of individual effort, despite flexibility
70 in care behaviour being observed in response to changed partner effort (Harrison et al. 2009).
71 This has triggered the development of models to include such flexibility, or negotiation in
72 ‘behavioural time’ (McNamara et al. 1999, 2003). Each parent is expected to adjust its effort
73 in response to its partner by monitoring each other’s activity pattern (Hinde 2006; Johnstone
74 et al. 2014) or the condition of the brood (Hinde & Kilner 2007; Lessells & McNamara 2012)
75 in a series of alternated bids (or bouts). It became clear that selection acts on a parent’s
76 behavioural response to its mate’s behaviour (McNamara et al. 1999), rather than on a
77 specific level of parental effort per se (Houston & Davies 1985). As a result of evolved
78 negotiation rules, parents may be able to exploit their mate, perhaps even by handicapping
79 themselves (Barta et al. 2002; Houston et al. 2005). Ultimately, this theory predicts that
80 negotiation could result in offspring faring worse under biparental care, implying a cost of
81 sexual conflict (Royle et al. 2002, 2006; Lessells & McNamara 2012). Recent observations in
82 great tits, *Parus major*, however, suggest a completely opposite pattern in which parents
83 appear to match each other’s investment, resulting in more turn taking and high brood visit
84 rates (Johnstone & Hinde 2006; Hinde 2006). These controversial observations inspired an
85 alternative negotiation model (Johnstone et al. 2014), which contrarily predicts enhanced
86 offspring fitness driven by behavioural coordination between parents that acts as a form of
87 reciprocity and reduces sexual conflict.

88 Taken together, the theoretical models on conflict resolution by negotiation described above
89 predict contrasting consequences for the offspring. Empirical tests for such consequences are
90 limited to a single study with captive zebra finches, *Taeniopygia guttata* (Royle et al. 2002,
91 2006). Furthermore, altered provisioning behaviour in response to changed partner effort is
92 expected to trigger a dynamic feedback mechanism with offspring begging behaviour
93 (Morales & Velando 2013). Thus parental negotiation rules may result not only from sexual

94 conflict over care, but also from changes in offspring behaviour (Parker et al. 2002b; Smiseth
95 et al. 2008; Thorogood et al. 2011). Therefore, empirical studies are urgently needed to fill
96 this knowledge gap on the mechanisms and consequences of parental negotiation, without
97 neglecting the multiple family cues that each parent may use to gain information (Houston et
98 al. 2005; Hinde & Kilner 2007).

99 Studies addressing this topic have typically examined the change in parental effort when a
100 focal bird's mate was either experimentally removed or handicapped (e.g. by feather clipping
101 or adding weights) in comparison with biparental control families (Sasvári 1986; Harrison et
102 al. 2009). A variety of behavioural responses have been reported, but partial compensation
103 was the most general outcome. Although such studies confirm a certain degree of individual
104 responsiveness towards their partners, two major concerns arise: first, mate handicapping
105 techniques are likely to change the perception of partner quality, so any observed change in
106 response behaviour may be attributed not solely to changed parental effort, but also to
107 lowered mate attractiveness (i.e. differential allocation, Sheldon 2000). Second, most of these
108 studies say little about the consequences of changes in parental strategies for offspring, and
109 thus the potential costs of negotiation. None the less, the overview of Harrison et al. (2009)
110 revealed two important insights, namely potential differences in both response behaviour
111 between the sexes (Griggio & Pilastro 2007) and between manipulation methods. Sexual
112 differences in parental care do occur and are generally explained in an evolutionary context
113 related to uncertainty of parentage, anisogamy and population sex ratio (Kokko & Jennions
114 2012). Although often neglected in mathematical models, sexual differences in negotiation
115 over parental care are also expected. For instance when costs and/or benefits of parental care
116 differ between males and females (Cezilly 1993; Sanz et al. 2000), but especially when both
117 sexes gather information differently about the brood's need and the partner's work effort
118 (Johnstone & Hinde 2006). In great tits for example, female parents may be better informed

119 as they spend more time with the young, compared to males which invest more time in
120 territory defence (Sanz et al. 2000). The better informed parent is then predicted to work
121 harder, respond more strongly to changes in brood need and compensate more strongly for
122 changes in partner effort (Johnstone & Hinde 2006). An elegant method to investigate such
123 parental negotiation rules depending upon available information entails experimental
124 manipulations of breeding pairs in a reversible way and in a range of treatment levels
125 (Houston et al. 2005). Indeed, the overview of Harrison et al. (2009) clearly indicated more
126 compensatory behaviour in (permanent) mate removal, relative to mate handicapping
127 experiments. Temporarily removing and reversibly restraining parents from providing full
128 care or information gathering may offer a fruitful research tool to assess the informative cues
129 that are important for applying parental negotiation rules.

130 Our aims were threefold. First, we investigated the consequences of negotiation by
131 comparing offspring development in biparental (both parents care for a full clutch) and
132 uniparental (female cares for a half clutch) families. Theoretical models predict negative
133 (Lessells & McNamara 2012) or positive (Johnstone et al. 2014) consequences for the
134 offspring, although empirical evidence is especially limited (Royle et al. 2002, 2006).
135 Second, we aimed to gain innovative insights into the applied negotiation rules of both
136 parents by temporarily manipulating the amount of information that each parent could gather
137 from their partner (Johnstone & Hinde 2006; Harrison et al. 2009). We therefore measured
138 male and female behavioural responses when their partner was temporarily restrained in
139 providing direct care. This was done in a set-up in which the partner was either visible or
140 invisible and thus with a different degree of potentially perceived information on partner
141 work effort. We expected a partial compensation response to be stronger when the partner
142 was invisible (cf. mate removal, Harrison et al. 2009), with potential differences between the
143 sexes. Finally, we simultaneously investigated offspring begging intensity, as this may form a

144 feedback mechanism that may impinge on parental provisioning strategies (Morales &
145 Velando 2013). We expected that the better informed sex may respond more strongly to
146 changes in brood need (Johnstone & Hinde 2006).

147

148 <H1>Methods

149 We used 26 male and 26 female adult Fife Fancy canaries, *Serinus canaria*, for the
150 experiment, originating from our own laboratory stock population. All birds were unrelated
151 first-year canaries. From 15 March 2012 onwards, males were housed in individual cages
152 (50x64 cm and 40 cm high, GEHU cages, Nijverdal, The Netherlands) for territorial
153 establishment and females were housed in one large internal aviary (2x2x2m). All birds
154 experienced a long light regime (14:10 h light:dark) and had access to seeds and water ad
155 libitum. Egg food was provided twice a week. After 5 weeks of long light regime, all birds
156 were paired by randomly allocating females to the male cages and nesting materials were
157 provided. Progress on nest building, egg laying and incubation was monitored daily. We
158 synchronized hatching within broods by keeping the first two eggs at room temperature (20
159 °C) and returning them after the third egg was laid. This minimized within-brood differences
160 in size facilitating cross-fostering (Hinde et al. 2009; Estramil et al. 2013). At hatching (day
161 0), chicks were individually marked with a unique within-nest colour on their back, using
162 nontoxic pens (Artline70N) which was reapplied when necessary. From then onwards, egg
163 food and germinated seeds were provided on a daily basis. Chicks were ringed with a unique
164 code on day 7. The research was approved by the Ethical Committee of the University of
165 Antwerp (ID: 2011-86).

166

167 <H2>Experimental set-up

168 Nests were alternately assigned to uniparental and biparental families ($N = 13$ nests per
169 family treatment; $N = 78$ chicks) on day 2. Meanwhile, chicks were cross-fostered to ensure
170 that any observed variation in chick begging and parental feeding was not attributed to
171 experience with their biological parents after hatching (Estramil et al. 2013). Cross-fostering
172 occurred as follows: nests of four chicks were split into two pairs, one chick pair being cross-
173 fostered to a uniparental nest to be raised by a female alone and the other cross-fostered to a
174 biparental nest. Biparental nests received two pairs of nestlings, to match an equal number of
175 chicks per adult and thus to apply a comparable workload per parent in both groups (Royle et
176 al. 2002, 2006). Only adult females were used in the uniparental group, because males do not
177 engage in brooding and were thus not expected to successfully raise the offspring on their
178 own. Nests were video recorded for almost 2 h (mean \pm 1SE: 108.7 ± 0.3 min) on days 9 and
179 12 (uniparental families) and days 9, 10 and 12 (biparental families) to assess parental
180 feeding and chick begging behaviours (for details see below). An additional manipulation
181 was performed in biparental nests: on days 10 and 12 the nests were temporarily split so that
182 each parent had to take care of two nestlings alone in a separate cage unit. On one of these
183 days, cages were placed opposite to and in contact with each other, so that the adults could
184 see into each other's nest and communicate with each other through the bars (visible partner
185 manipulation). On the other day, the cages were placed in two separate, identical rooms
186 (invisible partner manipulation), to exclude all visible and auditory contact between the
187 parents. The order of these manipulations was randomized between nests and alternated
188 within nests. This set-up enabled us to assess (1) effects of family structure on offspring
189 development, (2) differences in parental provisioning effort and chick begging behaviour
190 between uni- and biparental families on day 9 and (3) differences in temporarily split

191 biparental groups due to partner visibility on days 10 and 12 in biparental groups and (4) to
192 compare female effort in uniparental and split biparental families on day 12.

193

194 <H2>Chick begging and parental provisioning behaviour

195 We used the summed duration of all observed feeding bouts in all analyses as a proxy for
196 parental provisioning effort, with each individual chick being the experimental unit. Each
197 time begging was observed, nestling begging intensity was estimated as in Kilner (2001).
198 Briefly, an intensity score ranging from 1 (i.e. motionless nestling only with open gape) to 4
199 (gape open, head back, neck stretched and back vertical) was noted for each second that
200 begging was observed in the video fragment. Total begging effort was calculated as the sum
201 of all scores over the duration of begging. Finally, begging reward was calculated as the total
202 begging intensity divided by the number of parental feeds received. All videos were analysed
203 using The Observer XT software (Noldus Information Technology, Wageningen, The
204 Netherlands) and all provisioning and begging estimates were corrected for the duration of
205 the recorded video. The latter was done by dividing the total time of the observed behaviour
206 (min) by the length of the video (h).

207

208 <H2>Nestling development and molecular sex determination

209 Chicks were weighed daily from day 0 until day 14. Individual chick growth rate was
210 estimated as the regression slopes of chick body mass against age during the linear phase of
211 the growth curve (i.e. first 14 days). Growth rate determined via nonlinear Gompertz curves
212 gave very similar estimates (Pearson correlation: $r_{50} = 0.97$, $N = 52$, $P < 0.0001$).
213 Furthermore, body mass and tarsus length were measured at day 20 (i.e. at the fledgling

214 stage). Independence is reached at the age of 30 days, at which time chicks are no longer fed
215 by their parents. On this day, final chick body mass was measured and a blood sample (50 µl)
216 was collected from the alar wing vein for molecular sex determination. DNA was extracted
217 from red blood cells using Chelex resin-based DNA extraction (Walsh et al. 1991) or Qiagen
218 DNeasy kit methods applying the manufacturer's protocol. CHD genes were amplified by
219 PCR using the protocol of Griffiths et al. (1998). The amplified PCR product was separated
220 on a 1.5% agarose gel stained with ethidium bromide. Males were identified as having a
221 single CHD-Z band whereas females also have a CHD-W band.

222

223 <H2>Statistical analysis

224 Separate linear mixed models were applied to test for differences in chick development
225 (growth rate, body mass at day 20 and 30 and tarsus length) between family treatments
226 (uniparental and biparental). Additional mixed models were performed for body mass, but
227 corrected for size by adding tarsus length as an extra explanatory variable. Similar linear
228 mixed models were performed to test for behavioural differences (total begging intensity,
229 begging reward and parental feeding effort) between uniparental and biparental families on
230 day 9. Family treatment, chick mass and their interaction were added to the model as
231 explanatory variables. Finally, in a mixed model using backward stepwise elimination, we
232 tested whether male and female parents differed in parental provisioning effort during the
233 visibility manipulation (day 10 and day 12). Explanatory variables in this model include
234 experimental manipulation (visible or invisible partner), chick weight and chick begging
235 intensity, along with feeding sex as the main effect and as an interaction with all former
236 parameters. Total begging intensity and parental feeding effort had to be square root-
237 transformed to meet assumptions for normality. Given the genetic similarities among

238 nestlings within the original nest before cross-fostering and the similar environmental
239 conditions within each foster nest, both original nest ID and foster nest ID were added as
240 independent random factors to all these models to adjust for a bias in statistical independence.
241 Tests for potential sex differences in nestling development and biased provisioning towards
242 male or female chicks are presented in the Appendix. All analyses were performed in SAS
243 9.3 (SAS Institute Inc., Cary, NC, U.S.A.). Significant findings are indicated by $P < 0.05$,
244 tendencies by $P < 0.10$ and nonsignificant results by $P > 0.1$. Means ± 1 SE are presented
245 throughout the results.

246

247 <H1>Results

248 <H2>Comparison of uni- and biparental families

249 <H3>*Nestling development*

250 Several marked differences were observed between chicks raised in different family
251 treatments. Chicks from uniparental families were significantly heavier, both absolute (17.76
252 ± 0.50 g versus 15.97 ± 0.36 g; $F_{1,36} = 8.56$, $P = 0.006$; Fig. 1a) and corrected for tarsus
253 length ($F_{1,35} = 11.16$, $P = 0.002$) at fledging and tended to grow faster (0.60 ± 0.04 g/day
254 versus 0.55 ± 0.04 g/day; $F_{1,37} = 2.99$, $P = 0.092$) than chicks raised in biparental nests.
255 Similar patterns were observed for size-corrected body mass at independence ($F_{1,19} = 4.47$, P
256 $= 0.048$).

257

258 <H3>*Chick begging and parental provisioning (day 9)*

259 Chick begging behaviour and parental provisioning effort both differed strongly between
260 family treatments. Specifically, parental feeding effort was much lower in biparental families
261 (10.2 ± 1.8 min/h versus 24.2 ± 5.7 min/h; $F_{1,35} = 7.56$, $P = 0.009$; see Fig. 1b) and was
262 biased towards heavier chicks ($F_{1,35} = 14.53$, $P = 0.0005$). On the other hand, begging
263 intensity was significantly higher in biparental than uniparental families (respective scores:
264 783.0 ± 40.0 versus 509.4 ± 34.0 ; $F_{1,36} = 8.27$, $P = 0.007$; see Fig. 1c), which was
265 independent of the chicks' individual weight ($F_{1,35} = 0.0$, $P = 0.95$). As a consequence,
266 begging reward was also much higher in the uniparental treatment ($F_{1,36} = 23.74$, $P < 0.0001$).
267 Across treatments, offspring body mass had similar effects on both provisioning (interaction
268 term: $F_{1,34} = 2.57$, $P = 0.12$) and begging ($F_{1,34} = 0.09$, $P = 0.77$) behaviour.

269

270 <H2>Visibility manipulation (day 10 and 12)

271 The visibility manipulation experiment in the temporarily split biparental groups enabled us
272 to disentangle male and female provisioning strategies. Parental feeding effort increased
273 towards heavier chicks at a comparable rate for male and female parents (Table 1). Similarly,
274 feeding effort increased with chick begging intensity, but with a higher responsiveness to
275 begging in females than males (Table 1). Parents differed in provisioning effort depending on
276 the visibility of the partner. Specifically, male parents provided more food than female
277 parents and this sexual difference was even more pronounced when the partner was invisible,
278 relative to the visible set-up (see Table 1, Fig. 2). A post hoc test revealed that especially
279 males increased their workload when their partner became invisible (20.1 ± 0.5 min/h; $t_{59} =$
280 2.04 , $P = 0.046$), whereas females tended to decrease their feeding effort in such conditions
281 (2.8 ± 0.5 min/h; $t_{59} = -1.80$, $P = 0.077$; see Fig. 2). Furthermore, no significant differences in
282 food provisioning were observed between males (13.0 ± 0.5 min/h) and females (6.7 ± 0.6

283 min/h) in the visible set-up ($t_{59} = -1.51, P = 0.14$), which strongly contrasts with the invisible
284 set-up ($t_{59} = -4.67, P < 0.0001$). In addition, female provisioning effort towards chicks
285 measured on day 12 was almost two times lower during the invisible manipulation compared
286 to chicks from uniparental families on the same day ($F_{1,18} = 12.0, P = 0.003$).

287

288 <H1>Discussion

289 Our results support the existence of a costly sexual conflict over parental care. Offspring
290 from biparental families were observed to beg harder for parental resources, to weigh less as
291 fledglings and to tend to grow more slowly than uniparental families, despite similar parental
292 workloads. We further presented empirical evidence that these costs may relate to negotiation
293 and showed how males and females differ in their negotiation rules. The latter depended on
294 the available information on brood begging intensity and the mate's work effort. Below we
295 explain in detail how these results fit within the current theoretical framework of sexual
296 conflict over care and discuss the implications for other forms of family conflicts and their
297 resolution.

298

299 <H2>*Cost of sexual conflict*

300 Current theory on conflict resolution in species with biparental care predicts that each parent
301 is able to adjust the amount of care in response to its partner's effort: a behavioural response
302 called negotiation (McNamara et al. 1999). Despite a shortage of empirical tests, a current
303 debate exists on how negotiation takes place (Lessells 2012) along with its potential costs
304 (Lessells & McNamara 2012) or benefits (Johnstone et al. 2014) for the offspring (Royle et
305 al. 2002, 2006). Likewise, such offspring consequences are commonly neglected in mate

306 removal and handicapping studies (Harrison et al. 2009). Our results indicate that, when
307 controlling for an equal potential workload, parental provisioning effort towards each
308 offspring was only half as much in biparental nests compared to females caring alone, despite
309 higher offspring begging intensity in biparental nests. Furthermore, chicks from biparental
310 nests tended to grow more slowly and weigh significantly less as fledglings and at
311 independence, indicating lowered competitive abilities early in life. These results are
312 generally in line with a study on captive zebra finches, *Taeniopygia guttata*, which similarly
313 found less parental investment and less predictable food delivery in biparental nests (Royle et
314 al. 2006) and even a decrease in attractiveness of male chicks later in life (Royle et al. 2002).
315 To our knowledge, these are the only empirical studies that support a cost of sexual conflict
316 through negotiation over parental care as predicted by Lessells & McNamara (2012), and
317 which, however, are opposite to Johnstone et al.'s (2014) expectations.

318 If negotiation is indeed costly, one may then question why parents do not divide tasks and
319 care for only some of the offspring (Lessells 2002). Several taxon-specific hypotheses
320 suggest benefits of larger brood size (e.g. through thermoregulation) or inextricable task
321 division between the sexes (Lessells 2012). Our results may add another argument to this
322 discussion and suggest that an additional benefit of biparental care throughout an individual's
323 life may be overall increased offspring quantity, rather than quality, at least in some
324 songbirds (Smith & Härdling 2000; Royle et al. 2006). Specifically, we indicate that
325 uniparental females may opt to invest more in the quality of the current brood when they rely
326 only on themselves at the onset of the breeding period. This increased current investment is
327 expected to lower the female's general condition and may therefore be at the expense of
328 future reproductive investment and lifetime fitness (Trivers 1972; Royle et al. 2002). Such
329 trade-offs remain speculative and require further attention, but they may well hamper the
330 evolution of uniparental care.

331

332 <H2>*Sex-specific negotiation rules*

333 Our visibility manipulation revealed that the ability to observe the partner's activity pattern
334 and characteristics of the brood are important cues for parents to provide care (Hinde &
335 Kilner 2007). Moreover, males and females varied strongly in the cues used to define their
336 provisioning response, depending on both the degree of partner visibility and offspring
337 begging intensity. In detail, parents did not differ significantly in provisioning when mates
338 were visible to each other, although without the option to provide direct help. However, an
339 interesting sexual difference became explicit when mates were out of sight from each other,
340 with males showing increased and females decreased feeding effort. Such sexual differences
341 in negotiation rules may relate to an asymmetry in gathered information between the sexes
342 (Johnstone & Hinde 2006). Indeed, male and female canaries generally differ in provisioning
343 strategy (Kilner 2002), whereby females spend more time near the nest, invest less effort in
344 foraging and frequently receive food via allofeeding (Estramil 2014). This task division
345 probably leads to an asymmetry in information about partner work effort in favour of the
346 females (Johnstone & Hinde 2006). Mathematical models and observations in great tits
347 indicated that the parent better informed about the brood's need is expected to respond more
348 strongly to changes in offspring demand, work harder and compensate more strongly for
349 changes in partner effort (Johnstone & Hinde 2006). Females indeed appeared more sensitive
350 to offspring begging intensity (see also Kilner 2002). However, our observations are in
351 contrast with the last of these predictions, as our results suggest that well-informed females
352 do not work harder but keep private information and exploit their partner when they are out
353 of sight. Why females do not exploit their mate permanently is likely to depend on the
354 balance between mate exploitation and the female's urge to respond to increased offspring
355 begging behaviour.

356 Recent observations by Johnstone et al. (2014) indicated a form of cooperation between great
357 tit parents with turn taking in provisioning speeding up their feeding rate. We believe that the
358 contrasting findings may result from species-specific differences in the adequacy of
359 information gathering about partner effort. For example, the variation in caterpillar size
360 delivered by great tit parents (single-load species) is probably smaller than the variation in
361 amount of seeds collected and processed by canary parents (multiload species). This may
362 create a greater potential for cheating by the best informed parent in multiload species. Such
363 species-specific differences in information gathering may provide a promising future research
364 avenue. We therefore suggest a comparative study including a range of species with different
365 foraging strategies should be performed with an experimental set-up similar to ours.

366

367 <H2>*Integrated family conflicts*

368 Food provisioning towards each chick was lowered when both parents cared for their young.
369 It is therefore not surprising that we found amplified begging behaviour in biparental nests.
370 However, it remains unknown whether increased begging of biparental nestlings is the cause
371 or the consequence of suboptimal provisioning. On the one hand, offspring may increase
372 begging in response to their hunger status and thus as a reflection of slower development. On
373 the other hand, our results may also imply that parental negotiation results in greater sibling
374 competition and begging, which on its own can lead to a decrease in offspring condition and
375 growth (Kilner 2001; Royle et al. 2006). As confirmed earlier in canaries, sibling conflict
376 over care through begging may be energetically demanding, resulting in less resource
377 allocation towards growth (Kilner 2001). Furthermore, predictive models in parent–offspring
378 conflict theory incorporate costs of begging behaviour to maintain evolutionary stability
379 (Parker et al. 2002a). Without costs, begging would escalate without bounds. Whatever the
380 cause or consequence might be of poorer condition on increased biparental nestling begging,

381 the bottom line is that parental negotiation rules may affect chick begging behaviour, which
382 in turn is traded off against offspring growth and body mass. Parents, and here in particular
383 mothers, do not only respond to their mate's effort. Our results also indicate the importance
384 of chick begging behaviour (Parker et al. 2002a) and chick mass (Lessells & McNamara
385 2012) as determinants in providing care, and this closes the cycle of intrafamilial dynamics.
386 Our results therefore underline the importance of investigating joint interactions among all
387 family members (Hinde & Kilner 2007; Smiseth et al. 2008; Morales et al. 2009; Hinde et al.
388 2010) as indicated by our observed direct influence of sexual conflict over parental care on
389 offspring behaviour.

390

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396

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507 **Appendix**

508 **Differences between male and female offspring**

509 In this appendix we describe how we tested for potential sex differences in chick
510 development and for biased provisioning towards male or female chicks.

511 **Statistical methods**

512 Separate linear mixed models were run with a given estimate for chick development (growth
513 rate, body mass and tarsus length) as the dependent variable and family treatment, chick sex
514 and their interaction as categorical explanatory variables. Similar models were performed to
515 test for behavioural differences (total begging intensity and parental feeding effort) between
516 uniparental and biparental families on day 9. Family treatment, chick sex and their interaction
517 were added to the model as explanatory variables. All models included original nest ID and
518 foster nest ID as independent random factors to all models to adjust for a bias in statistical
519 independence.

520

521 **Results**

522 *Nestling development*

523 A sexual dimorphism was observed in growth rate (male: 0.63 ± 0.03 g/day; female: $0.54 \pm$
524 0.04 g/day; $F_{1,36} = 3.74$, $P = 0.061$), body mass of fledglings (male: 17.4 ± 0.4 g; female: 16.0
525 ± 0.5 g; $F_{1,35} = 6.14$, $P = 0.018$) and at independence (male: 19.3 ± 0.3 g; female: 18.5 ± 0.3
526 g; $F_{1,26} = 3.67$, $P = 0.067$) and tarsus length (male: 18.0 ± 0.1 mm; female: 17.4 ± 0.1 mm;
527 $F_{1,34} = 11.09$, $P = 0.002$). Overall, male fledglings were thus observed to be larger and
528 heavier than females. The observed sex differences were consistent across family treatments
529 for all the above parameters (treatment*chick sex interactions: all $P \geq 0.25$), except for tarsus

530 length for which a sexual size dimorphism tended to be more pronounced in uniparental
531 families ($F_{1,34} = 3.94$, $P = 0.055$).

532

533 *Chick begging and parental provisioning*

534 Chick sex did not influence parental provisioning ($F_{1,35} = 0.12$, $P = 0.73$) or begging intensity
535 ($F_{1,35} = 2.54$, $P = 0.12$) on day 9. Also across treatments, offspring sex had similar effects on
536 both provisioning (interaction term: $F_{1,34} = 0.24$, $P = 0.63$) and begging ($F_{1,34} = 0.35$, $P =$
537 0.56) behaviour.

538

539

540 **Table 1:** Result of the mixed model explaining variation in parental provisioning rules

Effect	<i>df</i>	<i>F</i>	<i>P</i>	Estimate	SE
Intercept				-2.92	1.60
Sex	1, 59	13.2	0.0006	-3.40	1.33
Manipulation	1, 59	0.01	0.94		
Begging	1, 59	16.1	0.0002	0.69	0.48
Mass	1, 59	34.1	<0.0001	0.58	0.10
Sex*Manipulation	1, 59	7.19	0.010	-2.30	0.86
Sex*Begging	1, 59	4.4	0.040	1.35	0.64
Sex*Mass	1, 58	1.53	0.22		

541

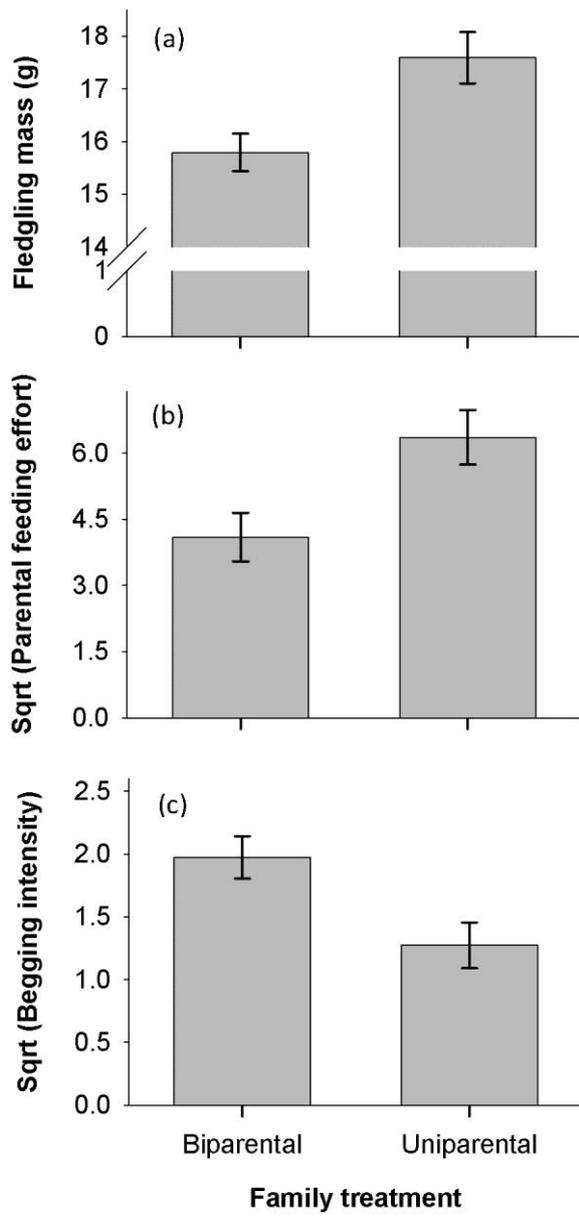
542 Provisioning rules were investigated during the visibility manipulation experiment in
 543 biparental families. Explanatory variables include parental sex, visible and invisible type of
 544 manipulation, offspring begging intensity and chick mass prior to the video recording.
 545 Estimated effect sizes with SE are presented for the significant predictors. Only female
 546 estimates are given for sex-specific effects, as males are treated as the reference term and set
 547 at zero in the model output. The model accounts for genetic and environmental similarities
 548 among chicks (see Methods).

549 Figure legends:

550 **Figure 1:** Difference in (a) fledgling mass, (b) chick begging intensity and (c) parental
551 feeding effort between uni- and biparental families on day 9. Mean \pm 1 SE values are based
552 on the parameter estimates of the statistical model.

553 **Figure 2:** Sexual difference in parental feeding effort during both temporary manipulations
554 of split biparental families. Mean \pm 1 SE values are based on the parameter estimates of the
555 statistical model.

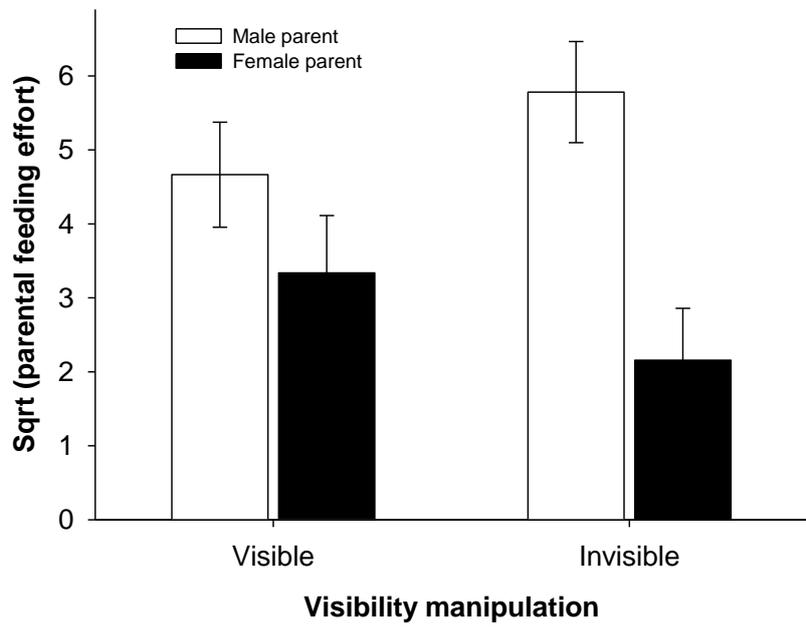
556 Figure 1:



557

558

559 Figure 2:



560