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3 Context dependent effects of an experimental increase of hunger level
4 in house sparrow nestlings
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26 **Abstract**

27 Exploring the links between parental supply and nestling demands and between nestling
28 demand and food supply is of central importance for understanding the evolution of
29 parent-offspring communication. It has been suggested that optimal food supply by
30 parents and begging effort of nestlings are context dependent, and we here test some
31 predictions of this hypothesis. House sparrow (*Passer domesticus*) nestlings were
32 experimentally fed with a pharmacological appetitive stimulant (cyproheptadine) that
33 increases nestling demands, and explore its effect on nestling growth (i.e. body mass
34 and tarsus length), which can be considered as the net payoff of inflated and costly
35 offspring demand. As assumed by the experimental protocol, nestlings with an
36 exaggerated demand were preferentially fed by parents. In accordance with the
37 hypothesis, net benefits in terms of growth were mainly detected in first breeding
38 attempt of parents that successfully reared three broods. Because costs associated with
39 parental feeding should be lower for first breeding attempts and for parents of higher
40 phenotypic quality (those able to successfully rear three clutches), our results provide to
41 our knowledge, the first experimental evidence supporting a dynamic role of costs of
42 food supply affecting net payoff of offspring demands, which may help to understand
43 the mechanisms allowing the evolutionary equilibrium between intensities of offspring
44 begging and parental provisioning.

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47 **Significance statement**

48 Both feeding and begging for food are costly activities for offspring and parents
49 respectively. Rewards of such behaviours in terms of food receiving and reproductive
50 success should vary depending on ecological conditions (i.e. food availability for
51 offspring and physical condition of parents). Here we pharmacologically exaggerated
52 appetitive of house sparrows (*Passer domesticus*) nestlings and explore its effect on
53 parental behaviour and on nestling growth (i.e. body mass and tarsus length). The
54 expected benefits were mainly detected for first breeding attempts and only in nests of
55 adults that were able to rear two more broods, that is, when costs of feeding the
56 offspring by adults are lower. Our results provide to our knowledge, the first
57 experimental evidence supporting dynamic outcomes of offspring demands and parental
58 provisioning, which is essential for understanding the evolution of parent-offspring
59 communication.

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63 Key words: costs of reproduction, cyproheptadine, family conflict, parent-offspring
64 communication, parental investment, parental response.

65 **Introduction**

66

67 In species with parental care offspring beg for food to their parents depending on need,
68 and parents adjust their feeding effort depending on signals of need and/or quality of
69 their offspring (Parker et al. 2002). Optimal offspring demand is however greater than
70 optimal parental supply (Trivers 1974). Thus, considering scenarios of scramble
71 competition among nestlings and/or of honest signalling of need is of central
72 importance to model the evolution of mechanisms regulating the effect of begging on
73 provisioning, and of provisioning on begging (Mock and Parker 1997; Kölliker 2003).

74 The effect of begging on provisioning have been largely investigated concluding
75 that parents should positively respond to offspring demands (Kilner and Johnstone
76 1997), which is adaptive for parents (Grodzinski and Lotem 2007). Parental decisions of
77 how to divide resources among nestlings within the same nest, however, do not only
78 depend on hunger level of nestlings signalled by their begging behaviour. Parents may
79 distribute resources randomly but also based on factors related to nestling hierarchy in
80 body mass and/or age (e.g., Cotton et al. 1999; Davis et al. 1999; and references
81 therein). The accuracy, reliability and meaning of the information exchanged between
82 offspring and parents, as well as parental responses to given information from nestlings,
83 is likely strongly context dependent (Royle et al. 2002). It may for instance depend on
84 number of siblings and of feeding adults in the nest (Roulin et al. 2000), or on whether
85 or not environmental conditions (i.e., food availability), including physical condition of
86 adults (i.e., associated costs), allow parents to meet offspring demands (i.e.
87 environmental context dependency of parental provisioning decision) (Davis et al.
88 1999).

89 Offspring demands would among other factors depend on food supply by
90 parents, but the effects are not consistent. Although it is generally assumed that food
91 supply will cause a reduction in begging levels and that food deprivation should
92 increase begging activity (Kilner and Johnstone 1997; Wells 2003), several studies have
93 found positive effects of parental food supply on offspring demand (Stamps et al. 1985,
94 1989; Lotem 1998; Krebs 2001; Mock et al. 2005). Such counterintuitive results have
95 recently been explained within the honest-signalling framework by Grodzinski and
96 Johnstone (2012). They modelled the effect of parental food supply on offspring
97 demands when variation in supply can be attributed to variation in the costs of parental
98 care (i.e. food availability, or the extent to which parents' future reproductive prospects
99 are damaged by provisioning current young (Parker et al. 2002)).

100 Thus, variation in costs associated with parental food supply due to, for instance,
101 variation in ecological (i.e. food availability) and/or physical conditions of parents will
102 also affect both optimal food demands by offspring and optimal food supply by parents.
103 Offspring should increase their begging activity in situations that favour expected parent
104 responses, while parents should respond to begging activity of offspring mainly in
105 situations of reduced costs of feeding. Davis et al. (1999) presented a model of
106 investment decisions faced by parents in a variety of environmental settings when
107 simultaneously raising several offspring of different ages, and with different levels of
108 resource need (i.e., hunger). They concluded that the optimal decision of parents
109 depends on environmental contexts. Feeding on the basis of short term need (i.e. hunger
110 level) was the most successful strategy only in environments of high food availability
111 (i.e. low cost of feeding).

112 The honest-signalling framework assumes the existence of costs associated with
113 the production of begging signal activity (for evidence of such costs, see e.g. Soler et al.

114 1999, 2014; Rodriguez-Girones et al. 2001; Moreno-Rueda 2010; Noguera et al. 2010;
115 Martín-Gálvez et al. 2011). These costs would overcome the extra feeding gained from
116 dishonest begging, thereby preventing the escalation of begging intensity (Godfray
117 1991,1995). However the marginal value of additional resources for offspring is not
118 static as it increases as overall food supply decreases and, thus, offspring should
119 increase their costly demands as food supply decreases (Kilner and Johnstone 1997;
120 Royle et al. 2002; Wells 2003). However, since costs of parental feeding should
121 negatively influence parental response to offspring signals of need and, thus, overall
122 food supply level (Davis et al. 1999; Grodzinski and Johnstone 2012), in scenarios of
123 elevated costs of feeding (i.e. low food availability and/or low parental energy reserves),
124 elevated begging behaviour would no longer be adaptive for offspring because the weak
125 responses in term of parental supply will hardly outweigh the costs of begging
126 (Grodzinski and Johnstone 2012). We know that optimal parental investment in feeding
127 the offspring is related to foraging costs (Jones 1988; Tinbergen and Dietz 1994; Naef-
128 Daenzer and Keller 1999; Schifferli et al. 2014) but, as far as we know the possibility
129 that costs of food supply influence optimal demand effort of offspring has never been
130 tested.

131 Here we test the above scenario assuming that optimal feeding effort of parents
132 in response to offspring demands, and the pay-off of signals of need of offspring depend
133 on environmental contexts. We explore the net benefits (i.e., nestling growth) of
134 exaggerated nestling demands in different environmental contexts implying different
135 costs of parental responses to nestling demands. Briefly, we provoked dishonest
136 offspring demand by experimentally feeding house sparrow (*Passer domesticus*)
137 nestlings with a pharmacological appetitive stimulant (cyproheptadine hydrochloride,
138 hereafter cyproheptadine) (Martín-Gálvez et al. 2011), and explored the effect on

139 nestling growth (i.e. body mass and tarsus length), which can be considered as the net
140 payoff of an inflated and costly signal of need (Martín-Gálvez et al. 2011; Mock et al.
141 2011). Cyproheptadine acts directly on the hypothalamus by blocking the activity of
142 serotonin on the hunger centre (Delitala et al. 1975). Although the mechanism of this
143 action as an appetite stimulant is unknown, it appears not to be due to a hypoglycaemic-
144 induced hyperphagia or an increase in endogenous growth hormones (Bergen 1964;
145 Stiel et al. 1970). Cyproheptadine is also used as an antihistaminic and has minimal side
146 effects in humans, consisting mainly of transient drowsiness (Homnick et al. 2004). Its
147 properties as appetitive stimulant have been shown in three species; the domestic fowl
148 (*Gallus gallus*) (Injidi and Forbes 1987; Muralidharan et al. 1998; but see, Rao and
149 Varadarajulu 1979), domestic pigeons (*Columba livia*) (Güntürkün et al. 1989) and
150 magpies (*Pica pica*) (Martín-Gálvez et al. 2011). Thus, consistent with previously
151 detected net effects of experimentally exaggerated demands (Martín-Gálvez et al. 2011),
152 we expect a net positive effect of cyproheptadine treatment on nestling growth in house
153 sparrow nestlings, but mainly in situations of feeding at relatively low costs for parents
154 (Davis et al. 1999).

155 House sparrows usually lay 4-5 eggs per clutch and start to incubate with the
156 third egg, which results in asynchronous hatching and where brood reduction is
157 common (Murgui 2011), even in captivity with *ad libitum* food (present study). Both
158 males and females feed the offspring and they breed more than once per breeding
159 season (Anderson 2006). Because of the extrinsic energetic costs of parental care
160 (Moreno et al. 1995, 1999) that will accumulate with subsequent breeding attempts of
161 the same season, previous breeding attempts should affect residual reproductive values
162 of adults (i.e. intrinsic costs of reproduction, Clutton-Brock 1991; Reznick et al. 2000).
163 Thus, during the breeding season, parental activity during later reproduction events

164 would be relatively more costly in terms of future reproductive prospects than that for
165 early breeding attempts (Heaney and Monaghan 1996; Nilsson and Svensson 1996;
166 Ghalambor and Martin 2000; Weggler 2006), thereby reducing feeding effort (Stodola
167 et al. 2009). As a proxy of costs associated with this intrinsic cost of reproduction
168 (hereafter Accumulative Parental Costs), we used the relative order in the breeding
169 season (hereafter Brood Order) when exploring the effect of the experiment in first,
170 second and third breeding events of the same pair.

171 In addition, because costs associated with parental activity are relatively higher
172 for parents of lower phenotypic quality (Verhulst et al. 1995; Hansson et al. 2000)
173 (hereafter Intrinsic Parental Costs), when studying the experimental outcome in first
174 broods, we used total number of successful breeding events during the same season as a
175 measure of parental quality.

176 Thus, with these assumptions in mind, the theoretical scenario of context-
177 dependent benefits of offspring demands predicts that the accumulative parental costs
178 should influence the expected benefits (increased nestling growth) associated with
179 experimentally dishonest solicitation of resources. Benefits should be relatively higher
180 in first than in subsequent breeding attempts. Moreover, and because of the intrinsic
181 parental costs (see above), benefits associated with the experimental dishonest signal of
182 need would be mainly manifested by nestlings of parents that were able to successfully
183 rear more broods.

184 We tested these predictions in a captive population of house sparrows under *ad*
185 *libitum* food conditions during different breeding attempts in the 2010 and 2011
186 breeding seasons. The assumed effects of cyproheptadine on nestling begging behaviour
187 and parental food allocation were tested in 2012. We therefore expect that nestlings in
188 experimental nests grow (i.e. tarsus length and body mass) better than those in control

189 nests, mainly for first clutches and for clutches reared by good quality parents (i.e. those
190 that successfully reared three different clutches in the same year).

191

192

193 **Material and Methods**

194

195 This study was performed during the 2010-2012 breeding seasons within a captive
196 population of house sparrows maintained in two aviaries in Hernán Valle, 60 km from
197 Granada, Spain. Each of these two aviaries consisted of four cages of ca. 50 m³ each,
198 interconnected by small holes (ca. 10 cm) through a central cage of ca. 40 m³ in which
199 food was provided. This allowed examination of nest-boxes and experimental
200 manipulation in absence of parents, which always flew to the other cages. This
201 organization of the aviaries considerably decreases potential stress to breeding birds.
202 More information of the conditions of the aviaries can be found in Soler et al. (2013).
203 At the beginning of the 2010 breeding season there were a total of 26 pairs in each
204 aviary, while at the beginning of the 2011 breeding season one of the aviaries had 55
205 males and 47 females, and the other had 47 males and 51 females. The number of next
206 boxes was always greater than number of sparrow pairs. During 2012, the behaviour of
207 nestlings in a subsample of nest-boxes was filmed. The birds were provided with *ad*
208 *libitum* access to commercial seed mix for canaries, nestling food for canaries with
209 honey and small pieces of fruit added (egg food with fruit, Bogena), cracked grains of
210 wheat and rice, fly maggots, apple and lettuce. More detailed information on aviaries
211 and sparrows can be found in Soler et al. (2011).

212 To minimize observer bias, blind methods were used when all behavioural data
213 were recorded and/or analysed. Pairs breeding in each nest-box were identified by a

214 unique combination of coloured tarsus-rings through direct observation and/or by video-
215 filming the entrance once the first egg was laid. Extra-pair paternity may influence
216 feeding rates of parents (Sejberg et al. 2000) and, consequently, the expected pay-off of
217 offspring begging displays. However, we know that extra-pair paternity is greatly
218 reduced in food-supplemented populations (Vaclav et al. 2003), which suggests that it is
219 quite reduced in our captive population where social monogamy during breeding is the
220 rule. In any case, for the analyses, we only used those breeding pairs that remained
221 together during the entire breeding season. From the beginning of the breeding season
222 all nest-boxes were at least checked every second day until clutch initiation, and
223 afterwards daily to detect full incubation, which allowed us to estimate hatching time.
224 Nest-boxes were checked daily beginning one day before estimated hatching date (10
225 days after laying the first egg) until the day of hatching, when we started the
226 pharmacological experiment.

227

228 Experimental design

229 Breeding pairs were randomly assigned to control or experimental treatment and these
230 statuses were maintained during the whole breeding season. At the day of hatching, all
231 nestlings were handled exactly in the same way and received the treatment. In
232 experimental nests, all nestlings were fed with cyproheptadine hydrochloride diluted in
233 mineral water while those in control nests were fed with mineral water. For the
234 experimental treatment, we prepared a solution of cyproheptadine (4 mg per ml of
235 water) and adjusted doses to body mass of experimental nestlings (0.016 mg of
236 cyproheptadine per g of nestling) based on our previous work (Martín-Gálvez et al.
237 2011). For the control treatment, nestlings received the same volume of water as
238 experimental nestlings of the same age. The treatment was repeated every second day

239 until 12 days after hatching. Nestlings were weighed (digital balance, accuracy 0.1mg)
240 every day before the treatment in order to adjust the daily drug doses, while tarsus
241 length was measured with a calliper (accuracy 0.01mm) once when nestlings were 12
242 days old.

243

244 Video-recordings

245 During spring of 2012, we video recorded 8 experimental broods in the middle of the
246 nestling period when nestlings were 5-7 days old. All nestlings received the treatment
247 the day of hatching and every second day until they were video-recorded. Only for these
248 video-recordings, a random selection of half the nestlings received only water, while the
249 rest were fed with cyproheptadine. In this way, we could test the effect of
250 cyproheptadine treatment within each nest, thereby avoiding confounding factors in our
251 analyses due to among nest variation. Each nestling was marked on the head with a
252 unique combination of white points (Tipp-Ex) for individual identification.

253 For recording we used a microcamera (Euroma, KPCS500) installed within the
254 nest-box connected to a recorder (Linux MPEG4) and to a monitor so that we could see
255 the nestlings and feeding adults. The video camera was put on just before left the aviary
256 after experimental feeding (ca 9:00-10:00 AM) and removed 2h 30 minutes later. For
257 our analyses we used the parental and nestling behaviour filmed from 30 to 60 minutes
258 after the start of recording. It assures that measurements were not affected by our
259 presence in the aviary. Recorded videos were analysed with the program Super play 1.3
260 software (<http://superplay.software.informer.com/>). For each adult visit we collected the
261 following binomial information for each nestling: (i) whether it did beg for food (i.e.,
262 opening the bill to feeding adult), (ii) whether it was the closest nestling to the

263 provisioning adult at the arrival time, (iii) whether its head was the highest while
264 begging, (iv) whether it was the first nestling starting to beg, and (v) whether it was fed.

265

266 Statistical analyses

267 *Treatment effects on nestling begging behaviour and parental food allocation*

268 Number of feeds received by nestlings did not differ from normal distribution
269 (Kolmogorov-Smirnov tests for continuous variables, $P > 0.2$) and thus was analysed by
270 means of a General Linear Model (GLM) with treatment as the fixed factor, body mass
271 and average time without being fed by parents before successful feeding as covariates,
272 which should influence the hunger level of nestlings. Nest identity and its interaction
273 with treatment were included in the models as random factors to account for the non-
274 independence of nestlings within the same nest while focusing on within nest
275 comparisons.

276 Experimental influence on variables considered to characterize nestling begging
277 behaviour was analysed in statistical models with identical independent factors as that
278 used for the number of feeds. As dependent variables, for each nestling, we considered
279 the number of parental visits where (i) it begged first, (ii) it occupied the closest
280 position to adults, (iii) it reached the highest elevation of nestling heads while begging,
281 and (iv) it was the first begging from their parent for food. All these dependent variables
282 were approximately normal distributed and, thus, we used General Linear Models to test
283 for the effects of independent factors. Residuals of these models did not differ from
284 normal distribution.

285

286 *Treatment effects of the appetitive stimulant on nestling growth*

287 Body mass and tarsus length of house sparrows were measured during different
288 breeding attempts in control and experimental nests. These measures followed a
289 Gaussian distribution (Kolmogorov-Smirnov tests for continuous variables, $P > 0.2$).
290 Since we were not interested in exploring inter-year variation and, to statistically
291 account for possible differences, tarsus length and body mass of nestlings from different
292 study years were standardized by applying the following equation: $X_i = (a_i - A) + Z$
293 where a_i is the value (i.e., tarsus length or body mass) in the year a , A is the average
294 value for the year a , and Z the average of values of both study years. Moreover,
295 variation in body mass and tarsus length among nests was statistically significantly
296 greater than the within nest variation after statistically controlling for experimental
297 treatment (GLM that included information of breeding attempt, experimental treatment,
298 nest identity nested within experimental treatment (random factor), and the interaction
299 between nests identity and breeding attempt (random factor); effect of the interaction
300 between nest identity and breeding attempt: tarsus length, $F = 6.42$, $df = 58,242$, $P <$
301 0.0001 ; body mass, $F = 3.95$, $df = 58,242$, $P < 0.0001$). Thus, we used mean values of
302 sparrow nestlings from each brood in subsequent analyses. Furthermore, brood size did
303 not affect average values of tarsus length ($F = 0.03$, $df = 1,138$, $P = 0.87$) or body mass
304 ($F = 1.95$, $df = 1,147$, $P = 0.164$) even after controlling for the statistically significant
305 effect of breeding attempt (on tarsus length ($F = 11.27$, $df = 2,138$, $P < 0.0001$) and
306 body mass ($F = 4.47$, $df = 2,147$, $P = 0.013$)). Thus, the information on brood size of
307 sparrow nests was no longer considered in our statistical models. Clutch size, brood size
308 at hatching and at fledging and brood reduction of first, second and third breeding
309 attempts of experimental and control pairs are reported in Table 1.

310

311 *Accumulative parental costs*

312 We collected information for 27 (56 successful broods) and 51 (98 successful
313 broods) breeding pairs in 2010 and 2011, respectively. Number of breeding attempts in
314 2010 (mean (SE) = 2.07 (0.16)) do not differ from that in 2011 (1.92 (0.11); $F = 0.66$, df
315 = 1, 76, $P = 0.42$). Tarsus length of nestlings in nine nests at different broods was not
316 measured and we did not use these nests in further analyses.

317 To explore differential experimental effects on nestling growth depending on the
318 accumulative parental costs, we only used information from pairs that did successfully
319 rear three broods (12 experimental and 10 of control treatment). We did not collect
320 information on tarsus lengths for the second broods in two pairs under control
321 treatments and thus sample size differed for different breeding attempts. The statistical
322 GLM testing for such effects included experimental treatment, brood order and the
323 interaction between these two factors as fixed effects; nest identity nested within
324 treatment and the interaction between this factor and brood order were included as
325 random factors to account for the within nest design of the data set.

326

327 *Intrinsic parental costs*

328 For analyses exploring differential experimental effects on first clutches of
329 breeding pairs that successfully reared (i.e., at least one nestling to fledging) one, two or
330 three clutches (i.e. intrinsic parental costs), we considered information from all first
331 successful breeding attempts (74 breeding pairs, 35 with experimental treatment (10, 13,
332 and 12 pairs did respectively rear one, two and three broods successfully) and 39 with
333 control treatment (11, 18, and 10 pairs did respectively rear one, two and tree brood
334 successfully)). The statistical GLM to explain the variation in body mass and tarsus
335 length (dependent variables) included treatment, number of successful breeding
336 attempts and the interactions between these two factors as fixed effects.

337 FDR (False Discovery Rate) method was used to adjust p-values for multiple
338 comparisons (i.e., testing the same prediction on tarsus length and body mass) by
339 *p.adjust* function of stats package in R 3.1.2 (<http://www.r-project.org/>). All other
340 statistical tests were performed in Statistica 10.0 (Statsoft Inc. 2011). Critical P-values
341 for rejecting null hypotheses (H_0) was set at < 0.05 .

342

343 **Results**

344

345 *Nestling survival and breeding attempt*

346 Survival rate of hatchlings in nests where at least one nestling fledged in our captive
347 population was 87.2% (N = 594), and it decreased from first (88.6%, N = 299) to
348 second (87.8%, N = 213) and third breeding attempts (80.5%, N = 82) (Chi-square =
349 8.77, df = 2, P = 0.012). Moreover, brood reduction mainly due to starvation of smallest
350 nestlings (results not shown) (see Table 1) occurs relatively frequently in our captive
351 population (36.0%, N = 153 nests). However, the increases in brood reduction from first
352 (31.2%, N = 77) to second (39.6%, N = 53) and third (43.82, N = 23) clutches did not
353 reach statistical significance (Chi-square = 1.67, df = 2, P = 0.43). These results suggest
354 that *ad libitum* food supply to the parents did not lessen sibling competition for food,
355 and that intensity of nestling competition for food was more intense in third clutches.

356

357 *Video recordings*

358 Analyses of video recordings of nests of house sparrows including nestlings
359 under the cyproheptadine and water treatments confirmed that those treated with the
360 appetitive stimulant were more often fed by parents than their control siblings
361 (treatment effect: F = 6.37; df = 1,7.7, P = 0.031) and that the effect of treatment was

362 similar in different experimental nests (experimental effect: $F = 0.92$; $df = 7,9$, $P =$
363 0.54), even after controlling for the random effects of nest identity ($F = 1.46$; $df = 7,7.4$,
364 $P = 0.31$), body mass ($F = 0.15$; $df = 1,9$, $P = 0.70$), and time since the last feeding ($F =$
365 3.98 ; $df = 1,9$, $P = 0.077$). The detected experimental effect corresponded to
366 intermediate values of effect size (partial eta squared = 0.45) and power (0.63). Thus,
367 our appetite stimulant experiment successfully influenced the amount of food received
368 by nestlings from parents. We, however, failed to detect experimental effects on
369 begging behaviour variables (i.e. begging frequency, position in the nest, begging order
370 at parent arrival to the nest, and head height during begging; $F < 1.49$, $P > 0.26$).

371

372 Accumulative parental costs and effects of cyproheptadine treatment

373 When comparing the effect of the experimental supplementation of the appetitive
374 stimulant in first, second and third broods of pairs that successfully reared three
375 clutches, we did not find evidence supporting a general effect of the appetitive stimulant
376 on body mass ($F = 1.02$, $df = 1,21.3$, $P = 0.32$) or tarsus length ($F = 2.60$, $df = 1,21.4$, P
377 $= 0.12$) after controlling for the effect of past successful events of reproduction (body
378 mass: $F = 3.78$, $df = 2,37$, $P = 0.032$; tarsus length: $F = 11.62$, $df = 2,37$, $P = 0.0002$).
379 Interestingly, the interaction between experimental treatment and brood order tended to
380 explain body mass ($F = 3.75$, $df = 2,37$, $P = 0.066$) but not tarsus length ($F = 1.90$, $df =$
381 $2,37$, $P = 0.16$). Specifically, treatment effects were only detected for first (body mass: F
382 $= 8.24$, $df = 1,20$, $P = 0.018$; tarsus length: $F = 5.46$, $df = 1,20$, $P = 0.030$) but not for the
383 other breeding events ($F < 2.44$, $df = 1,20$, $P > 0.135$). Nestlings from experimental first
384 broods were heavier and of longer tarsus length than those from control first broods
385 (Fig. 1). These results suggest that the effects of the appetitive stimulant depend on the

386 accumulative parental costs, i.e. the parental investment already made in the breeding
387 season, made the treatment effect more obvious for first than for subsequent broods.

388

389 *Intrinsic parental costs and effects of cyproheptadine treatment*

390 When comparing body mass and tarsus length of nestlings from first broods of
391 pairs with different parental quality (i.e. those that successfully reared either one, two or
392 three broods) tarsus length ($F = 5.24$, $df = 2,68$, $P = 0.014$), but not body mass of house
393 sparrow nestlings ($F = 0.01$, $df = 2,68$, $P = 0.99$) differed from pairs with a single brood
394 to those with three (Fig. 2). Moreover, tarsus length ($F = 3.71$, $df = 1,68$, $P = 0.16$) and
395 body mass ($F = 0.84$, $df = 1,68$, $P = 0.36$) of experimental nestlings did not differ from
396 control nestlings (Fig. 2). Finally and as predicted, the effect of the experiment on tarsus
397 length of nestlings from first brood depended on intrinsic parental costs, i.e. whether or
398 not a target pair reared one, two or three broods (Treatment x total of broods per pair, F
399 $= 4.57$, $df = 2,68$, $P = 0.028$), while a tendency was detected for body mass (Treatment x
400 total of broods per pair, $F = 2.50$, $df = 2,68$, $P = 0.090$). Treatment effect on body mass
401 tended to be apparent for pairs with a high parental quality, i.e. those that successfully
402 reared three broods (LSD post-hoc, $P = 0.054$, Fig. 2), while for tarsus length this effect
403 was detected for nests that reared a single brood (LSD post-hoc, $P = 0.038$, Fig. 2) and a
404 tendency was detected for those that reared three successful broods (LSD post-hoc, $P =$
405 0.06 , Fig. 2). Except for those that reared two successful broods, nestlings
406 experimentally fed with the appetitive stimulant were heavier and had tarsi longer than
407 those in control nests (Fig. 2). These results therefore suggest that the strength of the
408 experimental effect depends on parental characteristics (i.e. quality and/or willingness to
409 invest in reproduction) that predict events of successful breeding attempts.

410

411 **Discussion**

412

413 Our results confirmed the general positive effects of the appetitive stimulant
414 cyproheptadine on nestling growth, which was also found previously in magpies
415 (Martín-Gálvez et al. 2011), likely mediated by parents adjusting their efforts to the
416 hunger level of experimental nestlings. We found that the effects of the appetitive
417 stimulant on nestling growth were only detected in first broods. In addition, the effects
418 of the experiment in the first broods were greater in pairs that raised three broods than in
419 those raising two or one broods. Below we discuss possible methodological caveats and
420 the interpretation of these results as supporting the hypothesis that parental supply
421 response to nestling demands, as well as optimal offspring demands, are context
422 dependent. We also discuss alternative scenarios explaining our results.

423 The study was performed in aviaries with *ad libitum* resources for parents and,
424 thus, the possible confounding factor due to variation of resources in nature throughout
425 the breeding season was eliminated from our analyses. Eliminating variations due to
426 resource availability would reduce but not eliminate environmental variations
427 potentially affecting parental decisions (context-dependence). Here, we are not
428 interested in detecting the influence of resource availability for parents on nestling
429 phenotypes, but in other factors potentially affecting parental decisions. Thus, by
430 eliminating variation due to resource availability we are statistically restricting the
431 proportion of variance mainly related to the hypothesis tested.

432

433 *Appropriateness of our pharmacological experiment for increasing hunger levels.*

434 In accordance with previous studies (Martín-Gálvez et al. 2011, 2012), our
435 results confirmed a preferential feeding by parents of experimental nestlings, but failed

436 to detect an effect on nestling begging behaviour. Therefore, the drug may influence
437 other aspects of the begging display. We know for instance that in magpies it influences
438 mouth colouration of nestlings (DM-G and JJS unpubl. data) and that house sparrow
439 mouth colour varies within brood as a result of environmental context (Dugas 2012),
440 which affect detectability by parents and therefore provisioning (Dugas 2015). This
441 possibility could therefore explain our results.

442

443 *Appropriateness of using the number of breeding attempts as a surrogate for the costs*
444 *of reproduction in ad libitum condition*

445 The use of number of breeding events as indicative of intrinsic costs of
446 reproduction and of probability of reproducing several times during the same season as
447 a proxy of individual phenotypic quality of adults is not new (Thorogood et al. 2011).
448 Probability of laying subsequent clutches is related to experimental food supply (Nagy
449 and Holmes 2005a; Thorogood et al. 2011; Seward et al. 2014) and/or to intrinsic
450 phenotypic quality of adults (Hoffmann et al. 2015) and, on average, nestlings of multi-
451 brooded females are of better phenotypic quality than those from single-brooded (Nagy
452 and Holmes 2005b). In addition, reproductive success and quality of nestlings of second
453 and third clutches are typically lower than those of first clutches (Crick et al. 1993;
454 Antonov and Atanasova 2003; Serra et al. 2012; but see Kalinski et al. 2009). Thus,
455 food availability for nestlings in later reproductive attempts is likely reduced because of
456 the limited parental food supply due to accumulated costs of reproduction of parents.
457 The question however is whether these patterns also occur in our captive population
458 with *ad libitum* food availability for parents.

459 The hypothesis tested assumes considerable costs of feeding by adults and of
460 begging for food by nestlings in condition of *ad libitum* food availability. This kind of

461 assumptions has been previously discussed for a captive population of sparrows in
462 Israel (Dor and Lotem 2009) for which rate of nestling survival (66.5%) was even lower
463 than those found in natural populations in North American and Europe (66.1%- 67.5%)
464 (Dor and Lotem 2009), in Israel (74.6% (Singer and Yom-Tov 1988), cited in Dor and
465 Lotem 2009) and in France (80% - 94.8 %, Chastel and Kersten 2002). Survival rate of
466 hatching in nests where at least one nestling fledged in our captive population was
467 within the above range (see results) and decreased from first to third clutches.
468 Moreover, brood reduction in our captive population is similar or even larger than those
469 found in wild populations of this species in North America (42%, Mock et al. 2009)
470 and, our results showed that it increases from first to third clutches. In addition, in our
471 captive population most brood reduction events occurred because last hatched nestlings
472 became runts and then died (CR-C unpubl. data), which suggests starvation as the main
473 cause of nestling death. All these results show that *ad libitum* food supply to the parents
474 did not lessen sibling competition for food and, therefore, we think that our captive
475 population is appropriate for testing hypothetical context dependence of benefits
476 associated with an exaggerated level of hunger. Moreover, because brood reduction was
477 more likely to occur in third than in first broods, intensity of nestling competition for
478 food should be more intense in third clutches.

479

480 *Context dependent effects of showing hunger level in house sparrows*

481 In life history theory, cost of parental care is considered in the extent to which parent's
482 future reproductive prospects are damaged by provisioning current young (Stearns
483 1992; Parker et al. 2002). Thus, since effects of reproductive effort are accumulated
484 during the breeding season, costs of parental supply should be relatively larger for later
485 than for earlier reproductive events (i.e. accumulative parental costs, see Introduction).

486 Moreover, costs of parental food supply should be relative to energy reserves or
487 phenotypic condition of parents (i.e. intrinsic parental costs, see Introduction),
488 especially after controlling for the effects of accumulative parental costs. We explored
489 the context-dependent effects of increased appetite by comparing nestling growth
490 among breeding pairs that varied in their number of breeding attempts. On the one hand,
491 we only used pairs that successfully produced three broods to test the effects of the
492 accumulative parental costs. On the other hand, the influence of the intrinsic parental
493 costs was estimated by comparing nestlings from the first breeding events among pairs
494 that raised one, two and three broods.

495 We detected evidence suggesting that both accumulative and intrinsic parental
496 costs determined the outcomes of the pharmacological experiment concerning nestling
497 growth. Nestlings in experimental nests had longer tarsi and were heavier than those in
498 control nests, but mainly for first reproductive events of pairs that successfully reared
499 three broods, i.e. in those breeding attempts with the lowest accumulative parental costs.
500 Body mass, tarsus length and/or body condition are considered as determinants of
501 probability of local recruitment in birds (Moreno et al. 2005 and references therein), and
502 it is also the case in house sparrows (Ringsby et al. 1998; Cleasby et al. 2010).
503 Therefore, our results suggest an effect on fitness prospects of nestlings with
504 exaggerated hunger levels, but only during first clutches. These results fit well with the
505 predictions from Davis et al. (1999) and of Grodzinski and Johnstone (2012), who
506 respectively suggest that parents should feed on the basis of hunger level in situations of
507 high food availability, or of low costs of food supply. Thus our results confirm that
508 parental response to offspring demand is context dependent.

509 Previous experimental works in captive populations of house sparrows found
510 evidence of genetic variation in the level of parental effort, but parental response to

511 experimentally induced changes in nestlings begging behaviour was neither repeatable
512 across broods nor heritable across generations nor correlated to nestling begging (Dor
513 and Lotem 2010). These results were in any case tentatively interpreted by Dor and
514 Lotem (2010) as indicating that oscillating selection for high and low levels of parental
515 effort may covary with some other individual traits (Wolf et al. 2007), which otherwise
516 may be those related to costs of parental food supply in terms of reduced longevity
517 (Clutton-Brock 1991; Owens and Bennett 1994) or future reproductive outcomes
518 (Grodzinski and Johnstone 2012) as interpreted here. We do not know whether the
519 expected parental response to experimentally induced change in begging behaviour by
520 Dor and Lotem (2010) occurs for first and not for later breeding events as we detected
521 here and, thus, our results is the first evidence supporting a role of costs of food supply
522 determining parental response to offspring demands.

523 Our results also suggest that costs of parental food supply determine the
524 functionality of an increased food demand of nestlings because payoff of such increased
525 begging behaviour would be largely determined by the dynamic costs of parental care.
526 Only in contexts of relatively low costs of parental care, an increased demand of food
527 will result in a net benefit for offspring (Fig. 1 and Fig. 2) as expected by Davis et al.
528 (1999) and Grodzinski and Johnstone (2012). In this case, offspring may use cues and
529 signals given by parents or siblings (Kilner and Hinde 2008) to gather information about
530 parental costs of care and, accordingly, adjust their begging level and associated costs,
531 not only to the rate of food supply, but also to cues of costs of parental care (Grodzinski
532 et al. 2011). For house sparrows, we know that nestling begging intensity has a
533 relatively low genetic component with an important interaction between genetic and
534 environmental components, which would allow nestlings to adjust begging intensity to
535 environmental conditions and parental responses, related for instance to food

536 availability (Kedar et al. 2000; Dor and Lotem 2009). Further experimental
537 manipulation of costs associated with parental food supply that result in decreased food
538 demands by nestlings is needed for firm conclusions in favour of this hypothesis.

539 Summarizing, we found that net benefits associated with an experimentally
540 increased level of need (i.e. appetite) of nestlings were detected in situations of
541 relatively low costs of food supply, which is in accordance with the hypothesis that both
542 parental response to offspring need and optimal begging effort by nestlings were
543 context dependent. The assumption that parents and offspring behaviours are context
544 dependent is therefore essential for the comprehension of the mechanisms allowing the
545 evolutionary equilibrium between offspring begging and parental provisioning.

546

547

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549

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553

554 **Compliance with Ethical Standards**

555

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761 Table 1 Average clutch size, brood sizes at hatching and at fledging, and number of
 762 nestlings that died during the nesting period (brood reduction) of first, second, and third
 763 breeding attempt of experimental and control broods. Sample sizes (N), standard errors
 764 (SE) and 95% confidence intervals (CI) are also shown
 765

Breeding attempt	Experimental treatment	N	Mean	S.E.	-95% CI	+95% CI
Clutch size						
First	Exp.	37	4.35	0.16	4.03	4.67
	Control	40	4.70	0.13	4.45	4.95
Second	Exp.	26	4.81	0.21	4.36	5.25
	Control	27	5.11	0.20	4.70	5.53
Third	Exp.	13	4.46	0.35	3.70	5.23
	Control	10	4.60	0.31	3.91	5.29
Brood size at hatching						
First	Exp.	37	3.73	0.19	3.34	4.12
	Control	40	4.03	0.16	3.70	4.35
Second	Exp.	26	3.81	0.25	3.28	4.33
	Control	27	4.22	0.27	3.67	4.77
Third	Exp.	13	3.46	0.39	2.62	4.30
	Control	10	3.70	0.33	2.94	4.46
Brood size at fledging						
First	Exp.	37	3.41	0.19	3.02	3.79
	Control	40	3.48	0.18	3.11	3.84
Second	Exp.	26	3.31	0.26	2.76	3.85
	Control	27	3.74	0.32	3.09	4.40
Third	Exp.	13	2.69	0.33	1.98	3.41
	Control	10	3.10	0.31	2.39	3.81
Brood reduction						
First	Exp.	37	0.32	0.10	0.13	0.52
	Control	40	0.55	0.13	0.28	0.82
Second	Exp.	26	0.50	0.13	0.24	0.76
	Control	27	0.48	0.13	0.20	0.76
Third	Exp.	13	0.77	0.26	0.21	1.33
	Control	10	0.60	0.27	0.00	1.20

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770 Figure legends

771

772 Fig. 1 Body mass (g) and tarsus length (mm) (LS-means \pm SE) relative to brood order of

773 house sparrow nestlings from experimental (i.e. nestlings fed with the appetitive

774 stimulant) and control (i.e. nestlings fed with water) broods of pairs with three

775 successful broods

776

777 Fig. 2 Body mass (g) and tarsus length (mm) (LS-means \pm SE) of house sparrow

778 nestlings from experimental (i.e. nestlings fed with the appetitive stimulant) and control

779 (i.e. nestlings fed with water) in the first breeding attempt of the season in pairs that

780 successfully reared one, two or three broods

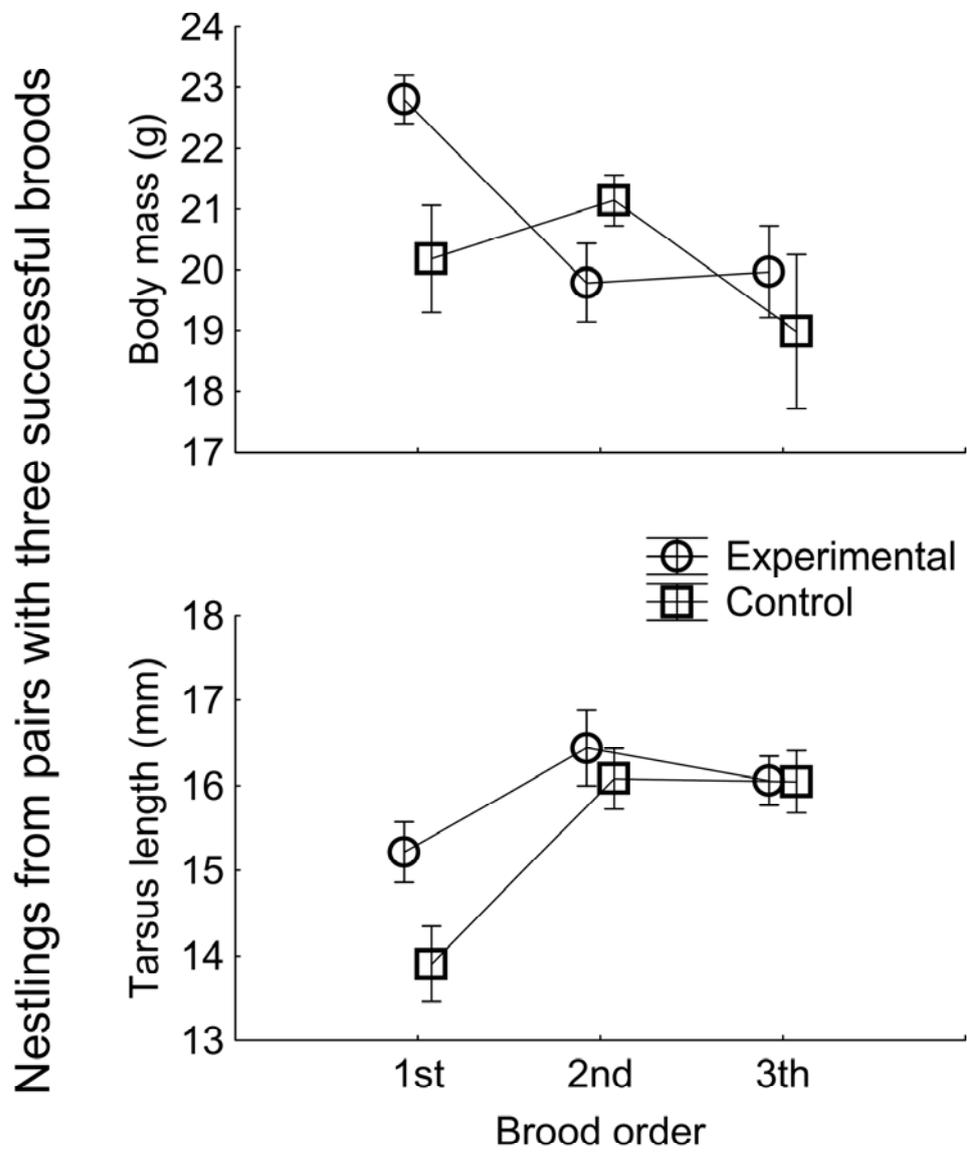
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785 Fig. 1



Accumulative parental costs

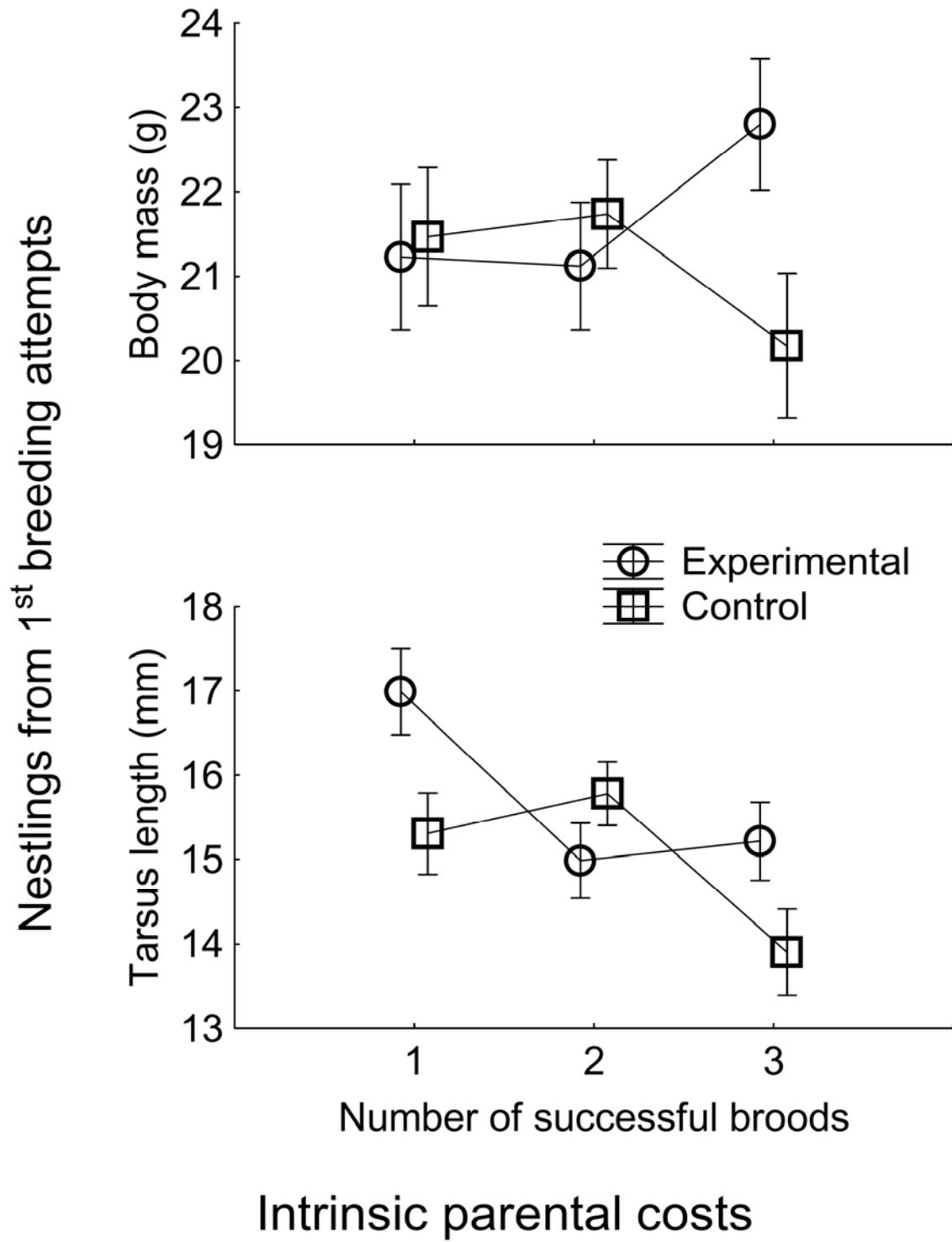
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789 Fig 2.

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