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Social context-dependent provisioning rules in red-winged fairy-wrens do not vary with signals of increased chick need

MacLeod, K.J.; Brouwer, L.

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1 **Social context dependent provisioning rules in red-winged fairy-wrens do**
2 **not vary with signals of increased chick need**

3

4 MacLeod, K.J.^{1,2,3} & Brouwer, L.^{4,5,6*}

5

6 ¹ Department of Biology, Pennsylvania State University, Mueller Laboratory, University Park, PA
7 16802, USA

8 ² Department of Ecosystem Science and Management, Pennsylvania State University, Forest
9 Resources Building, University Park, PA 16802, USA

10 ³ Department of Zoology, University of Cambridge, Downing Street, Cambridge, CB2 3EJ, UK

11 ⁴ Division of Ecology and Evolution, Research School of Biology, The Australian National
12 University, Canberra ACT 2601, Australia

13 ⁵ Department of Animal Ecology, Netherlands Institute of Ecology NIOO-KNAW, PO Box 50,
14 6700AB Wageningen, The Netherlands

15 ⁶ Department of Animal Ecology & Physiology, Institute for Water and Wetland Research, Radboud
16 University, Nijmegen, the Netherlands

17

18

19 * address correspondence to Dr Lyanne Brouwer, Department of Animal Ecology
20 & Physiology, Institute for Water and Wetland Research, Radboud University,
21 P.O. Box 9100, 6500 GL Nijmegen, the Netherlands; l.brouwer@myscience.eu
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34 **Abstract**

35 Individuals should adjust investment in parental care in order to maximize
36 current and future reproductive success. In cooperative breeders, where helpers
37 assist with raising offspring, larger groups may allow for a reduction in
38 investment (load-lightening) of each individual. Additionally, the type of
39 individual and thus the social context can play an important role in individual
40 investment. Less attention has been paid to how provisioning rules vary across
41 ecological contexts, though theory suggests that individuals can only afford to
42 reduce their investment when nestling starvation is unlikely, thus under mild
43 conditions. Here, we test whether previously reported provisioning rules based
44 on social context vary with ecological conditions, by experimental manipulation
45 of signals of chick need, in the cooperatively breeding red-winged fairy-wren
46 (*Malurus elegans*). Previous work in this species has shown that all group
47 members load-lighten with additional male helpers, whereas effort remains
48 constant in response to the number of female helpers in the group. We show that
49 experimental begging playback resulted in all individuals increasing their
50 provisioning rates, indicating that our treatment was perceived as increased
51 chick need. However, in contrast to our prediction, increased chick need did not
52 stop individuals from reducing their investment with an increasing number of
53 male helpers in the group. These results suggest that despite some flexibility in
54 parental effort, individuals use strict rules with respect to group composition,
55 suggesting that individual provisioning effort is based on multiple integrated
56 cues, and responses to changes in the environment are highly context-
57 dependent.

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59 **Keywords:** additive care, cooperative breeding, helping behaviour, load-
60 lightening, *Malurus*, parental investment, playback

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84 **Introduction**

85

86 In species that provide care to offspring, individuals should adjust their
87 investment in costly care behaviour, such as provisioning of food to offspring, in
88 order to maximize current and future reproductive success (Stearns, 1992). In
89 biparental species, investment decisions are not only conditional upon the
90 demands of the young (Kilner & Drummond, 2007), but also on the investment
91 or characteristics of one's partner (Sheldon, 2000). In cooperatively breeding
92 species, not only the breeding pair, but also the helpers that assist with raising
93 offspring, should strategically adjust their investment in care behaviours, as
94 alloparental care incurs significant costs (Taborsky 1984; Heinsohn & Cockburn
95 1994). If individuals reduce their own investment according to the investment of
96 their group members, there is a "load-lightening" effect ("compensation"); in
97 contrast, if there is no adjustment to the care provided by others, or if
98 compensation is incomplete, an individual's care has an "additive" effect
99 (Hatchwell & Davies 1990; Hatchwell 1999). Accordingly, investment decisions
100 by breeders and helpers in cooperative groups can vary according to the number
101 (Balshine et al. 2001; Savage, Russell & Johnstone 2015) and effort (Wright,
102 1998) of group members. Individual effort itself might depend on the type of
103 individual, for example, parental investment might depend on whether or not an
104 individual is likely to breed in the near future, which may vary among the sexes
105 (Clutton-Brock et al., 2002). However, until recently the role of social context
106 (e.g. the number and sex of the helpers) on breeder and helper investment
107 patterns received little attention (but see Brouwer, Van de Pol & Cockburn 2014;
108 Adams et al. 2015).

109

110 Various aspects of the ecological environment can also influence parental
111 investment. For example, parental provisioning rate has been shown to decrease
112 with increasing risk of predation in 10 bird species (Ghalambor, Peluc, & Martin,
113 2013) and low food availability decreases maternal sensitivity to offspring
114 signals in stitchbirds (*Notiomystis cincta*; Low, Makan & Castro 2012). Not
115 surprisingly, harsh conditions might result in food deprivation, which will result
116 in higher begging intensity (Drummond & Garcia Chavelas, 1989; Leonard, Horn,
117 Gozna, & Ramen, 2000; Lotem, 1998). Because ecological conditions often
118 determine the value of extra parental care (Davies & Hatchwell, 1992), ecological
119 context will also interact with social context to determine parental investment.
120 Thus the compensatory or additive nature of parental investment may vary
121 according to the harshness of the environment. Indeed, a comparative study
122 showed that investment is more likely to be compensatory when the likelihood
123 of nestling starvation is low (Hatchwell, 1999). However, how flexible
124 investment decisions are with respect to social and ecological context has
125 received little attention. Recently, a study on long-tailed tits (*Aegithalos*
126 *caudatus*) showed that adjustment of provisioning effort to others varied among
127 years, suggesting that provisioning rules are dependent on environmental
128 variables (Adams et al., 2015). In addition, female superb fairy-wrens (*Malarus*
129 *cyaneus*) with helpers were able to reduced their investment (load-lightening, by
130 reducing egg size), but only under good conditions (Langmore, Bailey, Heinsohn,
131 Russell, & Kilner, 2016). Whether the interaction of parental investment between
132 social and ecological context is a general pattern remains unknown, yet this

133 could improve our understanding of cooperative systems and how they may
134 plastically respond to environmental change.

135

136 In this study, we investigate provisioning behaviour of dominant breeders
137 and helpers across varying social contexts by experimental manipulation of the
138 perceived ecological conditions, through simulating increased chick need with a
139 nestling playback experiment. We use the facultative cooperatively breeding red-
140 winged fairy-wren (*Malurus elegans*) as a model system. Parental investment has
141 been shown to depend on social environment in this species, with both additive
142 care and load-lightening occurring depending on group composition. All group
143 members decrease their provisioning rates with an increasing number of male
144 helpers (load-lightening), but not female helpers (additive care) (Brouwer et al.,
145 2014). This is in spite of male and female helpers feeding at similar rates, and not
146 differing in the type of food they provide (Brouwer et al., 2014). Second, high
147 rates of extra-pair paternity (Brouwer, Van De Pol, Atema, & Cockburn, 2011)
148 and a difference in future prospects between male and female helpers, indicate
149 likely variation in the benefits of investing in offspring care.

150

151 We predict that simulated increased chick need through playback of chick
152 begging will result in increased provisioning rates, but that the response will
153 depend on group composition and vary among different type of group members.
154 Load-lightening should only occur when group members can afford to reduce
155 their investment, thus when the likelihood of nestling starvation is low
156 (Hatchwell & Russell, 1996). Thus, we predict that in response to perceived
157 increased chick need, the previously reported load-lightening pattern with an

158 increasing number of male helpers should disappear and become additive care,
159 similar to the response to the number of female helpers (Brouwer et al. 2014).
160 Furthermore, we predict that, irrespective of group composition, dominant
161 females will show a stronger response to increased chick need than dominant
162 males and helpers, because high rates of extra-pair paternity (57 %) (Brouwer et
163 al., 2011) mean that they are most highly related to the offspring and thus gain
164 most benefits from successfully raising the brood. In addition, we predict that
165 male helpers show a stronger response than female helpers, because males are
166 more likely to inherit the natal territory and would therefore benefit more from
167 recruiting new group members who will later help them (Brouwer et al., 2014;
168 Russell & Rowley, 2000), in line with group augmentation theory (Kokko,
169 Johnstone, & Clutton-Brock, 2001).

170

171

172 **Methods**

173 Study area and data collection

174

175 Data were collected during the 2015 breeding season in a population of red-
176 winged fairy-wrens at Smithbrook Nature Reserve, near Manjimup, Western
177 Australia (34 ° 20 ' S, 116 ° 10' E) that has been studied since 2008 (Brouwer et
178 al., 2011). This reserve is a 95 ha area of state-owned karri forest (*Eucalyptus*
179 *diversicolor*) (for more details on habitat see Rowley et al. 1988). The main study
180 area comprised around 65 territories in which >99 % of the adult birds were
181 colour-banded with unique combinations. Territories were regularly checked to
182 determine breeding activity and to confirm group composition. In each group, a

183 'dominant' pair raises young with the help of subordinate helpers of both sexes.
184 Social status was based on behavioural observations, plumage variation, and age
185 (Russell & Rowley, 2000). Adult birds are sexually dimorphic, so breeder and
186 helper sex is easily determined visually (Rowley et al., 1988).

187

188 Nests, once discovered, were checked at least twice a week to monitor the
189 progress of nest building, egg laying, and chick hatching. Nests are incubated by
190 the dominant female for approximately 15 days and clutch size variation is
191 limited (98 % of nests have 2 or 3 eggs, (Lejeune, van de Pol, Cockburn, Louter, &
192 Brouwer, 2016). Broods are provisioned by group members until fledging at
193 around 12 days (Rowley et al., 1988). Nestlings can be accurately aged based on
194 characteristics like colour and the presence of wing buds (Rowley & Russell,
195 1997). Plural breeding, where more than one female in the group builds a nest
196 (Brouwer et al., 2011), were excluded from our experiments given that in these
197 rare instances helpers may divide their efforts between the nests of the primary
198 and the secondary breeder.

199

200 Recording of playback stimuli

201 Experimental playbacks were created from recordings of natural begging at
202 nests. To obtain these recordings, a camouflaged dummy recorder was placed
203 20-30 cm from the nest opening the day before recording was to take place. The
204 dummy was swapped for the camouflaged recording device (Zoom Handy
205 Recorder H5, Zoom Corporation, Tokyo, Japan) at least fifteen minutes before
206 recording began. Nests were recorded when nestlings were aged 8 and 10 days
207 old (day 1 being the day of hatching), for at least one hour. Sound files were

208 recorded as broadcast wave files at 48 kHz sampling rate. Times of day when
209 begging may be reduced, such as very early morning or in the middle of the day
210 when temperatures were highest, were avoided.

211

212 Playback sound files were created using the free software AudacityR
213 (“Audacity(R): Free Audio Editor and Recorder,” 2014;
214 <https://www.audacityteam.org>). Each playback contained only begging calls
215 from a single nest, recorded on a single day. The first 5 minutes of every raw
216 recording were deleted to remove noises associated with, and in case chicks
217 were momentarily disturbed by, placement of the recorder. Periods of chick
218 begging were identified, excised from the recording, and copied into a separate
219 file. From these excerpts, segments including adult calls, calls from other birds,
220 or other significant background noises such as traffic, were removed. The edited
221 excerpts were run together, with any gaps of silence removed, so that the
222 resulting playback was continuous natural begging with no other stimuli (mean
223 playback duration 126 s). Three recordings/playbacks were made for each chick
224 age (8 and 10 days old), at five different nests, all of which contained two chicks.

225

226 As a control, recordings of background noise from the study area were
227 used for playback (*sensu* Burford et al. 1998). Control recordings and playback
228 files were created in the same way as above, using recordings that were made at
229 least 30 m from any known nests. Control recordings were free of calls of red-
230 winged fairy-wrens, predatory birds or birds that should cause alarm (any such
231 calls were excised from the recording in Audacity). Three control playbacks were
232 made at three different locations (mean recording duration 37 min 15 s).

233

234 *Playback experiment*

235 The first experiment was performed when chicks were 7 or 8 days old. By this
236 stage nestlings are no longer brooded by the female, so her contribution can be
237 compared to that of other group members. Each experiment consisted of two
238 treatments per nest (control and experimental playback in random order), which
239 lasted for at least 1 hour (with groups larger than four birds being observed for
240 1.5 hours), separated by a break of 30 min during which time no noise was
241 played to allow all birds to feed with no additional stimuli. To increase sample
242 sizes the experiment (again, a control and an experimental playback in random
243 order) was performed at each nest two days later, thus when chicks were 9 or 10
244 days old. Due to nest predation, we were not able to perform a second test on all
245 nests, but our set-up with both experimental and control playback performed
246 within the same group on the same day ensures there is no bias due to variation
247 between days and chick ages.

248

249 As with the recording equipment, a camouflaged dummy speaker was
250 placed directly behind the nest at least one day before the experiment. At least
251 fifteen minutes before the experiment commenced, the dummy speaker was
252 replaced by a camouflaged rechargeable portable Bluetooth speaker (Trek
253 Micron: TDK Corporation, Tokyo, Japan), connected to an iPhone 4s (Apple Inc,
254 USA). The presence of a speaker did not alter provisioning rates (average
255 provisioning rates were in the same range as those previously reported without
256 auditory playback or playback equipment: Brouwer et al. 2014). The first feeding
257 visit to the nest after the initial fifteen minutes had elapsed marked the start of

258 the experiment; similarly, the first feed after the half hour break between
259 treatments marked the start of the second part of the experiment. Treatment
260 order (control/experimental) was determined by coin toss to minimise effects of
261 time of day, and within treatment, which of the recordings was used was
262 determined using a random number generator (www.random.org). Nests were
263 never played playbacks created using recordings of their own nestlings or those
264 of their neighbours. Playback volume was matched to natural amplitude of
265 background noise and the natural average volume of chick begging respectively.
266 The volume of chick begging was determined by measuring volume at 4 nests
267 prior to the start of the experiment using a sound meter application [Decibel X,
268 SkyPaw Co. Ltd, Vietnam, <http://skypaw.com/decibel10.html>; used on iPhone 4s,
269 Apple Inc, USA]). In day 7 & 8 trials, playbacks were subsequently played at 60-
270 65 dBA, while in day 9 & 10 trials, playbacks were played at the higher volume of
271 75-80 dBA (variation due to natural fluctuation in volume in recordings).
272 Measurements of average background noise were measured in the same way
273 (standing at least 20 m from any known nest) and control playbacks were
274 subsequently played at 40-50 dBA, mimicking the natural range, in order to
275 adequately control for speaker noise while also not providing a potential
276 deterrent (which playing background noise at unnaturally high volumes might
277 be).

278

279 To mimic the natural situation, birds were only subjected to playback
280 when approaching the nest. During each treatment, playbacks were started when
281 a bird was <10 cm from the nest opening, and continued for 5 seconds (average
282 length of a begging bout in fairy-wrens; MacGregor & Cockburn 2002).

283 Observations and control of the playback were done from a hide placed between
284 6 and 8 m from the nest, which was put up at least one day before the
285 experiment to minimize disturbance. The identity of each bird that brought food
286 to the nest was recorded, allowing calculation of each individual's provisioning
287 rate, and the total number of feeds provisioned to chicks by the whole group. In a
288 few cases where the vegetation surrounding the nest was dense, the identity of
289 the provisioning bird could not be identified (<1 % of feeds), in which case these
290 feeds were included in the count of group feeds and equally distributed among
291 all members of the group.

292

293 In total, we observed 290 feeding visits from 78 individuals, in 42 trials of
294 22 groups with varying group composition (0-3 male helpers, 0-2 female
295 helpers). Mean group size was 3.7 ± 0.9 S.D. (range 2-6). Group sex ratio
296 (proportion male) was on average 0.54 ± 0.2 S.D. (range 0.25 to 0.8). Group size
297 was not correlated with brood size (Spearman's $\rho = 0.23$, $P = 0.31$).

298

299 Statistical analyses

300 In order to determine whether the experimental playback treatment was
301 successfully perceived as increased chick need, we first analysed whether the
302 total feeding rate of a group per hour was significantly higher with the
303 experimental treatment compared to the control playback treatment on the
304 same day, using a paired t-test.

305

306 To test whether ecological context (perceived chick need) influenced individual
307 provisioning decisions, the number of feeds per bird per hour (transformed

308 using $\log_{10}(x+1)$ to normalize data) was fitted as a normal response variable in a
309 LMM. Identity of the group, trial (control and experimental observations of a
310 group within same day) and individual were included as nested random
311 intercepts to control for repeated observations. In addition, we fitted the number
312 of feeds using a Poisson distribution with the duration of the observation (on log
313 scale) as an offset. Our data was over-dispersed and to account for this, subject
314 identity was added as a random intercept (Harrison, 2014). The results from the
315 Poisson regression provided qualitatively similar results (Table A1). To
316 investigate whether load-lightening in the presence of male helpers became
317 additive in response to the experimental treatment, the covariate number of
318 male helpers, fixed factor playback treatment and their interaction were
319 included in the analysis. To test our prediction that dominant females would
320 respond stronger to the playback treatment than other group members, status of
321 the individual (dominant male, dominant female, helper male, helper female)
322 and its interaction with playback treatment were also included as fixed factors.
323 Subsequently this interaction allowed us to test whether helper males responded
324 more strongly than helper females by investigating the contrasts using a post-
325 hoc test. We also accounted for brood size (2 or 3 chicks), chick age, and the
326 number of helper females by including them as covariates.

327

328 Statistical analyses were performed in R (version 2.4.2) (R Core Team
329 2015, <https://www.r-project.org>) using packages lme4 (Bates, Mächler, Bolker,
330 & Walker, 2015) and phia (De Rosario-Martinez, 2015). All effects were mean
331 centred before including them in the model, allowing for interpreting main
332 effects in the presence of (non-significant) interactions in a full model

333 (Schielzeth, 2010). Significance was based on comparing the final model with a
334 reduced model without the predictor of interest using likelihood ratio tests.
335 Feeding rates in Fig. 1b were corrected for the number of helper males in the
336 group by calculating the difference between the observed values and the
337 predictions from the male helper effect (Table 1). Means are reported ± 1
338 standard error throughout except where otherwise stated.

339

340 Ethical Note

341 Although fairy-wrens are highly tolerant of human disturbance around the nest
342 site, we minimized the time at the nest setting up equipment and made sure the
343 birds returned to provision after this was done. The Western Australian
344 Department of Biodiversity, Conservation and Attractions gave permission for
345 fieldwork and the ANU Animal Experimentation Committee licensed our field
346 research. Permission for colour-banding was given by the Australian Bird and
347 Bat Banding Scheme (ABBBS).

348

349 **RESULTS**

350

351 *Response to experimental treatment*

352 Groups responded to our begging playback treatment as would be expected if it
353 was perceived as a signal of increased chick need: experimental begging
354 playback treatment significantly increased total feeding rates to the chicks
355 compared to control playback treatment at both chick ages (control vs
356 experimental: 7-8 days old, 15.7 ± 1.37 vs. 23.2 ± 2.12 feeds/h, paired $t = -3.79$,

357 d.f. = 22, $P = 0.001$; 9-10 days old, 23.1 ± 2.14 vs. 31.4 ± 3.20 feeds/ h; paired $t = -$
358 4.58, d.f. = 17, $P < 0.001$).

359

360 *Response to social and ecological context*

361 As previously reported (Brouwer et al 2014), individual provisioning rates of all
362 group members decreased with an increasing number of male helpers (load-
363 lightening), but not with the number of female helpers (additive care), (Fig. 1,
364 Table 1). However, in contrast to our prediction increased chick need did not
365 result in load-lightening in the presence of male helpers to become additive care:
366 provisioning rates declined with an increasing number of helper males in both
367 the control and playback treatments (Fig. 1; Table 1: Treatment \times number of σ
368 helpers).

369

370 *Variation in response due to type of group member*

371 Dominants responded stronger to the begging playback than helpers (Fig. 2),
372 however, in contrast to our prediction, dominant females did not respond more
373 strongly to the experimental playback than other group members (Fig. 2a; Table
374 1 interaction treatment \times status). In addition, our prediction that helper males
375 would invest more compared to helper females was also not supported (Fig. 2a;
376 post-hoc $\chi^2_1 = 0.001$, $P = 0.92$). Finally, the patterns were similar when
377 considering the relative change in investment of different type of group
378 members (Fig. 2b).

379

380

381 DISCUSSION

382 Understanding how key behaviours, such as parental care, might vary based on
383 social and ecological context could improve our understanding of how species
384 may plastically respond to environmental changes. Although considerable
385 plasticity has been demonstrated in parental investment of cooperative breeders
386 in response to a variety of ecological conditions, little attention has been paid to
387 how responses to social and ecological contexts (Adams et al., 2015). In this
388 study, we experimentally manipulated chick begging signals through begging
389 playback thereby mimicking harsh conditions, in the cooperatively breeding red-
390 winged fairy-wren. We found that individual provisioning rate decreased
391 according to the number of male helpers, independent of whether signals of
392 perceived chick need were at normal or experimentally elevated levels, thus
393 differences in offspring provisioning depending on social environment were
394 consistent across ecological contexts. In addition, there was no evidence that
395 individuals likely to gain more from future benefits showed a stronger response
396 to increased chick hunger. Together these results enforce the importance of the
397 social environment for investment decisions in cooperative breeders; individuals
398 of different status and sex showed consistent patterns in provisioning behaviour
399 even when overall feeding rates were increased in accordance with chick need.

400

401 *Increased chick need did not result in additive care*

402 Our experimental treatment resulted in increased provisioning rates, indicating
403 that the begging playback was perceived as a signal of hunger. However, in
404 contrast to our prediction, there was still load-lightening in the presence of male
405 helpers, whereas a reduction in investment is only expected when individuals
406 can afford to do so. Yet, although a comparative analysis of 27 cooperatively

407 breeding species showed that, across species, the occurrence of additive care is
408 significantly associated with a higher rate of nestling starvation (Hatchwell,
409 1999), evidence for plasticity in provisioning rate based on cues related to
410 nestling starvation is mixed. Luck (2002) demonstrated that compensatory and
411 additive investment strategies may be exhibited in the same species depending
412 on landscape characteristics that are linked to food availability: rufous
413 treecreepers (*Climacteris rufa*) in a fragmented, disturbed landscape with
414 decreased food availability did not reduce feeding rates as the number of nest
415 attendants increased, while load-lightening was observed in an undisturbed
416 landscape, where food was more abundant (Luck 2002). Conversely, in the
417 ground tit (*Parus humilis*), investment by breeders varies according to the
418 presence/absence of helpers regardless of the quality of the foraging
419 environment (Lu, Yu, & Ke, 2011).

420

421 This lack of consistency suggests that parental investment in addition to
422 being sensitive to cues of chick need or other environmental cues relating to the
423 likelihood of chick starvation, might also be dependent on other factors, such as
424 the relative costs of plastically increasing investment. Such costs may be reduced
425 in temperate or tropical habitats, where the costs for parents of increasing their
426 feeding effort is relatively low due to greater food abundance and mild
427 environmental conditions (Lu et al., 2011). There may also be temporal variation
428 in cue sensitivity. For example, a long-term study of how breeders respond to
429 group size in the acorn woodpecker (*Melanerpes formicivorus*) demonstrated
430 that load-lightening becomes more likely when chicks are older (> 7 days) and
431 the likelihood of brood reduction decreases (Koenig & Walters, 2012). Although

432 group members were responsive to experimentally elevated chick begging in our
433 study, the relatively short time-window in which we conducted the experiment
434 may not have been sufficient to result in a change in provisioning rules. If each
435 individual carefully considers its investment compared to others and the need of
436 the brood, more time might be needed to change care from load-lightening to
437 additive care.

438

439 *Investment did not vary with current and potential future benefits*

440 As typical for many species of the fairy-wren genus, many offspring are sired by
441 males from outside the social group (Brouwer et al., 2017). As a result, dominant
442 females have the highest relatedness to the offspring and thus benefit most from
443 raising young. However, in contrast to our prediction, dominant females did not
444 respond more strongly to increased chick need compared to other group
445 members. Possibly the extra costs of increasing provisioning even more do not
446 outweigh the benefits of increased offspring production, particularly because
447 dominant females already incur the costs of egg production, incubation and
448 brooding of the chicks. Alternatively, these additional costs to breeding females
449 may mean that females lack the flexibility of care that males have because they
450 may be working closer to their maximum capacity (Low et al., 2012).

451

452 Surprisingly, we found that dominant males too showed a strong
453 response to increased chick need, despite the fact that the offspring they care for
454 are often unrelated, and future helpers are costly for them as they compete for
455 extra-group matings (Brouwer et al 2011). A study in closely-related superb
456 fairy wrens (*Malarus cyaneus*) also showed that dominant males, but not

457 females, responded strongly to increased chick begging (MacGregor & Cockburn,
458 2002). This sex difference was attributed to differences in time spent at the nest:
459 breeding female superb fairy-wrens spend more time at the nest than their male
460 counterparts, and therefore potentially are better able to accurately assess chick
461 condition (in other words, they were “not fooled” by the playback experiment)
462 (MacGregor & Cockburn, 2002). In their study, dominant males may have
463 increased their feeding rates in order to compensate for the dominant females’
464 lack of response (MacGregor & Cockburn, 2002). However, this is an unlikely
465 explanation for the strong male response in our study, because all group
466 members, including dominant females, increased feeding rates in response to
467 increased begging. Alternatively, the costs of not responding to nestlings (e.g.
468 nestling starvation) may outweigh the benefits, such as reduced workload or
469 increased opportunities to solicit for extra-pair copulations. Dominant males
470 might be able to cope well with the costs of working harder and the
471 opportunities for increasing their chances of more extra-pair copulations might
472 be few since extra-pair mate choice seems to be based on moult date long before
473 the breeding season starts (Brouwer et al. 2011).

474

475 Despite the fact that male helpers are more likely to inherit the territory
476 than females (Russell & Rowley 2000) and thus would benefit more from
477 recruiting new group members who will later help them (Kokko *et al.* 2001;
478 Clutton-Brock 2002), we did not find that helper males responded to increased
479 chick need more strongly than female helpers. Such a pattern was shown in
480 cooperative meerkats (*Suricata suricatta*), where philopatric females fed
481 proportionally more than males in response to begging playback (English, Kunc,

482 Madden, & Clutton-Brock, 2008). As for other group members, however, further
483 increasing investment might not outweigh the costs this incurs, because future
484 group members might also be costly as being in a group with more female
485 helpers reduces survival (Lejeune et al, 2016).

486

487 *Cues for investment decisions*

488 The consistent provisioning patterns across contexts that we found suggest that
489 group composition is an important cue that is used by individuals as a basis for
490 provisioning decisions. However, in red-winged fairy-wrens it remains unclear
491 what information group composition actually provides. Why is the number of
492 helper males an important cue to individuals in red-winged fairy-wren groups,
493 particularly given that the number of helper females does not appear to be an
494 important cue? Previously, we hypothesised that helper males may be perceived
495 as being more reliable, given that they are less likely to disperse mid-season than
496 helper females (Brouwer et al., 2014; Russell & Rowley, 2000). Based on this
497 idea group members should base their investment decisions without presuming
498 that female help will be available.

499

500 Alternatively, males and females might use different cues on which to
501 base their investment decision. For example, in the closely related superb fairy-
502 wren it was shown that dominant females did not respond to increased nestling
503 begging, whereas both dominant and helper males did (MacGregor & Cockburn,
504 2002). In contrast, both helpers and dominants did use the same provisioning
505 rules in Arabian babblers (*Turdoides squamiceps*) (Wright 1998). In red-winged
506 fairy-wrens there is no indication that males and females use different cues,

507 since all group members respond in a similar way to the number of helper males
508 and there is no difference in overall investment among the sexes (Brouwer et al.,
509 2014) and the response to increased chick begging does not vary consistently
510 among males and females (Fig. 2). It is thus likely that both chick need and
511 investment of others are important cues, although when individuals show load-
512 lightening and thus have lower nest visitation rates, the signals of chick need
513 might become less important and individuals might rely more on what other
514 group members do. Nevertheless, although unlikely, we cannot rule out the
515 possibility that males and females use different cues, as this would require
516 playback experiments targeting focal individuals (e.g. one sex) only rather than
517 the whole group simultaneously. Here, we did not use such a design since we
518 were specifically interested in differences in responsiveness to chick cues within
519 the context of the group, not to the responses other individuals. Future
520 experiments targeting begging playback to helper males and females separately
521 might shed light on whether males and females use different cues, though in
522 practice such experiments are very difficult to perform for larger group sizes and
523 when birds arrive at the nest simultaneously or shortly after another.

524

525 *Conclusions*

526 Red-winged fairy-wrens show considerable complexity in provisioning rules,
527 displaying status-dependent differences in provisioning rates and a mix of
528 additive and load-lightening care according to group composition, which was
529 independent of chick need. The combination of responsiveness to group
530 composition, but individual and across-context consistency in provisioning rules,
531 reinforces the importance of considering social environment when investigating

532 resource investment in offspring. Furthermore, the quick response to increased
533 chick need indicates some flexibility in investment decisions. A fuller
534 understanding of the cues used by individuals (and how those cues may interact)
535 will further illuminate how we might expect key behaviours (such as parental
536 care), and cooperative species more generally, to respond to patterns of global
537 environmental change (Sih, Ferrari, & Harris, 2011).

538

539

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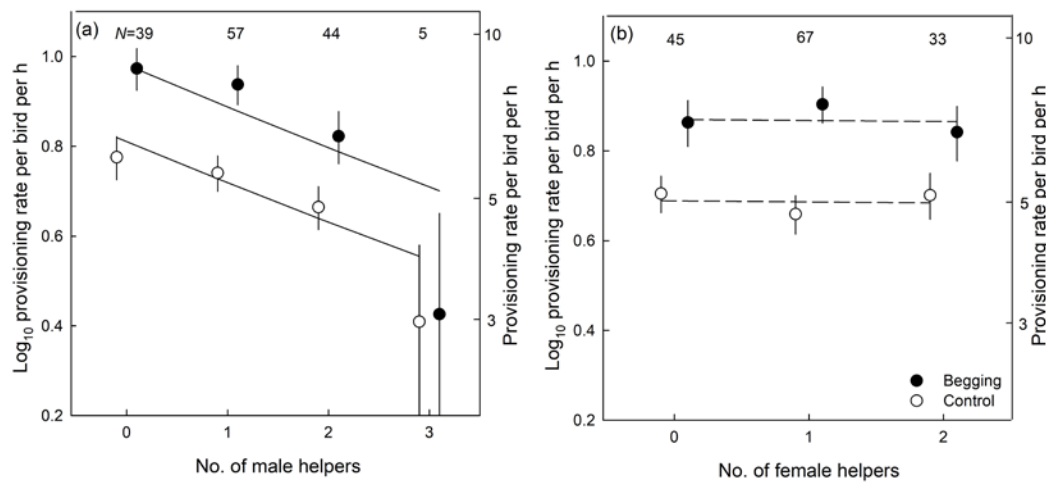
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729 Table 1. Results of a linear mixed model (LMM) examining provisioning rates in
 730 response to control and experimental (begging) playback at the nest.

	Estimate ± S.E.	<i>df</i>	<i>X</i> ²	<i>P</i>
Intercept	0.80 ± 0.03			
Treatment*	0.11 ± 0.02	1	24.4	<0.01
Number of ♂ helpers	-0.09 ± 0.04	1	6.2	0.01
Number of ♀ helpers	-0.002 ± 0.04	1	0.002	0.97
Status [§]		3	15.4	<0.01
♂ Dominant	0.05 ± 0.05			
♂ Helper	-0.07 ± 0.05			
♀ Helper	-0.17 ± 0.06			
Brood size	0.16 ± 0.06	1	6.7	<0.01
Chick age	0.06 ± 0.02	1	6.8	<0.01
Treatment × number of ♂ helpers	-0.02 ± 0.03		0.62	0.43
Treatment* × status [§]		3	5.7	0.13
Treatment × ♂ Dominant	0.04 ± 0.05			
Treatment × ♂ Helper	-0.07 ± 0.06			
Treatment × ♀ Helper	-0.08 ± 0.06			
Random effects				
σ ² _{Group}	<0.001			
σ ² _{Trial}	0.02			
σ ² _{Individual}	0.02			

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 732 Reference categories are as follows: *control; § ♀ Dominant. Provisioning rates
 733 were measured as the log₁₀-transformed number of feeds of a bird per hour. *N* =
 734 290 observations.

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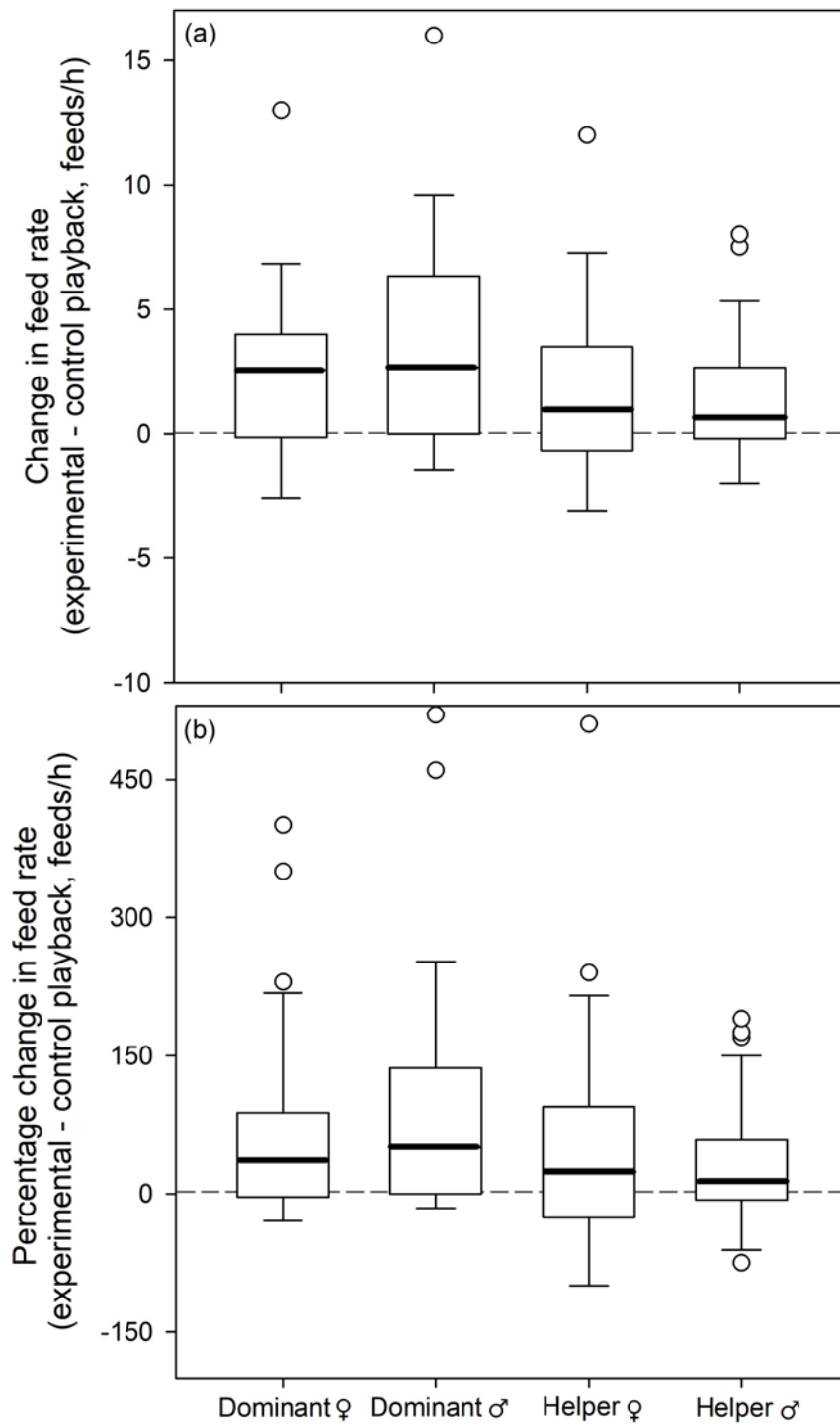


746

747 Fig. 1. The average provisioning rates per bird per hour in relation to a) the
 748 number of male helpers in the group and b) the number of female helpers in the
 749 group (corrected for the number of male helpers). Numbers on top indicate the
 750 number of observations. Error bars represent standard errors. Trendlines show
 751 the predictions according to the model (Table 1), with solid lines indicating
 752 significant and dashed lines indicating a non-significant association.

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756 Fig. 2. Boxplots showing the a) absolute and b) relative increase in provisioning
 757 rates in response to begging playback (experimental - control) for dominant and
 758 helper red-winged fairy-wrens of both sexes. Boxes represent the median, and

759 upper and lower interquartile ranges; whiskers represent minimum and
760 maximum values, with outliers shown as circles.
761

762 Table A1. Results of a generalized linear mixed model (GLMM, Poisson
763 distribution) examining the number of feeds to nestlings in response to control
764 and experimental (begging) playback at the nest.

	Estimate ± S.E.	<i>d.f.</i>	<i>X</i>²	<i>P</i>
Intercept	-2.46 ± 0.07			
Treatment*	0.29 ± 0.05	1	28.1	<0.001
Number of ♂ helpers	-0.26 ± 0.10	1	3.95	0.047
Number of ♀ helpers	-0.14 ± 0.12	1	1.32	0.25
Status [§]		3	15.0	<0.01
♂ Dominant	0.08 ± 0.12			
♂ Helper	-0.23 ± 0.13			
♀ Helper	-0.48 ± 0.15			
Brood size	0.26 ± 0.17	1	1.9	0.17
Chick age	0.17 ± 0.05	1	10.3	0.001
Treatment × number of ♂ helpers	-0.04 ± 0.07	1	0.29	0.59
Treatment* × status [§]		3	2.88	0.41
Treatment × ♂ Dominant	0.11 ± 0.12			
Treatment × ♂ Helper	-0.09 ± 0.13			
Treatment × ♀ Helper	0.08 ± 0.15			
Random effects				
σ ² _{Group}	0.02			
σ ² _{Trial}	0.09			
σ ² _{Individual}	0.11			
σ ² _{Observation}	0.03			

765
766 Estimates are on a log scale. Feed rate was offset by observation duration. *N* =
767 290 observations.

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