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1 **Parental provisioning behaviour in a flock-living passerine, the**
2 **Vinous-throated Parrotbill *Paradoxornis webbianus***

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22

23 **Abstract**

24 The amount of food delivered by parents to their chicks is affected by various life
25 history traits as well as environmental and social factors, and this investment
26 ultimately determines the current and future fitness of parents and their offspring. We
27 studied parental provisioning behaviour in vinous-throated parrotbills *Paradoxornis*
28 *webbianus*, a species with an unusual social system that is characterised by flock-
29 living, weak territoriality and variable nesting dispersion. Parental provisioning rate
30 had a positive influence on chick mass gain, suggesting that provisioning rate is an
31 effective measure of parental investment in this species. Males and females fed
32 nestlings at approximately the same rate, and no other carers were observed at nests.
33 Parents coordinated provisioning rates so that they mostly fed chicks synchronously.
34 However, the extent to which parents coordinated provisioning was associated with
35 their social environment, synchrony being positively related to local breeding density
36 and negatively to nearest-neighbour distance. The rate at which parents provisioned
37 nestlings showed the same relationships with social measures, being greatest at higher
38 density and when neighbours were closer. Visit rate was also related to chick age, but
39 not to brood size, brood sex ratio, extra-pair paternity, laying date, temperature,
40 parents' body characters, time of day or year. We conclude that a breeding pairs'
41 social environment plays an important role in determining parental investment,
42 probably through its effects on the opportunities that parents have for foraging with
43 conspecifics.

44

45

46 **Keywords** breeding density · group foraging · provisioning rate · *Paradoxornis*

47 *webbianus* · vinous-throated parrotbills

48

49 **Introduction**

50

51 In altricial bird species, fledging weight is largely dependent on the amount of food
52 delivered by parents during the nestling period (Naef-Daenzer and Keller, 1999) and
53 the condition of offspring at fledging is known to have important consequences for
54 subsequent survival of the offspring (Tinbergen and Boerlijst 1990; Magrath 1991;
55 Lindén et al. 1992; Both et al. 1999, MacColl and Hatchwell 2002). Therefore, high
56 investment in offspring in the current breeding attempt may bring high fitness returns
57 for both parents and chicks. However, provisioning involves energy expenditure by
58 parents, which might have a negative effect on their survival and future breeding
59 opportunities (Lindén and Møller 1989; Clutton-Brock 1991). Accordingly, parental
60 investment in chicks should be the result of a trade-off between current and future
61 benefits for each parent.

62 Provisioning rates are known to be influenced by a number of factors relating to
63 life histories, such as brood size (Nur 1984), extrapair paternity (Wright 1998) and
64 nestling sex ratio (Nishiumi et al. 1996; Westerdahl et al. 2000), and also
65 environmental conditions, such as breeding density (Silleet et al. 2004) and food
66 abundance (Naef-Daenzer et al. 2000). Furthermore, the influence of these ecological
67 factors on parental provisioning behaviour may also depend on the social system, such
68 as the number of carers providing food (Houston and Davies 1985; Hatchwell 1999;
69 Valencia et al. 2006) and the territorial system of the species concerned. For example,
70 in territorial species parental provisioning rates may depend on territory size and
71 quality, while in non-territorial breeding systems, food can not be monopolised and
72 parents often forage in groups so that parents may have to share resources with other
73 individuals (Krause and Ruxton 2002). Overall, provisioning behaviour reflects the

74 phylogeny, ecology and social behaviour of a species and its variation within and
75 between species has played an important role in determining the evolution of parental
76 investment.

77 We studied parental provisioning behaviour in the vinous-throated parrotbill
78 *Paradoxornis webbianus*, a small passerine (ca. 10 g) that is a common resident in
79 South Korea. Parrotbills are found in bush and scrub in diverse habitats ranging from
80 marshlands and lowlands to mountainous regions. They are not strictly territorial but
81 instead form large (ca. 50 – 150 individuals), stable flocks in the non-breeding season,
82 and during the breeding season, paired adults are frequently observed in small flocks
83 (ca. 3 – 10 individuals), even though they are not cooperative breeders. They breed in
84 monogamous pairs, building an open-cup nest and laying an average clutch size of 5
85 eggs; the nestling period is about 12 days (Kim et al. 1995). Parental roles from nest
86 building, through incubating to provisioning are similar for males and females (Kim
87 1998). They occasionally show territorial behaviour against other birds around the
88 nest during early breeding stage (nest building), but generally they do not defend
89 territories as distinct areas against intruders. This lack of territoriality during the
90 breeding season generates a variable number of close neighbouring breeders; some
91 breeding pairs have several closely neighbouring pairs while others are solitary (Kim
92 1998; Lee et al. 2009a).

93 The objectives of this study were to describe the pattern of parental
94 provisioning behaviour in this non-territorial breeding system, and to determine the
95 factors influencing parental behaviour, with a particular focus on the influence of the
96 species' unusual social system.

97

98 **Methods**

99

100 Fieldwork

101

102 The fieldwork was carried out during two breeding seasons (April - August, 2005 and
103 2006) at Buyoung-ri, Yangpyeong-gun, Gyonggi-do, South Korea (37°32'N
104 127°20'E). The study area is approximately 140 ha and consists of woodland with
105 scrub and bush at its margins, reedbeds around a stream running through the study
106 area, and farmland and gardens. There were five winter flocks, consisting of 60-120
107 individuals each, in the study area. As part of a study of the genetic structure of the
108 population, prior to each breeding season, almost all birds (> 90%, n = 651) in the
109 study area were caught using mist nets during the winter preceding each breeding
110 season (i.e. December - January, 2004-05, 2005-06). We measured the body mass (g)
111 and tarsus length (mm) of all captured birds, and ringed them with metal rings and
112 unique combinations of colour rings. Blood samples (ca. 10 µl) were also taken from
113 their brachial vein in the wing (n = 650) and stored in absolute ethanol for molecular
114 sexing and parentage analysis.

115 We searched intensively for nests in the study area during two breeding seasons.
116 Once found, nest locations were recorded to an accuracy of 10m using GPS, with
117 which we calculated nearest-neighbour distance and local breeding density: the
118 number of neighbouring nests within 200 m from a focal nest. We used a 200 m
119 criterion in the calculation of local breeding density because the breeding home range
120 of this species is about 100 m from their nests and thus birds breeding within 200 m of
121 one another have a high probability of contacting each other (Kim 1998). We
122 identified the breeding pairs at each nest by direct observation and video-recording.

123 Any unringed breeding birds were caught using mist nets, ringed, measured and bled
124 during the incubation period. We sexed breeding pairs by morphological difference
125 (e.g. cloaca shape) and/or molecular sexing (Griffiths et al. 1998). All known
126 breeding attempts were closely monitored via regular visits at 1-3 day intervals. We
127 filmed provisioning behaviour in 26 nests (15 in 2005, 11 in 2006), when the chicks
128 were 7-9 days old; at this stage, parents usually stop brooding chicks during the day
129 and parental provisioning rate reaches an asymptote (Kim 1998). No parents were
130 filmed at more than one nest. In 2005, we filmed nests using a micro camera set (Sony
131 MC-1 video camera, Sony DSR-11 VTR and Sony DV 270 ME videotape), which
132 gave 260 min of continuous recording. In 2006, we used a videocamera handycam (8
133 mm) with 120 min tape, placed on a tripod about one metre from the nest. In all cases,
134 the video camera was camouflaged to reduce disturbance to parents and any nests in
135 which parents showed unnatural behaviour in response to the presence of the
136 videocamera were excluded from the analysis. We calculated provisioning rate as the
137 mean number of feeding visits per brood per hour. We do not know the exact feeding
138 time but only feeding frequency per hour in observations conducted in 2005 but we
139 know the exact time of provisioning by males and females in 2006 with which we
140 analysed the relative timing (i.e. synchrony) of provisioning by males and females.
141 Provisioning timing between parents was regarded as synchronous when both parents
142 fed chicks within one minute of each other. We also measured the body mass of
143 chicks before and after videotaping, from which we inferred the amount of food
144 delivered by parents. Chicks were ringed and bled at the age of 8 or 9 days old for
145 further analysis.

146

147 Factors analysed and statistics

148

149 In order to analyse the effect of local breeding density on the coordination of
150 provisioning between male and female, we used robust fitting of linear regression,
151 which is appropriate when the data contain outliers. We fitted multiple linear
152 regression (MLR) models to analyse variables associated with provisioning rate by
153 parents. We first carried out normality test for each variable (Shapiro-Wilk test,
154 Shapiro and Wilk 1965) and then applied appropriate transformation using the Box-
155 Cox transformation if necessary. In a maximal model, we included age of chicks when
156 videotaping, brood size, brood sex ratio, the presence of extra-pair young (EPY), first-
157 egg laying date, local breeding density, nearest-neighbour distance, recording start
158 time to control for the effect of the time of the day and mean temperature to
159 investigate any effect of ambient weather. We also included their two-way
160 interactions and quadratic terms in the model. Local breeding density and nearest-
161 neighbour distance were strongly correlated each other (Spearman's rank correlation:
162 $r_s = -0.69$, $n = 26$, $P < 0.0001$), so we made two different maximal models, one of
163 which included local breeding density with the other variables, while the other
164 included nearest-neighbour distance with the other variables. In addition, the number
165 of parameters we tested were more than our data points ($n = 26$) so we conducted our
166 analyses with several separate models, each with an acceptable number of parameters
167 (ca. 9 parameters; Burnham and Anderson 2002). We achieved minimal adequate
168 models by putting all of the significant terms and nearly significant terms from each
169 model into the same model and then removed non-significant terms until all terms in
170 the model were significant (see Crawley 2007 for details). We also calculated effect
171 size (r , Pearson's product-moment correlation) for the significant terms, following the
172 suggestion by Nakagawa and Cuthill (2007). Detailed methods for molecular sexing
173 of nestlings and parentage analysis can be found in Lee et al. (2009a, b). Means are

174 presented with standard deviation throughout. All statistical analyses were carried out
175 in R 2.7.0 (R Development Core Team 2008).

176

177 **Results**

178

179 Parental provisioning patterns

180

181 The mean number of visits by parents per brood per hour was 7.0 ± 3.0 ($n = 26$) and
182 there was no difference between years in the mean provisioning rates by parents
183 (2005: 6.8 ± 3.0 , $n = 15$; 2006: 7.1 ± 3.1 , $n = 11$; Wilcoxon rank sum test, $W = 76.5$, P
184 $= 0.8$). No provisioning visits by non-parents were observed. The amount of food
185 delivered by parents, inferred by total brood mass change during the period of
186 observation, was significantly correlated with provisioning rates (Spearman's rank
187 correlation: $r_s = 0.54$, $n = 26$, $P < 0.001$; Fig. 1) indicating that provisioning rate is a
188 valid and meaningful measure of investment.

189 Averaged across all nests ($n = 26$), male parrotbills fed chicks slightly more
190 frequently than females (males 54%, females 46%, total visits = 337), but at each nest
191 there was no significant difference in the feeding frequency between males and
192 females (sign test, $n = 26$, $P = 0.85$). Morphological characteristics were not
193 correlated with the provisioning rate for either sex (male body mass $r_s = -0.18$, $n = 22$,
194 $P = 0.40$; male tarsus length $r_s = -0.23$, $n = 22$, $P = 0.30$; female body mass $r_s = 0.23$,
195 $n = 22$, $P = 0.30$; female tarsus length $r_s = 0.24$, $n = 22$, $P = 0.30$).

196 Of the variables included in the maximal models, only three remained as
197 significant terms in the minimal adequate models (Table 1). Firstly, chick age was
198 positively related to provisioning rate ($P < 0.05$; Table 1), even though the range of

199 ages in our samples was narrow (7 – 9 days old). Secondly, local breeding density had
200 a positive effect on provisioning rate ($P < 0.01$; Fig. 2a, Table 1). Finally, there was a
201 quadratic relationship between provisioning rate and nearest neighbour distance, with
202 the highest feeding rates found when neighbours were closer together ($P < 0.01$; Fig.
203 2b, Table 1).

204 All other variables, such as brood size, brood sex ratio, the presence of EPY,
205 laying date, mean temperature, time of day and their quadratic terms and two-way
206 interactions failed to explain the pattern of provisioning rate by parents. The incidence
207 of EPY in a brood did not affect significantly the amount of either paternal
208 provisioning (males without EPY: 3.7 ± 0.54 , $n = 16$; males with EPY: 2.9 ± 0.37 , $n =$
209 7 ; Wilcoxon rank sum test, $W = 66.5$, $P = 0.5$) or maternal provisioning (females without
210 EPY: 3.1 ± 0.28 , $n = 16$; females with EPY: 2.7 ± 0.54 , $n = 7$; $W = 66.5$, $P = 0.5$).
211 Similarly, the proportion of total feeds by males was not different in nests with and
212 without EPY (% provisioning by males without EPY: $52\% \pm 3.6$, $n = 16$; males with
213 EPY: $53\% \pm 3.1$, $n = 7$; $W = 51$, $P = 0.76$).

214

215 Provisioning and the social environment

216

217 There was a highly significant positive correlation between the provisioning rates of
218 males and females at the same nest ($r_s = 0.64$, $n = 26$, $P < 0.001$; Fig. 3). Such a
219 correlation could arise because parents were foraging in the same habitat to meet the
220 demands of a single brood, but from the smaller sample of nests for which the times
221 of all feeds were available there was also strong evidence that parents synchronized
222 the timing of provisioning visits with each other. The average provisioning rate per
223 hour was low (male: 4.0 feeds/h ± 1.70 ; female: 3.5 ± 1.74 ; $n = 10$), so the probability

224 that visits would be synchronized is small if they occurred at random. However, over
225 70 % of visits (total visits = 73 at 10 nests) were synchronized, i.e. they occurred
226 within one minute of a feed by their partner.

227 Interestingly, the extent to which a breeding pair matched the timing of their
228 provisioning visits was related to the local breeding density (Fig. 4). With more
229 neighbouring pairs, focal breeding pairs decreased the synchrony of provisioning
230 visits (Robust regression analysis: $t = -3.15$, $df = 9$, $P = 0.01$; Fig. 4a). Similarly, the
231 degree of synchrony was lower when the nearest neighbouring nest was closer ($t =$
232 5.08 , $df = 9$, $P < 0.001$; Fig. 4b).

233

234

235 **Discussion**

236

237 In this study, we explored several variables that are expected to influence parental
238 provisioning behaviour in birds. We found that parents at the same nest provision
239 their chicks at similar rates, and they also appear to synchronise their visits to the nest,
240 suggesting that males and females forage in close proximity to each other. In the
241 analysis of parental provisioning rates, our results showed that chick age was a factor
242 affecting the provisioning rate by parents, which is very common pattern observed in
243 most birds (Kim 1998; Sanz and Tinbergen 1999; Sethi and Bhatt 2007; Falconer et al.
244 2008). However, brood size did not affect provisioning rate in this study. This may be
245 due to the fact that brood size of most nests (21 out of 26 nests) lay in a small range (4
246 to 6 chicks) during our observation periods, which may not be large enough to
247 generate differences in provisioning rates during our observation periods. We also
248 found that provisioning rate was not affected by brood sex ratio, nor the presence of
249 extra-pair young; the latter result contrasts with several studies that have reported an

250 effect of extra-pair paternity on parental provisioning rates (e.g. Dixon et al. 1994;
251 Ewen and Armstrong 2000), although many other studies have found no such effect
252 (Wright 1998; Peterson et al. 2001; Dickinson 2003; Bouwman et al. 2005).
253 Provisioning rates were significantly related to local breeding density indicating that
254 there are foraging benefits from breeding in proximity to conspecifics. A similar
255 relationship was observed with nearest neighbour distance, although in this case
256 maximum provisioning rate was observed at intermediate density, suggesting that
257 there may be density-related costs such as increased competition and food depletion
258 around nests in some cases. Furthermore, those factors also significantly affected the
259 extent to which males and females forage together. We focus on this relationship
260 between provisioning and density in the rest of the discussion.

261 An explanation for these patterns is suggested by the social organisation of this
262 species, which is characterised by weak territoriality and flock-living. As reported
263 previously, nest distribution varies from solitary to loosely colonial (Kim 1998; Lee et
264 al. 2009a) and breeding birds in high local density often forage together (J-W Lee,
265 personal observation), which may be one explanation for the frequent observations of
266 small flocks during the breeding season. If some benefit of flocking, such as anti-
267 predator vigilance or improved foraging efficiency, causes the coordination between
268 males and females, we would expect a positive correlation between partners'
269 provisioning rates, as observed. Furthermore, the need for a pair to coordinate their
270 foraging behaviour decreases as the number of alternative 'flocking partners'
271 increases; in other words, breeding pairs experience fewer foraging constraints with
272 increased local breeding density. That is, by foraging in a group with conspecifics,
273 parents could increase their current survival probability as well as foraging efficiency,
274 and this may lead to an increased provisioning rate (Krause and Ruxton 2002). The

275 function of flocking as an anti-predator strategy is well documented (Elgar 1989). For
276 example, improved detection of predators and/or the dilution of predation risk by
277 flocking will increase the probability of survival for individuals during the breeding
278 season (Lima 1995; Roberts 1996). In addition, flocking could increase foraging
279 efficiency if the spatial distribution of prey is patchy and it is temporally
280 unpredictable (Ranta et al. 1998; Naef-Daenzer 2000), so that individual search times
281 for a food patch are reduced (Ranta et al. 1993). Foraging individuals in flocks could
282 also increase foraging efficiency through reduced vigilance (Cresswell 1994);
283 collectively these could lead to an increased provisioning rate. It is therefore likely
284 that group foraging will be favoured in at least some non-territorial species and the
285 same effect might be expected for males and females in territorial species, which may
286 be one of the factors promoting a matched provisioning between pair members (Hinde
287 2006; Johnstone and Hinde 2006). However, little is known about how group
288 members coordinate their behaviour in foraging groups (Rands et al. 2003).

289 Another possible explanation is that the observed provisioning pattern in this
290 study might simply reflect the differences in habitat quality and associated food
291 availability because social factors such as breeding density and nearest-neighbour
292 distance are often strongly correlated with habitat quality (Holmes et al. 1996). For
293 example, increased provisioning rates at higher local breeding density may simply
294 result from more pairs choosing to nest in areas of higher food availability, rather than
295 an effect of density on opportunities for group foraging. Similarly, the extent of
296 coordination between parents could also be correlated with habitat quality. For
297 example, pairs breeding at low density may live in poor habitat where it is more
298 advantageous to forage as a pair. However, we have no direct evidence that breeding
299 density is related to food availability in this species. Rather, we argue that local

300 breeding density seems to be determined principally by the availability of nest sites
301 (Lee et al. 2009a). For example, a garden or yard with lots of available nest substrate
302 often shows high breeding density, although this area is often far away from foraging
303 sites (J-W Lee, personal observation). In addition, frequent observations of foraging
304 groups during the breeding season suggest that breeding birds experience some
305 benefits from flocking, irrespective of habitat quality. Therefore, our results linking
306 provisioning frequency to social environment are suggestive, but must be interpreted
307 with caution, and ultimately experimental approaches that control for habitat quality
308 are needed to differentiate between the effect of social factors and habitat quality on
309 provisioning behaviour in this species.

310 To conclude, our study showed that parental provisioning rates in vinous-
311 throated parrotbills were positively related to breeding density and nearest-neighbour
312 distance. In a territorial species, this result might be interpreted as a consequence of
313 resource monopolisation by despotic individuals, but that clearly is not case in the
314 non-territorial parrotbills. Instead, the dispersion of nests might be expected to match
315 the availability of resources, resulting in no density effect on provisioning rates
316 (Fretwell and Lucas 1969). The fact that we find a positive effect of density on
317 provisioning suggests that social factors play an important role in determining
318 parental investment. The underlying mechanisms that generate this relationship are
319 unknown but are probably related to the parrotbill's small size and vulnerability to
320 predators, and hence to the benefits of group-foraging. Therefore, this study suggests
321 that a good understanding of a species' social structure during the breeding season
322 may be critical in understanding parental investment strategies, even in species
323 without cooperative brood care.

324

325 **Zusammenfassung**

326

327 **Fütterverhalten von Eltern bei einem in Gruppen lebenden Singvogel, dem**

328 **Braunkopf-Papageischnabel *Paradoxornis webbianus***

329

330 Die Menge an Futter, die Eltern ihren Küken bringen, wird sowohl durch
331 verschiedene Life-history Eigenschaften als auch von sozialen und Umweltfaktoren
332 bestimmt. Dieses elterliche Investment bestimmt letztlich die jetzige und zukünftige
333 Fitness von Eltern und Nachwuchs. Wir untersuchten das Fütterverhalten im
334 Braunkopf-Papageischnabel, einer Art mit einem unüblichen Sozialsystem, das sich
335 durch Gruppenleben, schwache Territorialität und variable Nestverteilung auszeichnet.
336 Die Rate, mit der der Eltern Futter anbringen, hatte positiven Einfluss auf die
337 Gewichtszunahme von Küken. Dies suggeriert, dass die Fütterrate ein gültiges Maß
338 für elterliches Investment dieser Art ist. Männchen und Weibchen fütterten ihre
339 Nestlinge zu sehr ähnlichen Raten; außer den Eltern wurden keine anderen Individuen
340 an Nestern beobachtet. Eltern koordinierten ihre Fütterraten derart dass die Küken
341 meistens synchron gefüttert wurden. Die Stärke dieser synchronisierten Fütterung war
342 jedoch mit dem sozialen Umfeld assoziiert, - positiv mit lokaler Nestdichte und
343 negativ mit der Entfernung zum nächsten Nachbarn. Die Fütterrate verhielt sich
344 ähnlich in Bezug auf die sozialen Variablen, sie war am größten in hoher Nestdichte
345 und wenn die Entfernung zu Nachbarn am geringsten war. Die Rate der Nestbesuche
346 zeigte ebenso einen Zusammenhang mit dem Alter der Küken, jedoch nicht mit
347 Gelegegröße, Gelege, Geschlechterverhältnis, Fremdpatenschaften, Legedatum,
348 Temperatur, körperliche Merkmale der Eltern, Tages- oder Jahreszeit. Wir schließen
349 daraus, dass das soziale Umfeld eines Brutpaares eine wichtige Rolle für elterliches
350 Investment spielen kann, möglicherweise mittels seines Effekts auf die Gelegenheit
351 zur Nahrungssuche in innerartlichen Gruppen.

352

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364

365

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367

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479

480

481 Table 1. Results from minimal adequate MLR Models exploring variables associated
482 with parental provisioning rates.

| | <i>n</i> | <i>df</i> | <i>t</i> | <i>P</i> | <i>r</i> | 95% CI |
|---|----------|-----------|----------|----------|----------|---------------|
| Minimal adequate model 1 | | | | | | |
| Age | 26 | 23 | 2.285 | 0.03 | 0.43 | 0.22 – 0.64 |
| Local breeding density | 26 | 23 | 3.411 | 0.002 | 0.58 | 0.32 – 0.84 |
| Minimal adequate model 2 | | | | | | |
| Age | 26 | 22 | 3.276 | 0.003 | 0.57 | 0.36 – 0.78 |
| Nearest-neighbour distance | 26 | 22 | 2.714 | 0.01 | 0.50 | 0.10 – 0.90 |
| Nearest-neighbour distance ² | 26 | 22 | -2.960 | 0.007 | -0.53 | -0.93 – -0.14 |

483 Model 1 and model 2 included local breeding density and nearest-neighbour distance,
484 respectively.

485

486

487 **Figure legends**

488

489 **Fig. 1.** The correlation between change in brood mass before and after videotaping
490 and provisioning rate ($n = 26$). Provisioning rate was the mean number of nest visits
491 per brood per hour by parents. Each data point represents one nest.

492

493 **Fig. 2.** The relationship between parental provisioning rates and (a) local breeding
494 density, and (b) nearest-neighbour distance. Provisioning rate was the mean number
495 of nest visits per brood per hour by parents. Local breeding density was estimated as
496 the number of neighbouring nests within 200 m from a focal pair. Each data point
497 represents one nest.

498

499 **Fig. 3.** The correlation between male and female provisioning rates at the same nest
500 ($n = 26$). Provisioning rate was the mean number of nest visits per brood per hour by
501 each individual. Each data point represents one nest.

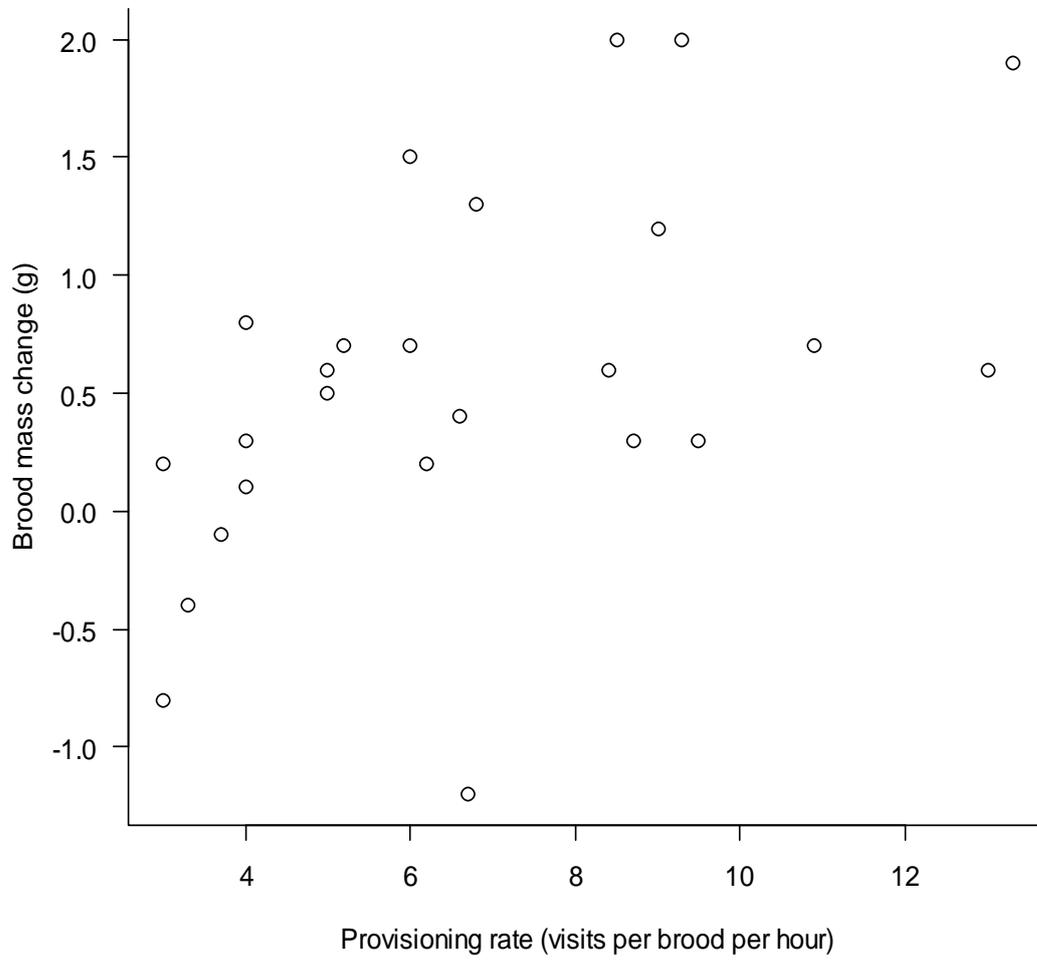
502

503 **Fig. 4.** The relationship between the degree of synchrony of nest visits by males and
504 females at the same nest and (a) local breeding density, and (b) nearest-neighbour
505 distance. Local breeding density was estimated as the number of neighbouring nests
506 within 200 m from a focal pair. Each data point represents one nest.

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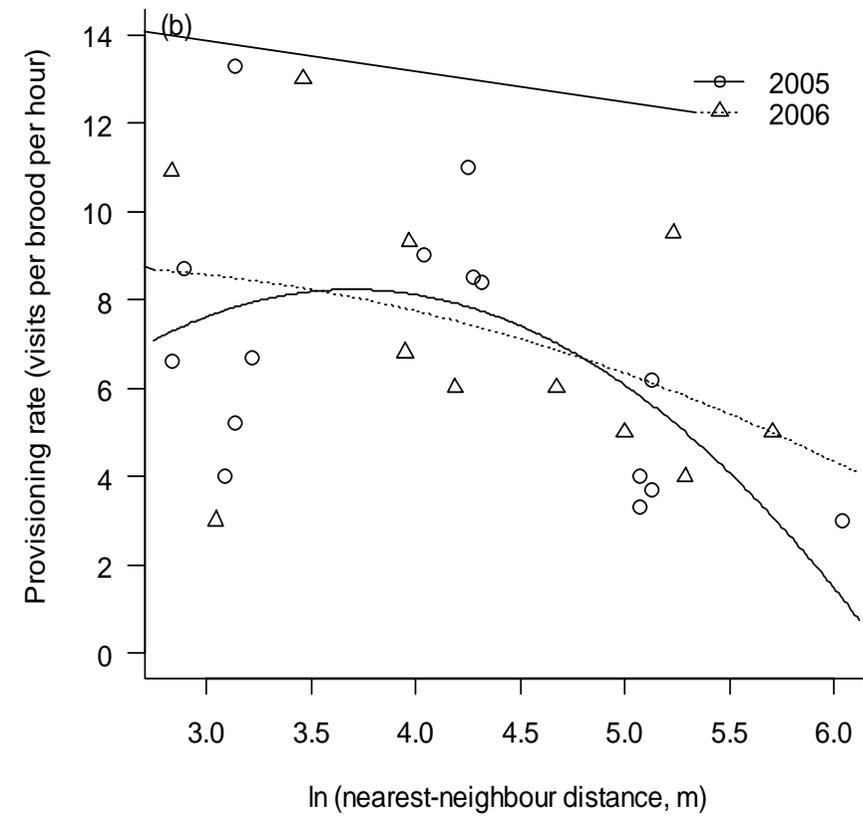
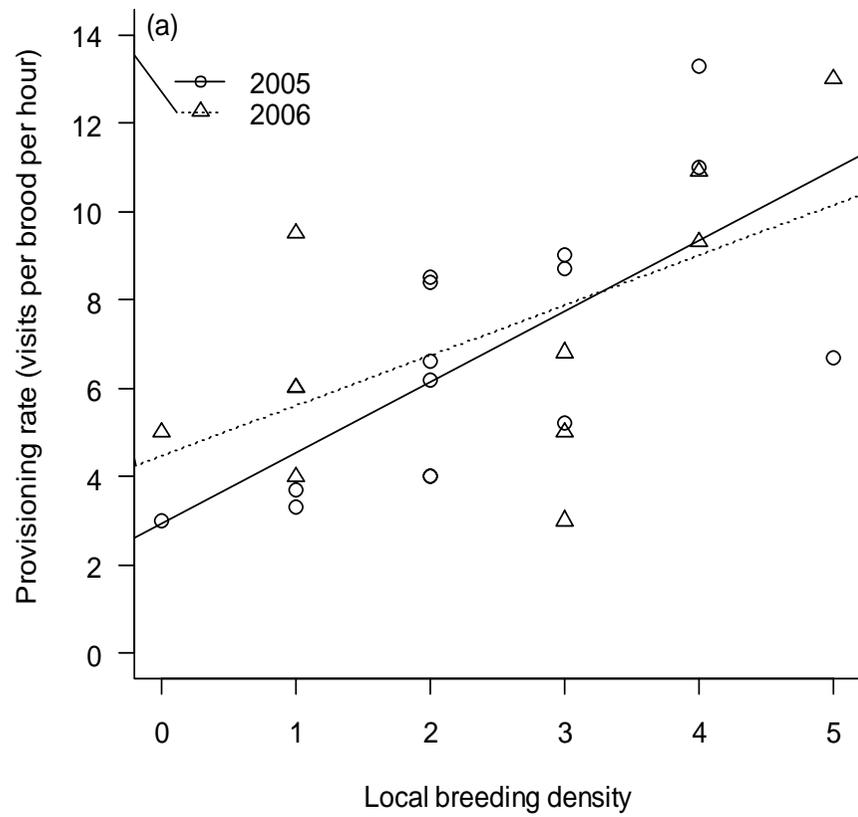
509



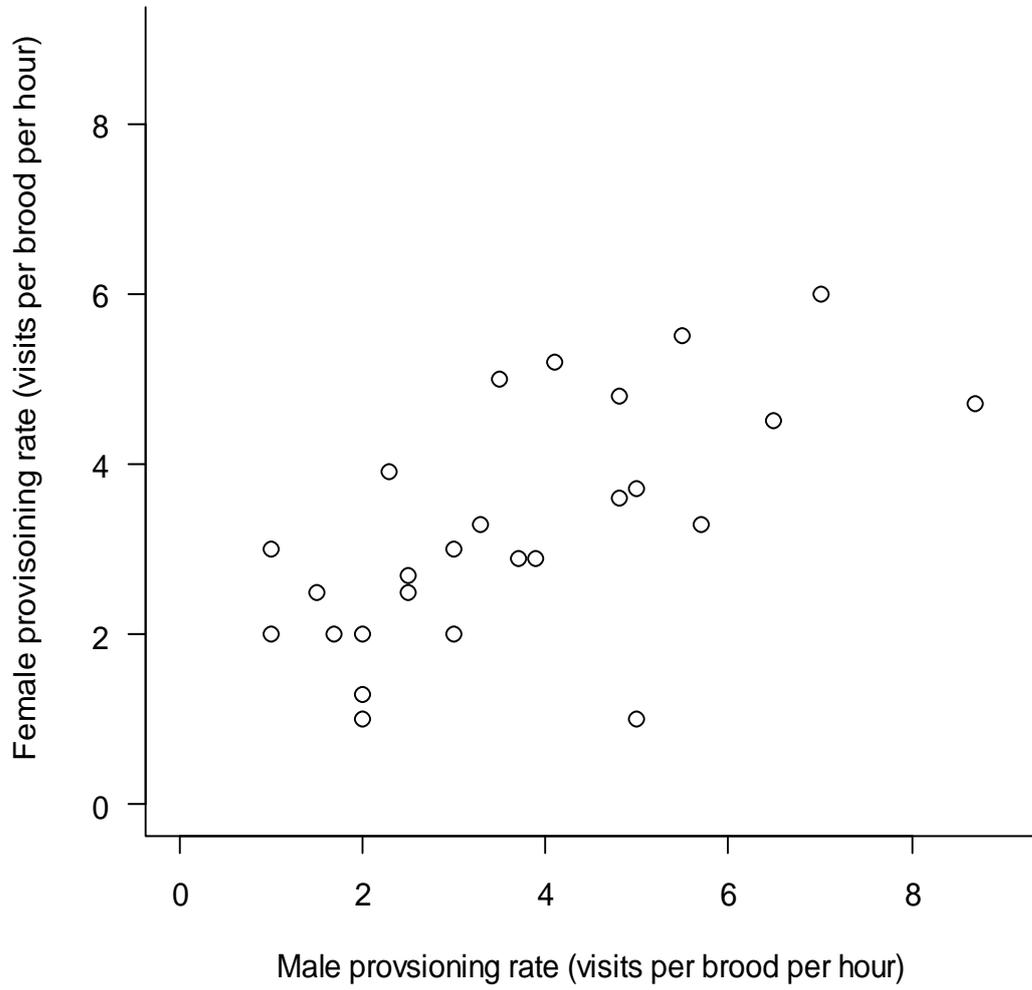
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511

512 Fig. 1.



513
 514 Fig. 2.
 515



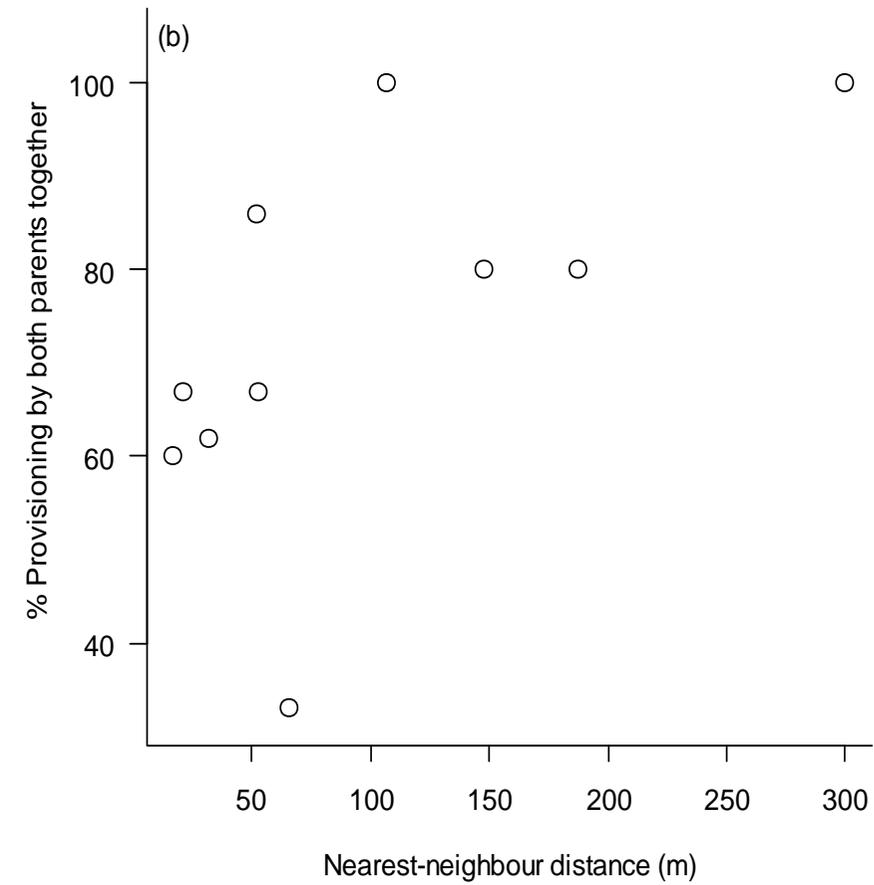
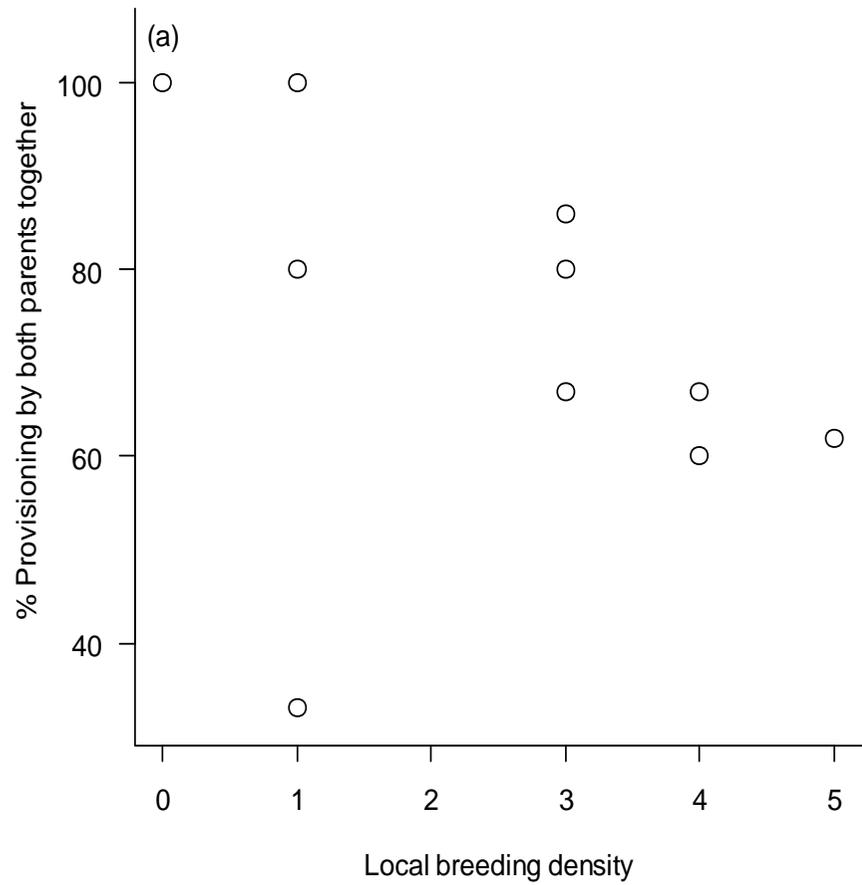
517

518

519 Fig. 3.

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522
523
524 Fig. 4.