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1 Parental effort according to dispersal

2 **Food availability modulates differences in parental effort between**
3 **dispersing and philopatric birds.**

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18 Dispersal entails costs and might have to be traded off against other life-history traits.
19 Dispersing and philopatric individuals may thus exhibit alternative life-history
20 strategies. Importantly, these differences could also partly be modulated by
21 environmental variation. Our previous results in a patchy population of a small
22 passerine, the collared flycatcher, suggest that, as breeding density, a proxy of habitat
23 quality, decreases, dispersing individuals invest less in reproduction but maintain a
24 stable oxidative balance whereas philopatric individuals maintain a high reproductive
25 investment at the expense of increased oxidative stress. In this study, we aimed at
26 experimentally testing whether these observed differences between dispersing and
27 philopatric individuals across a habitat quality gradient were due to food availability, a
28 major component of habitat quality in this system. We provided additional food for the
29 parents to use during the nestling rearing period and we measured subsequent
30 parental reproductive effort (through provisioning rate, adult body mass and
31 plasmatic markers of oxidative balance) and reproductive output. Density-dependent
32 differences between dispersing and philopatric parents in body mass and fledging
33 success were observed in control nests, but not in supplemented nests. However,
34 density-dependent differences in oxidative state were not altered by the
35 supplementation. Altogether, our results support our hypothesis that food availability
36 is responsible for some of the density-dependent differences observed in our
37 population between dispersing and philopatric individuals, but other mechanisms are
38 also at play. Our study further emphasizes the need to account for environmental
39 variation when studying the association between dispersal and other traits.

40 Keywords: parental care, dispersal, breeding density, habitat quality, oxidative stress,
41 reproductive output

42 **Introduction**

43 Dispersal has long been recognized as a key process in ecology and evolution in the
44 wild. In particular, it allows individuals to escape adverse conditions, reduces local
45 extinction risk in metapopulations and maintains gene flow between populations,
46 shaping local adaptation and speciation processes (Clobert et al. 2001). At the
47 individual level, dispersal has been shown to entail costs, e.g. the development of
48 morphological structures for mobility, the mortality risks during movement and
49 settlement in new habitats or the loss of familiarity with the habitat and social
50 environment (Bonte et al. 2012). Therefore, strong selective pressures should favor
51 dispersal of individuals bearing traits allowing them to reduce such costs (Clobert et al.
52 2009; Clobert et al. 2012). In the last decade, a growing number of studies have shown
53 that between-individual variation in dispersal often correlates with variation in
54 behavioral, morphological and physiological traits (Clobert et al. 2009; Ronce and
55 Clobert 2012; Debeffe et al. 2014). Such correlations can strongly affect population
56 dynamics (Bowler and Benton 2005; Phillips et al. 2006; Duckworth and Badyaev 2007;
57 Clobert et al. 2009; Hanski 2012) and evolution (Garant et al. 2005; Edelaar and Bolnick
58 2012), because dispersing individuals are not a random sample of the population.
59 Such correlations may reflect differential investment in phenotypic and life-history
60 traits between dispersing and philopatric individuals. As a result of these different
61 strategies, dispersing and philopatric individuals might eventually reach the same
62 fitness (Bélíchon et al. 1996; Julliard et al. 1996; Marr et al. 2002). Correlations between
63 dispersal and life history traits have been well described at the interspecific level
64 (Stevens et al. 2013; Stevens et al. 2014), although patterns are often inconsistent
65 between taxa (Stevens et al. 2014). Among vertebrates, empirical studies showed strong

66 variation between, but also within, species in the existence and direction of correlations
67 between dispersal and other life-history traits such as reproductive performance or
68 survival (reviewed in B elichon et al. 1996; Doligez and P art 2008).

69 Correlative studies may however fail to find predicted relationships between dispersal
70 and other phenotypic or life-history traits, or may even find opposite relationships, if
71 these relationships are influenced by environmental conditions (Clobert et al. 2009;
72 Cote et al. 2010). First, individual phenotype (e.g. sex and age), behavior or life-history
73 strategy can shape emigration and immigration responses to environmental variation
74 (Clobert et al. 2009; Le Galliard et al. 2012). An example of such phenotype-dependent
75 dispersal decisions is matching habitat choice, where a phenotype's fitness depends on
76 environmental conditions and each phenotype makes an adaptive decision to disperse
77 from its less favorable habitats toward its most favorable ones. Such a mechanism has
78 been experimentally demonstrated in various taxa including lizards (Cote and Clobert
79 2007; Bestion et al. 2015), fishes (Cote et al. 2013) and insects (Karpestam et al. 2012).

80 Additionally, dispersing and philopatric individuals may differ in their phenotypic or
81 life-history response to environmental conditions (van Noordwijk and de Jong 1986;
82 Price et al. 1988; Stearns 1989). Surprisingly, we currently know little about such a
83 differential response, because the effects of the post-dispersal environment on the
84 covariation between dispersal and other traits have mostly been investigated
85 correlatively so far (Myers and Krebs 1971; Duckworth and Badyaev 2007; Meylan et
86 al. 2009; R ecapet, Zahariev, et al. 2016; but see R ecapet, Daniel, et al. 2016). These
87 studies could therefore not exclude an effect of differential habitat choice between
88 dispersing and philopatric individuals. Whether and which environmental conditions
89 could causally alter phenotypic and life-history differences between dispersing and
90 philopatric individuals still needs to be experimentally explored, by manipulating

91 habitat characteristics without influencing habitat choice.

92 Previous results in a patchy population of collared flycatchers *Ficedula albicollis* suggest
93 that dispersing individuals produce less offspring than philopatric individuals when
94 breeding density decreases in their post-dispersal breeding habitat, but incur lower
95 physiological costs in terms of oxidative stress (Récapet, Zahariev, et al. 2016). In this
96 population, high local breeding density could reflect high habitat quality, and in
97 particular high food availability, because density is positively correlated with average
98 local breeding success (Doligez et al. 2004). However, high local density could also
99 generate high level of intraspecific competition during breeding, and thus low food
100 availability (Van Horne 1983). Therefore, the environmental factors at the origin of the
101 density-dependent differences between dispersing and philopatric individuals in
102 reproductive effort and output currently remain unknown.

103 To experimentally test whether food availability shapes differences between dispersing
104 and philopatric individuals in breeding strategies in this population, we provided
105 additional food to adults during the nestling feeding period. Food supplementation
106 has previously been shown to improve reproductive output in many species, including
107 the pied flycatcher *Ficedula hypoleuca*, a sister species of the collared flycatcher
108 (Verhulst 1994; Siikamäki 1998). By manipulating food availability after habitat choice
109 and settlement, we could ascertain that the observed differences were not biased by
110 differential habitat selection according to the treatment. We compared subsequent
111 reproductive effort, measured through parents' provisioning rate, body mass and
112 plasmatic markers of oxidative state (reactive oxygen metabolites and antioxidant
113 capacity), and the resulting reproductive output (nestlings' body mass and fledging
114 probability) between supplemented and control parents depending on their dispersal
115 status. If the differences previously observed between dispersing and non-dispersing

116 individuals were the result of different responses to food availability, we predict that
117 density-dependent differences between dispersing and philopatric individuals should
118 be reduced in food-supplemented nests compared to control nests. In that case, if low
119 breeding density is associated to low habitat quality and in particular low food
120 availability, the effect of food supplementation should be stronger in low-density
121 habitats. Conversely, if low breeding density is associated to low intraspecific
122 competition for food resources and thus high food availability, the effect of the food
123 supplementation should be stronger in high-density habitats. Other mechanisms than
124 food availability during nestling provisioning may also explain the density-dependent
125 differences between dispersing and philopatric individuals, such as the frequency of
126 aggressive social interactions (Duckworth 2008) or differential habitat choice according
127 to life-history strategies (habitat matching). In these cases, food supplementation is not
128 expected to influence density-dependent differences between dispersing and
129 philopatric individuals.

130 **Material and methods**

131 *Study population and definition of dispersal*

132 The study was conducted during spring 2014 on the island of Gotland, Sweden
133 (57°07'N, 18°20'E). Collared flycatchers bred in artificial nest boxes erected in 8
134 spatially discrete forest patches, with 17 to 42 breeding pairs per patch. Patches ranged
135 from 4.2 to 15.4 ha (mean \pm S.D. = 8.7 \pm 3.6) and contained between 24 and 77 nest
136 boxes (mean \pm S.D. = 48 \pm 18) regularly spaced, resulting in an average between nest
137 boxes distance of 37 to 48 meters (mean \pm S.D. = 42.5 \pm 4.2). The distance between
138 patches ranged from 680 to 5770 meters (mean \pm S.D. = 2869 \pm 1410), with only 2 pairs

139 of patches out of 28 being less than 1km apart (Figure S1). Nests were surveyed every
140 second day starting from 27 April to estimate laying date, clutch size, incubation date
141 and hatching date. 136 males and 147 females from 147 nests were caught inside nest
142 boxes when feeding 6 to 12-day-old nestlings (mean nestling age when catching the
143 parents \pm S.E. = Females: 9.7 ± 1.2 ; Males: 9.3 ± 1.3). Upon capture, birds were
144 identified (using individually numbered rings), weighed (to the nearest 0.1g), their
145 tarsus length was measured (to the nearest 0.1mm by a single observer, C.R.) and a
146 blood sample was taken (see below). Birds could be aged as yearlings or older adults
147 (i.e. 2 years old or older) based on plumage characteristics (Svensson 1992) or previous
148 capture history. Nestlings were ringed when 8 days old and weighed when 12 days
149 old. Nests were checked at the end of the season to record fledging success for each
150 nestling.

151 Local breeding density was measured as the proportion of available nest boxes
152 occupied by flycatchers in a patch. A nest box was considered available to flycatchers
153 when it contained no nest from another species (mainly great tit *Parus major* and blue
154 tit *Cyanistes caeruleus*) up to five days after the earliest egg-laying date for flycatchers in
155 the same patch. Nesting cavities are a major limiting resource for hole-nesting
156 passerines such as collared flycatchers and their availability is constrained by the
157 earlier settlement of resident birds (i.e. tit species). Measuring density relative to
158 available nest boxes rather than all nest boxes in the patch should therefore reflect
159 more accurately the attractiveness of a patch and the intensity of intra-specific
160 competition for cavities. Using the overall proportion of nest boxes occupied by
161 flycatchers (i.e. not accounting for nest box occupancy by species that start breeding
162 earlier) as a measure of local breeding density yielded similar results despite slightly
163 weaker effects than the proportion of available boxes occupied by flycatchers (results

164 not detailed). Conversely, using the number of pairs per surface unit as a measure of
165 density led to no effect, either alone or in interaction with dispersal status and
166 treatment, on any of the behavioral, physiological and reproductive response variables
167 (results not detailed). Therefore, this last measure did not appear relevant to catch
168 habitat quality and we only reported the effects of the density relative to available nest
169 boxes and referred to it as “density”. Local density, defined at the patch scale, was
170 previously found to influence dispersal decisions (Doncaster et al. 1997; Doligez et al.
171 2004) and differences in oxidative balance and reproductive success between
172 dispersing and non-dispersing individuals (Récapet, Zahariev, et al. 2016).

173 The landscape of the study area was spatially fragmented, with breeding forest patches
174 separated by fields, pastures and meadows unsuitable for breeding in this species.
175 Dispersal was defined as a change of patch between the year of the study and the last
176 previous record of the individual, either as an adult (breeding dispersal) or a nestling
177 (natal dispersal). This binary definition of dispersal is more appropriate than dispersal
178 distance between nest boxes given the patchiness of the study area (Doligez et al. 1999).
179 Because we had only 8 natal philopatric individuals for 21 natal dispersers in our
180 sample, we could not separate natal from breeding dispersal in the analyses and thus
181 pooled all individuals here according to their natal or breeding dispersal status.
182 Although these two processes are expected to be under different constraints (Paradis et
183 al. 1998), we found no interaction between age and dispersal status on reproduction
184 and oxidative stress in a previous study in the same population (Récapet, Zahariev, et
185 al. 2016) and restricting the data to breeding dispersal status did not qualitatively
186 change the results of the present study. We excluded previously unringed adults (N =
187 119, i.e. 42%), whose dispersal status was uncertain because a fraction of local breeders
188 are missed every year and thus immigrants consist of a mix of local birds and true

189 dispersing birds. We also excluded adults last caught in 2011 or before (N= 5, i.e. 2%)
190 because individuals that were missed for two or more years were likely to have
191 attempted to breed during these years and be missed, and their dispersal status was
192 therefore uncertain as well. However, we included 27 individuals last recorded in 2012.
193 Indeed, if these individuals had skipped reproduction in 2013, we correctly determined
194 their dispersal status. Some of them could have bred but be missed (due to temporary
195 emigration out of the study area or early breeding failure), in which case their actual
196 dispersal status might be incorrectly assigned (see discussion in Doligez et al. 2012).
197 Because dispersal was found to be repeatable in this population (Doligez et al. 2002;
198 Doligez and Pärt 2008) and because excluding these individuals did not change the
199 direction of our results, we however assumed that dispersal status determined with a
200 year of gap for these individuals indeed reflected their dispersal behavior. Our final
201 dataset included 85 females and 74 males of known dispersal status, coming from 121
202 different nests. Only one male was caught twice on different nests (i.e. was
203 polygynous).

204 *Food supplementation*

205 Food availability was manipulated by providing 30g live maggots (larvae of *Calliphora*
206 *erythrocephala*, Fibe AB, Kungsängen, Sweden) daily to half of our nests (N = 60
207 supplemented nests) from 2 to 12 days post-hatching in transparent containers
208 attached to nest boxes. The start of the food supplementation concurred with the
209 explosion of energetic demands at the beginning of nestlings' growth. The amount of
210 food provided corresponded to approx. 150 individual larvae of 200mg or 25 larvae per
211 nestling given the average brood size of 6 nestlings. Thus, the food supplementation
212 spared about half of the 360 daily parental visits (on average 24 visits per hour times 15

213 hours calculated from the measures of parental provisioning rates described below).
214 Thus, food was not provided *at libitum*. Accordingly, in nearly all cases, feeders were
215 empty on each refilling visit. Limiting the amount of food provided prevented
216 nestlings to be fed exclusively on maggots, which represented high energy but low
217 quality food compared to natural food items. Control nests (N = 61) received no food,
218 but were also visited daily to control for disturbance linked with human presence.
219 Broods that hatched on the same day were assigned either to the control or
220 supplemented treatment group alternatively in space within study patches to ensure a
221 homogeneous spatio-temporal distribution of treatments. The supplemented and
222 control nests did not differ in laying date (W = 1926, P = 0.62) or brood size at the
223 beginning of the experiment (i.e. on day 2; W = 2031, P = 0.27).

224 *Cross-fostering*

225 The dispersal behaviour of breeding adults might influence the quality of their
226 offspring through (i) genetic effects, (ii) pre-hatching effects (including breeding
227 habitat choice and maternal effects) and/or (iii) post-hatching investment in nestling
228 care. We were here interested in post-hatching parental responses to the
229 supplementation treatment in relation to dispersal status. Therefore, nestlings were
230 cross-fostered when two days old to dissociate pre-treatment effects of the parental
231 dispersal status from effects linked to the treatment. Nestling body mass and survival
232 were then analyzed in relation to their foster parents' dispersal status and experimental
233 treatment. Nestlings were cross-fostered between 3 broods hatched on the same day
234 and with similar body mass (i.e. with a difference in brood average body mass < 1g on
235 day 2). Whenever possible, all nestlings were exchanged with nestlings from the 2
236 other broods, so that experimental parents reared none of their own nestlings but

237 nestlings coming from two other broods. Partial cross-fostering were conducted when
238 only one suitable other brood was available or when brood sizes were too different. For
239 practical reasons, exchanges were performed within breeding patches whenever
240 possible (663 out of 1017 nestlings) or between nearby patches. Nests with a high early
241 mortality (≥ 3 dead hatchlings on day 2) were not cross-fostered but were included in
242 the supplementation experiment and the analyses if there was at least one nestling
243 alive on day 2.

244 *Parental provisioning rate*

245 When nestlings were 5 days old, parental provisioning rate was recorded during one
246 hour using a camouflaged camera located at least 6 meters from the nest box. Only one
247 nest was not recorded due to technical failure. At the beginning of the recording
248 period, the experimenter emptied the feeders on the nest box when necessary and
249 recorded the number of nestlings as well as their satiation level measured as their
250 response to the experimenter whistling on a 0-3 scale: (0) unreactive nestlings; (1) up to
251 two nestlings begging but stopping within a few seconds; (2) most nestlings begging
252 but stopping within a few seconds; (3) most nestlings begging continuously. This
253 variable controlled for parental motivation to feed nestlings. Video recording were
254 analyzed by two experimenters blind to the dispersal status of the parents and the
255 breeding density around the nest, although the feeders were visible on the video.
256 Provisioning rate was calculated for each parent as the number of feeding events per
257 hour and per nestling, starting from the first feeding event until the end of the
258 recording. This accounted for the parents' latency to resume feeding visits, which
259 could be influenced by the birds' response to the disturbance when setting the camera.
260 Three nests for which the feeders had not been properly emptied before the test were

261 excluded from the analyses. Five birds that resumed feeding less than 20min before the
262 end of the recording were excluded, because (i) their latency to resume feeding was
263 much longer (> 47min) than other individuals (< 35min), possibly indicating outlying
264 individuals in terms of parental care or response to experimental disturbance, and (ii)
265 they were observed feeding at most 3 times, thus their provisioning rate could not be
266 measured reliably. Individuals that did not resume feeding visits during the hour of
267 recording (N = 17) were also excluded because it was not possible to know whether
268 they were absent from the surroundings during the recording or too disturbed by the
269 presence of the camera. Including them with a provisioning rate of zero did however
270 not qualitatively change the results (not detailed here). The final dataset for
271 provisioning rate thus included 135 individuals from 105 nests, including 10 females
272 that were not caught while feeding nestlings.

273 *Blood markers of oxidative state*

274 A 40 μ L blood sample was taken from the brachial vein into heparin-coated Microvette
275 tubes (Sarstedt, Nümbrecht, Germany) for both parents when feeding nestlings. Blood
276 samples were maintained at 5°C in the field before being centrifuged in the evening to
277 separate plasma from red blood cells. Plasma and red blood cells were then stored at -
278 80°C until analyses in the laboratory.

279 The level of antioxidant defences may not accurately predict the level of oxidative
280 damages and these two components should always be measured simultaneously
281 (Costantini and Verhulst 2009). Because of the low amount of plasma available per
282 individual, we chose here to focus on two markers of oxidative state, describing
283 respectively oxidative damages and non-enzymatic oxidative defences: the reactive
284 oxygen metabolites (ROM) and the plasma total antioxidant capacity. ROMs are

285 organic hydroperoxides and act as precursors of long-term oxidative damage on
286 biomolecules. Antioxidant capacity was here measured as the capacity of plasma to
287 oppose the oxidative action of the hypochlorous acid HClO. This measure thus reflects
288 the concentrations of ascorbate (vitamin C), flavonoids, carotenoids, glutathione and
289 albumin, which are efficient scavengers of HClO, but not tocopherols (vitamin E) and
290 ubiquinol, which are less reactive toward non-radical oxidants (Folkes et al. 1995; de
291 Groot and Rauen 1998; Pattison et al. 2003; Pennathur et al. 2010). This measure of
292 antioxidant capacity is also independent of uric acid (Costantini 2011).

293 These oxidative state markers were measured using the d-ROMs test and the OXY
294 adsorbent test respectively (Diacron International, Grosseto, Italy), following protocols
295 previously used in the collared flycatcher (Récapet, Zahariev, et al. 2016). These tests
296 have been successfully used in birds to assess the cost of reproduction (Beaulieu et al.
297 2011; Stier et al. 2012). Each oxidative state marker was measured on five different
298 plates. Because less than 20 μ L of plasma was available for many individuals, only a
299 subset of individuals was measured in duplicate to estimate the coefficients of
300 variation (CVs). The inter-plate CVs were 8% and 13% on 11 duplicates for the d-
301 ROMS and OXY tests respectively and the intra-plate CVs were both 6% on 11
302 duplicates. The final sample consisted of 72 supplemented individuals (55 philopatric
303 and 17 dispersing) and 68 controls (50 philopatric and 18 dispersing) for ROMs and 83
304 supplemented individuals (63 philopatric and 20 dispersing) and 81 controls (58
305 philopatric and 23 dispersing) for antioxidant capacity.

306 *Statistical analyses*

307 To test whether food supplementation altered the dispersal-dependent responses to
308 breeding density in terms of parental effort, we examined the three-way interaction

309 between dispersal status, food supplementation and breeding density on provisioning
310 rate, adult body mass and markers of oxidative state using linear mixed models
311 (LMM). Because selective pressures acting on dispersal differ between sexes in this
312 species (Pärt 1995), the two-way interaction between sex and dispersal status was
313 included in all models. Because (i) adult body mass and physiological parameters vary
314 over the course of the nestling feeding phase (Récapet, Zahariev, et al. 2016) and (ii) the
315 effect of the supplementation on these parameters might increase with the duration of
316 the experiment, we also included time since hatching as a covariate (reflecting both
317 nestling age and the duration of the supplementation since supplementation always
318 started 2 days after hatching) and its interaction with treatment when modeling adult
319 body mass and markers of oxidative stress (parental feeding date was not concerned
320 because it was always recorded when nestlings were 5 days old). However, it was not
321 kept in any of the final models and we therefore do not detail the associated statistics
322 in the results. Pair and breeding patch were included as random effects to account for
323 the non-independence of the two members of a pair and for spatial environmental
324 variation. When modeling adult body mass, tarsus length was included as a covariate
325 to control for body size. Finally, for provisioning rate, brood size, nestlings' satiation
326 level and the starting hour of the recording, which have all previously been shown to
327 influence parental provisioning behavior, were added as fixed effects and the
328 recording day was added as a random effect to account for climatic variation between
329 days.

330 To evaluate the resulting effects on reproductive output, we examined the three-way
331 interaction between foster parents' dispersal status, food supplementation at the foster
332 nest and breeding density on nestling body mass when 12 days old, which is a
333 predictor of future juvenile survival and recruitment in the collared flycatcher (Lindén

334 et al. 1992), and on fledging probability. Nestling body mass was analyzed using a
335 linear mixed model, while fledging probability for each nestling was analyzed using a
336 generalized linear mixed model (GLMM, with a logit link function and a binomial
337 error distribution). We analyzed males and females separately to avoid the redundancy
338 of breeding data when both members of the pair were of known dispersal status.
339 Hatching date was included as a fixed covariate and foster nest, nest of origin and
340 patch were included as random effects. When analyzing nestling body mass, the time
341 of weighing was also included as a fixed covariate.

342 Adding adult's age (yearling vs. older adult) as a covariate for all variables measuring
343 reproductive effort and output did not qualitatively change the results, therefore we do
344 not detail the associated statistics. Due to the very small number of ringed yearlings
345 found in 2014 in the experimental patches (12 yearlings out of 159 adults in total), the
346 interaction between age and other variables could not be tested.

347 All models were run using the R software (R Core Team 2016). Fixed effects were
348 selected by stepwise backward elimination. Selection criteria were the p-values of type-
349 III F-tests for LMM, with denominator degrees of freedom calculated using
350 Satterthwaite's approximation (R package 'lmerTest', function anova, Kuznetsova,
351 Brockhoff & Christensen 2013) and the p-values of type-III Wald chi-square tests for
352 GLMM (R package 'car', function Anova, Fox & Weisberg 2011). No selection was
353 performed on random effects, which were kept in all final models.

354 *Ethics statement.*

355 Permission for catching and ringing adult and young birds was granted by the Ringing
356 Centre from the Museum of Natural History in Stockholm (license number 471:M009 to
357 C.R.). Permission for blood taking and experimental procedures was granted by the

358 Ethical Committee for Experiments on Animals in Sweden (license number C 108/7).

359 **Results**

360 *Reproductive effort*

361 *Provisioning rate*

362 The three-way interaction between dispersal status, breeding density and food
363 supplementation treatment on provisioning rate was not significant ($F_{1,110} = 0.09$, $P =$
364 0.77). However, provisioning rate per nestling was higher for dispersing compared to
365 philopatric individuals ($F_{1,117} = 10.71$, $P = 0.001$; estimate \pm SE for dispersing compared
366 to philopatric individuals: 0.5 ± 0.2 ; Table 1). Provisioning rate also decreased with
367 breeding density in control nests ($F_{1,70} = 8.79$, $P = 0.004$; estimate \pm SE: -1.8 ± 0.6) but not
368 in supplemented ones ($F_{1,39} = 0.59$, $P = 0.45$), leading to a significant interaction
369 between breeding density and supplementation treatment on provisioning rate ($F_{1,61} =$
370 6.40 , $P = 0.014$; Figure 1). Provisioning rate per nestling also decreased with increasing
371 brood size ($F_{1,87} = 29.01$, $P < 0.001$; estimate \pm SE: -0.3 ± 0.1). Provisioning rate did not
372 depend on nestlings' satiation level ($F_{3,83} = 1.04$, $P = 0.38$) or the time of the day when
373 provisioning rate was recorded ($F_{1,79} = 0.002$, $P = 0.97$).

374 *Adult body mass*

375 The three-way interaction between dispersal status, breeding density and food
376 supplementation treatment on adult body mass was significant ($F_{1,145} = 7.75$, $P = 0.006$;
377 Table 1; Figure 2). In control nests, adult body mass increased with breeding density in
378 dispersing birds (post-hoc test: $F_{1,19} = 12.30$, $P = 0.002$, estimate \pm SE: 2.63 ± 0.75) but not

379 in philopatric birds ($F_{1,5} = 0.14$, $P = 0.73$). Conversely, in supplemented nests, adult
380 body mass did not depend on density either in dispersing or philopatric birds (both P
381 > 0.21). Body mass also increased with tarsus length ($F_{1,150} = 19.44$, $P < 0.001$; estimate \pm
382 SE: 0.44 ± 0.10) and was higher in females compared to males ($F_{1,95} = 10.20$, $P = 0.002$;
383 estimate \pm SE: -0.29 ± 0.09).

384 *Markers of oxidative state*

385 The three-way interaction between dispersal status, breeding density and food
386 supplementation treatment on the two markers of oxidative state was not significant
387 (ROM concentration: $F_{1,126} = 1.77$, $P = 0.185$; antioxidant capacity: $F_{1,152} = 0.03$, $P =$
388 0.873). However, the relation between ROM concentration and breeding density
389 differed between dispersing and philopatric birds (interaction between dispersal status
390 and breeding density: $F_{1,129} = 4.01$, $P = 0.047$; Table 1; Figure 3). ROM concentration
391 tended to increase with breeding density in philopatric individuals ($F_{1,81} = 2.83$, $P =$
392 0.096 ; estimate \pm SE : 0.173 ± 0.103) but not in dispersing ones ($F_{1,6} = 0.33$, $P = 0.59$).
393 ROM concentrations did not depend on the food supplementation treatment ($F_{1,94} =$
394 0.01 , $P = 0.92$; none of the two- and three-way interactions with dispersal and density
395 was significant: all $P > 0.18$).

396 None of the interactions between dispersal status, food supplementation and/or
397 breeding density on antioxidant capacity was significant (all $P > 0.19$). We found a
398 significant interaction between sex and dispersal status on antioxidant capacity ($F_{1,155} =$
399 5.33 , $P = 0.022$; Table 1): antioxidant capacity was lower in dispersing females
400 compared to philopatric ones ($F_{1,83} = 4.66$, $P = 0.034$; estimate \pm SE: -19.6 ± 9.1); whereas
401 no such difference was found in males ($F_{1,72} = 1.53$, $P = 0.22$). Antioxidant capacity did
402 not depend on the supplementation treatment ($F_{1,154} = 2.13$, $P = 0.15$) or breeding

403 density ($F_{1,154} = 1.31$, $P = 0.25$).

404 ***Reproductive output***

405 *Nestling body mass*

406 Nestling body mass when 12 days old did not differ between dispersing and
407 philopatric foster mothers ($F_{1,65} = 0.25$, $P = 0.62$; none of the two- and three-way
408 interactions with food supplementation treatment and/or breeding density was
409 significant: all $P > 0.24$). Nestling body mass tended to be higher for dispersing
410 compared to philopatric foster males ($F_{1,51} = 3.44$, $P = 0.069$; estimate \pm SE for
411 dispersing compared to philopatric males: 1.06 ± 0.57 ; none of the two- and three-way
412 interactions with food supplementation treatment and/or breeding density was
413 significant: all $P > 0.16$). In both analyses (with resp. females or males of known
414 dispersal status), nestling body mass did not depend on the supplementation
415 treatment ($P > 0.48$), breeding density ($P > 0.89$) or their interaction ($P > 0.37$). Nestling
416 body mass decreased with hatching date ($P < 0.007$; Table 2) but did not depend on the
417 time of the day when the nestlings were weighed ($P > 0.26$).

418 *Fledging probability of nestlings*

419 None of the two- and three-way interactions of dispersal with food supplementation
420 treatment and/or breeding density was significant (all $P > 0.41$). Fledging probability
421 was higher when the foster female was dispersing ($X^2_1 = 3.94$, $P = 0.047$; estimate \pm SE
422 for dispersing compared to philopatric females: 1.53 ± 0.77). Fledging probability was
423 higher in supplemented compared to control nests ($X^2_1 = 6.22$, $P = 0.013$; estimate \pm SE
424 for supplemented compared to control nests: 1.71 ± 0.69 ; Table 3) but it did not depend

425 on breeding density ($X^2_1 = 0.11$, $P = 0.75$) nor its interaction with the food
426 supplementation treatment ($X^2_1 = 0.15$, $P = 0.70$).

427 Conversely, fledging probability differed between foster dispersing and philopatric
428 males but this effect depended on both breeding density and supplementation
429 treatment (three-way interaction: $X^2_1 = 6.10$, $P = 0.014$; Table 3; Figure 4). In control
430 nests, there was a significant interaction between male dispersal status and breeding
431 density ($X^2_1 = 7.29$, $P = 0.007$), because fledging probability increased with breeding
432 density in philopatric males ($X^2_1 = 6.21$, $P = 0.013$; estimate \pm SE: 10.22 ± 4.10) while it
433 was independent of breeding density in dispersing males ($X^2_1 = 2.24$, $P = 0.13$). In
434 supplemented nests, fledging probability did not depend on dispersal status ($X^2_1 =$
435 2.51 , $P = 0.11$), breeding density ($X^2_1 = 0.01$, $P = 0.91$) or their interaction ($X^2_1 = 0.59$, $P =$
436 0.44).

437 In both analyses, fledging probability decreased with increasing hatching date ($P <$
438 0.002 , Table 3).

439 **Discussion**

440 Differences in life-history traits between dispersing and philopatric individuals have
441 frequently been reported in empirical studies (Bélichon et al. 1996; Doligez and Pärt
442 2008), but their origin remains poorly understood. Previous results in the collared
443 flycatcher have shown that differences between dispersing and philopatric individuals
444 in oxidative state and reproductive output depended on local breeding density
445 (Récapet, Zahariev, et al. 2016). Through a manipulation of food availability after the
446 onset of breeding, here during the nestling feeding period, we investigated whether
447 such phenotypic differences between dispersing and philopatric birds were due to
448 food availability. In control nests, we observed density-dependent differences in adult

449 body mass between dispersing and philopatric individuals and, despite the low
450 sample sizes, in fledging probability between dispersing and philopatric males, but
451 these differences disappeared in supplemented nests. Density-dependent differences in
452 oxidative damages and non-density-dependent differences between dispersing and
453 philopatric females in antioxidant capacity and fledging success were however
454 unaffected by the food supplementation treatment. These results confirm that some of
455 the differences observed between dispersing and philopatric individuals depend on
456 food availability, whereas other differences might either be fixed or depend on other
457 environmental factors, unidentified at this stage.

458 Interestingly, inspection of the effects of dispersal and density in control nests in this
459 population across years 2012 and 2013 (Récapet, Zahariev, et al. 2016) and 2014 (this
460 study) showed that the differences between dispersing and philopatric individuals
461 were also sensitive to the temporal variation of the environment (Tables S1 to S5).
462 Environmental conditions in 2014 strongly differed from 2012 and 2013, with highly
463 unfavorable meteorological conditions (heavy rainfall and low temperatures), which
464 resulted in very high nestling mortality rate and thus poor reproductive output in 2014
465 compared to previous years, especially 2012, which had been a very favorable year
466 (mean fledging success in control nests \pm S.D. = 4.7 ± 2.6 in 2012, 3.0 ± 2.4 in 2013 and
467 1.5 ± 2.0 in 2014, to be compared to the average fledging success from 1980 to 2011 = 3.6
468 ± 0.6). Many of the effects observed in 2014 in control nests were cancelled (antioxidant
469 capacity) or even reversed (ROMs, fledging success of females) when conditions were
470 more favorable; some others were either unchanged (body mass) or their temporal
471 variation was difficult to assess due to low sample size (fledging success of males).
472 This suggests that both generally favorable environmental conditions and food
473 supplementation resulted in altering part of the observed differences between

474 dispersing and philopatric individuals. Further longitudinal data would be necessary
475 to better understand the potential impact of temporal environmental variation on
476 density-dependent differences between dispersing and philopatric individuals.

477 *Role of food availability in mediating the density-by-dispersal interaction on body mass*
478 *and reproduction*

479 In line with previous studies in pied flycatchers (Verhulst 1994; Siikamäki 1998), our
480 food supplementation was successful at increasing nestling survival until fledging. In
481 supplemented nests, the effect of breeding density on adult body mass and fledging
482 probability was cancelled out. The decrease in provisioning rate with increasing
483 density in control nests, independently of dispersal status, also disappeared in
484 supplemented nests, mainly because of an increase in provisioning rate in high-density
485 habitats (Figure 1). Food availability thus played a role in mediating the density-
486 dependence of these traits and in particular the differences between dispersing and
487 philopatric individuals in patterns of density-dependence on adult body mass and
488 fledging probability, although the last result remains to be confirmed with more
489 statistical power. Interestingly, for these two traits, the difference between control and
490 supplemented nests was observed at low densities (Figures 2 and 4). This confirms that
491 food availability was more constrained in low-density than high-density habitats and
492 that density reflects habitat quality rather than intraspecific competition level in this
493 population.

494 *Different responses to breeding density between dispersing and philopatric birds*

495 When considering only control nests, fledging probability increased with breeding
496 density in philopatric males only, whereas adult body mass increased with breeding

497 density in dispersing individuals (males and females) only. Despite the small sample
498 sizes for dispersing males, the significance of the interaction between density and
499 dispersal status in control nests speaks for an actual density-dependent difference
500 according to dispersal. The general directions of these effects confirm that high-density
501 habitats are also high-quality breeding habitats as previously reported (Doligez et al.
502 2004), because measures of adult condition or success increase when density increases.
503 Nevertheless, the fact that either body mass (for dispersing individuals) or
504 reproductive success (for philopatric males) increases but not both simultaneously
505 suggest a trade-off between parental condition and nestling survival until fledging, so
506 that both may not increase simultaneously (Ardia and Clotfelter 2007; Jacquin et al.
507 2012). Dispersing individuals would favor reproductive success at the cost of a higher
508 reproductive effort when habitat quality decreases, while philopatric males maintain
509 the same reproductive effort at the expense of reproductive success. This scenario
510 however remains speculative at this stage, because differences in markers of oxidative
511 stress did not mirror differences in adult body mass and because temporal variation in
512 these relationships remains to be explained. Nevertheless, an increase in oxidative
513 stress and a decrease in adult body mass can represent two alternative mechanisms to
514 explain reproductive costs. Confirming that dispersing and philopatric individuals use
515 different strategies along a trade-off between reproductive effort and reproductive
516 output would require experimental confirmation, for example by simultaneously
517 manipulating reproductive effort (e.g. using brood size manipulation) and
518 environmental conditions (e.g. nest box density).

519 ROM level also increased with breeding density in philopatric individuals only,
520 independently of the food supplementation. This relation is opposite to the decrease of
521 ROM level with increasing breeding density observed in philopatric individuals in the

522 same population in years 2012 and 2013 (Récapet, Zahariev, et al. 2016; Table S2).
523 Although the effect of breeding density on ROM level was reversed in 2014 compared
524 to previous years, an interaction between breeding density and dispersal status was
525 found in all three years. This confirms the importance of environmental conditions in
526 determining the differences between dispersing and philopatric individuals in
527 oxidative state.

528 *Differences between dispersing and philopatric birds independent of density and food*
529 *supplementation*

530 Philopatric individuals had a lower provisioning rate and lower fledging probability
531 per nestling than dispersing ones, independently of patch breeding density or food
532 supplementation. Consistent with previous results in this population (Récapet,
533 Zahariev, et al. 2016; Table S3), dispersing females also had a lower antioxidant
534 capacity compared to philopatric ones. This suggests that dispersing females had a
535 higher reproductive effort which translated into a higher reproductive success,
536 independently of the environment. However, the difference in fledging probability
537 according to female dispersal status was reversed in 2012 and 2013 compared to 2014
538 (Récapet, Zahariev, et al. 2016; Table S4). Therefore, environmental variability in
539 factors besides density and food availability seems to influence the fledging success of
540 dispersing females.

541 Without precise information on the number and type of prey brought back to the nest,
542 provisioning rate remains difficult to interpret. In fact, provisioning rate in control
543 nests was lower in high density, high quality patches, without resulting in a lower
544 fledging probability. High quality patches may thus also be characterized by high
545 quality prey items enabling individuals to achieve similar fledging success than in

546 lower quality habitats despite a lower provisioning rate. Although we have no
547 information on the type and size of preys brought by the parents in this study, longer
548 provisioning intervals have been found to be associated with larger or more numerous
549 prey items brought in a single feeding visit in several passerine species (Nour et al.
550 1998; Grieco 2002; Schwagmeyer and Mock 2008). Prey size is in turn an important
551 determinant of the total volume of prey brought to the nest (Grundel 1987) and
552 eventually of reproductive success (Schwagmeyer and Mock 2008).

553

554 In conclusion, our experimental study indicates that, in collared flycatchers, some
555 differences in reproductive effort and reproductive success between dispersing and
556 philopatric individuals are dependent on food availability. The food supplementation
557 increased the body mass of dispersers and the fledging success of philopatric males in
558 low-quality habitats, thus mitigating the dispersal-dependent effects of habitat quality
559 observed in control nests. Most studies of dispersal-dependent traits (reviewed in
560 Ronce and Clobert 2012) have described differences in one given context, without
561 investigating within-individual variation and in particular the role of environmental
562 variation beyond its effect on dispersal decisions (but see Ims 1990; Meylan et al. 2009;
563 Hoset et al. 2010). A deeper understanding of associations between dispersal and other
564 traits should therefore require paying more attention to their flexibility across varying
565 environmental conditions and seeking to measure or manipulate environmental
566 factors, including food availability, before drawing conclusions from observed
567 phenotypic differences between dispersing and non-dispersing individuals.

568

569

570 **Authors' contributions**

571 C.R., B.D. and P.B. designed the study; C.R. carried out the fieldwork; C.R. extracted
572 the data from part of the video recordings; C.R. analyzed the data; C.R., P.B. and B.D.
573 drafted the manuscript. All authors gave final approval for publication. The authors
574 hereby declare that they have no competing interests.

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588 **Data accessibility statement**

589 Analyses reported in this article can be reproduced using the data provided by Récapet
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591

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753

754

755 Figure 1: Provisioning rate per hour and per nestling as a function of breeding density
756 and food supplementation treatment. Breeding density was modeled as a continuous
757 variable in the linear mixed model describing provisioning rate, but three classes of
758 breeding density were defined for the sake of illustration, based on the distribution of
759 breeding density in the study patches: “low” (from 43 to 50% of available nest boxes
760 occupied), “intermediate” (from 65 to 73%) and “high” (from 80 to 91%).

761

762 Figure 2: Adult body mass as a function of breeding density and food supplementation
763 treatment for philopatric and dispersing individuals. Breeding density was modeled as
764 a continuous variable in the linear mixed model describing body mass, but three
765 classes of breeding density were defined for the sake of illustration (cf. Figure 1).

766

767 Figure 3: Concentration of reactive oxygen metabolites (ROM) as a function of
768 breeding density and dispersal status (dispersing vs. philopatric individuals). Breeding
769 density was modeled as a continuous variable in the linear mixed model describing
770 ROM concentration, but three classes of breeding density were defined for the sake of
771 illustration (cf. Figure 1).

772

773 Figure 4: Number of fledged nestlings as a function of breeding density and food
774 supplementation treatment for philopatric and dispersing males. Breeding density was
775 modeled as a continuous variable in the generalized linear mixed model describing the
776 number of fledglings, but three classes of breeding density were defined for the sake of
777 illustration (cf. Figure 1). Note that the general analysis was thus not performed using
778 classes with low sample sizes as illustrated here.

779 Table 1: Linear mixed-effect models best describing adult body mass, oxidative state
780 markers and provisioning rate. The sample size and the partition of the variance are
781 given for each model. The effect of sex is expressed as males vs. females.

Effect	Estimate \pm S.E.	F	Num. d.f.	Den. d.f.	P
Provisioning rate per nestling					
<i>V_{residual} = 0.40 (N = 135 adults), V_{pair} = 0.04 (N = 105 pairs), V_{date} = 0.08 (N = 15 dates), V_{habitat} = 0.00 (N = 9 patches)</i>					
Brood size	-0.3 \pm 0.1	29.01	1	87	< 0.001
Density	-1.6 \pm 0.6	0.75	1	69	0.389
Dispersal	0.5 \pm 0.2	10.71	1	117	0.001
Supplementation	-1.5 \pm 0.7	4.24	1	57	0.044
Density x Supplementation	2.4 \pm 1.0	6.40	1	61	0.014
Adult body mass					
<i>V_{residual} = 0.31 (N = 160 adults), V_{pair} = 0.03 (N = 120 pairs), V_{habitat} = 0.00 (N = 9 patches)</i>					
Tarsus length	0.44 \pm 0.10	19.44	1	150	< 0.001
Sex	-0.29 \pm 0.09	10.16	1	95	0.002
Density	0.24 \pm 0.54	3.56	1	105	0.062
Dispersal	-1.75 \pm 0.64	0.56	1	135	0.455
Supplementation	-0.32 \pm 0.60	4.96	1	101	0.028
Density x Dispersal	2.27 \pm 0.90	0.37	1	142	0.547
Density x Supplementation	0.38 \pm 0.79	4.95	1	106	0.028
Dispersal x Supplementation	2.78 \pm 0.96	8.30	1	138	0.005
Density x Dispersal x Suppl.	-3.73 \pm 1.34	7.75	1	145	0.006
Adult reactive oxygen metabolites					
<i>V_{residual} = 0.0202 (N = 135 adults), V_{pair} = 0.0018 (N = 107 pairs), V_{habitat} = 0.0000 (N = 9 patches)</i>					
Density	0.143 \pm 0.103	0.19	1	107	0.668
Dispersal	0.299 \pm 0.130	5.27	1	127	0.023
Density x Dispersal	-0.365 \pm 0.182	4.01	1	129	0.047
Adult total antioxidant capacity					
<i>V_{residual} = 1403 (N = 159 adults), V_{pair} = 0.00 (N = 119 pairs), V_{habitat} = 0.00 (N = 9 patches)</i>					
Sex	1.1 \pm 6.9	6.06	1	155	0.015
Dispersal	-19.6 \pm 8.6	0.23	1	155	0.632
Sex x Dispersal	32.5 \pm 14.1	5.33	1	155	0.022

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783 Table 2: Linear mixed-effect models best describing the body mass of 12-day-old
 784 nestlings. The sample size and the partition of the random variance are given beside
 785 each model.
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Effect	Estimate \pm S.E.	F	Num. d.f.	Den. d.f.	P
Nestling body mass (foster mother of known dispersal status)					
<i>V_{residual} = 1.09 (N = 339 nestlings), V_{foster} = 0.90 (N = 69 nests), V_{origin} = 0.52 (N = 89 nests), V_{habitat} = 0.40 (N = 9 patches)</i>					
Hatching date	-0.16 \pm 0.06	7.94	1	66	0.006
Nestling body mass (foster father of known dispersal status)					
<i>V_{residual} = 1.25 (N = 276 nestlings), V_{foster} = 1.90 (N = 59 nests), V_{origin} = 0.51 (N = 78 nests), V_{habitat} = 0.21 (N = 9 patches)</i>					
Hatching date	-0.21 \pm 0.07	8.37	1	56	0.005

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790 Table 3: Generalized linear mixed-effect models best describing fledging probability of
 791 nestlings. The sample size and the partition of the random variance are given beside
 792 each model.

Effect	Estimate \pm S.E.	χ^2_1	P
Fledging probability (foster mother of known dispersal status)			
<i>N = 503 nestlings, $V_{foster} = 5.78$ (N = 85 nests), $V_{origin} = 0.34$ (N = 108 nests), $V_{habitat} = 0.27$ (N = 9 patches)</i>			
Hatching date	-0.42 \pm 0.13	10.08	0.002
Supplementation	1.71 \pm 0.69	6.22	0.013
Dispersal	1.53 \pm 0.77	3.94	0.047
Fledging probability (foster father of known dispersal status)			
<i>N = 444 nestlings, $V_{foster} = 5.55$ (N = 75 nests), $V_{origin} = 0.000$ (N = 100 nests), $V_{habitat} = 0.000$ (N = 9 patches)</i>			
Hatching date	-0.58 \pm 0.15	15.32	< 0.001
Supplementation	9.20 \pm 4.02	5.23	0.022
Density	9.16 \pm 3.83	5.72	0.017
Dispersal	14.52 \pm 5.91	6.03	0.014
Supplementation x Density	-11.21 \pm 5.38	4.33	0.037
Supplementation x Dispersal	-17.74 \pm 8.16	4.73	0.030
Density x Dispersal	-22.00 \pm 8.80	6.26	0.012
Suppl. x Density x Dispersal	30.46 \pm 12.33	6.10	0.014

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