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Food supplementation mitigates dispersal-dependent differences in nest defence in a passerine bird.

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1 **Food supplementation mitigates dispersal-dependent differences in**
2 **nest defence in a passerine bird.**

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10 **Abstract**

11 Dispersing and non-dispersing individuals often differ in phenotypic traits (e.g. physiology,
12 behaviour), but to what extent these differences are fixed or driven by external conditions
13 remains elusive. We experimentally tested whether differences in nest-defence behaviour
14 between dispersing and non-dispersing individuals changed with local habitat quality in
15 collared flycatchers, by providing additional food during the nestling rearing period. In control
16 (non-food supplemented) nests, dispersers were less prone to defend their brood compared
17 to non-dispersers, whereas in food supplemented nests dispersing and non-dispersing
18 individuals showed equally strong nest defence. We discuss the importance of dispersal
19 costs versus adaptive flexibility in reproductive investment in shaping these differences in
20 nest-defence behaviour between dispersing and non-dispersing individuals. Irrespective of
21 the underlying mechanisms, our study emphasizes the importance of accounting for
22 environmental effects when comparing traits between dispersing and non-dispersing
23 individuals, and in turn assessing the costs and benefits of dispersal.

24

25 Keywords: dispersal, anti-predator behaviour, parental care, personality, habitat quality,

26 *Ficedula albicollis*

27 Introduction

28 Dispersal, defined as the movement of individuals between breeding sites or between birth
29 site and first breeding site [1], is a fundamental process in ecology. Dispersal decisions are
30 frequently driven by interactions between environmental factors and individuals' phenotype
31 [2] and natural selection might favour the functional integration of dispersal with phenotypic
32 traits that reduce dispersal costs [3]. In particular, aggressiveness is often associated with
33 dispersal in vertebrates [4]. Thus dispersal is predicted to be associated with fixed
34 differences in phenotype defining a dispersal syndrome [5,6]. However, natural selection is
35 also expected to favour flexibility, allowing individuals to adjust decisions to environmental
36 conditions. Thus, dispersing individuals may differ in their response to environmental
37 conditions and, in this case, the variation observed between dispersing and non-dispersing
38 individuals would be conditional on the environment rather than fixed [7]. Because most
39 studies on dispersal syndromes so far did not manipulate environmental conditions after
40 individuals' settlement, whether phenotypic differences between dispersing and non-
41 dispersing individuals are fixed or conditional on the environment remains unclear.

42 To explore these two alternatives, we manipulated habitat quality in a patchy
43 population of collared flycatchers *Ficedula albicollis* by providing additional food during the
44 nestling rearing period. We then tested the effects of food supplementation on the level of
45 temerity of the breeders depending on their between-patch dispersal status in the context of
46 defence against nest predators just before fledging.

47

48 Material and methods

49 The study was conducted in spring 2014 on a population of collared flycatchers breeding on
50 the island of Gotland, Sweden (57°07'N, 18°20'E). Nest boxes were monitored regularly in
51 eight study patches to record breeding data and weigh and measure (tarsus length) 12-day
52 old nestlings. Parents were caught when chicks were 6 to 12 days old, aged (yearlings vs.

53 older adults) based on plumage characteristics [8] (age uncertain for one individual), and
54 weighed. Dispersal was defined as a change of patch between birth and the first capture as a
55 breeder (natal dispersal) or between successive captures as a breeder (breeding dispersal).
56 Non-dispersing individuals did not change plot between successive captures (see [9] for a
57 discussion of this definition of dispersal in this population). We excluded previously unringed
58 adults (N = 94), which were of uncertain dispersal status because a fraction of local breeders
59 are missed every year and breeding dispersal is frequent in flycatchers.

60 Food availability was manipulated by providing 30g live maggots daily to half of our
61 nests (N = 86 supplemented nests) from 2 to 12 days post-hatching in transparent containers
62 attached to nest boxes. Control nests (N = 82) received no food, but were also visited daily.
63 Treatments were assigned to nests homogeneously in space and according to hatching date
64 within study plot. Food supplementation had positive effects on nestling survival (and in turn
65 brood size) but did not alter nestling body mass (Supplementary Information 2).

66 Adult nest defence was measured when chicks were 13-days old by placing a stuffed
67 nest predator (European red squirrel *Sciurus vulgaris*) on the entrance hole. To avoid
68 premature fledging, nest box entrance was closed during the test. The stuffed squirrel was
69 left for no longer than 5min from the arrival of the second parent and no longer than 15 min
70 from the observer's arrival. If no adult was seen, it was removed after 10 min. An observer
71 hidden under a camouflage net at least 8 meters from the nest box recorded the behaviour of
72 the breeding pair (Table S1). Behavioural responses during the 4.5 min following an
73 individual first sighting were available for all but three individuals and were thus used in the
74 analyses. Based on a multivariate analysis of the data (Supplementary information S1), a
75 nest defence score was computed using the behaviours that best described the intensity of
76 the response: (i) time spent within 2 meters of the box, (ii) number of movements around the
77 box and (iii) whether the individual attacked the dummy (Table 1). Similar scoring procedures
78 have been used in other studies of nest defence [10,11]. Nest defence was measured for
79 128 individuals from 91 nests. The supplemented (N = 51) and control nests (N = 40) had

80 similar laying dates (Wilcoxon rank-sum test: $W = 903$, $P = 0.350$) and brood sizes ($W = 886$,
81 $P = 0.257$) at the start of the supplementation treatment.

82 The effect of individuals' dispersal status in interaction with the supplementation
83 treatment on nest defence score (ordinal variable) was analysed using a cumulative-link
84 mixed-effects model [12] with package 'ordinal' in R [13]. As in many bird species, females
85 and yearlings dispersed more than males and older adults (ratio of females to males among
86 dispersing and philopatric individuals: 25:10 and 42:51 respectively, $X^2_1 = 6.02$, $P = 0.010$;
87 ratio of yearlings to older adults: 7:28 and 2:90 respectively, Fisher's exact test: $P = 0.002$).
88 Therefore, we included sex and age, as well as their interaction with supplementation.
89 Breeding density in the patch, measured as the fraction of available nest boxes occupied by
90 flycatchers, is likely to reflect natural variability in local competition and/or habitat quality as
91 denoted by its positive association with breeding success [14]. We thus controlled for it by
92 adding the interaction of dispersal with breeding density. Dispersers did not differ from
93 philopatric individuals in patch density (mean \pm SE = 0.674 ± 0.030 and 0.737 ± 0.015
94 respectively; $t_{51} = 1.92$, $P = 0.061$) or body mass (mean \pm SE = 13.0 ± 0.1 g in both groups;
95 $t_{53} = -0.52$, $P = 0.60$). Time of the day was included as a fixed covariate. Nest and observer
96 were included as random effects. Adding the interactions of dispersal status with either brood
97 size or average nestling body mass to correct for a potential confounding effect of brood
98 value yielded similar results (not detailed here). Non-significant effects (starting with
99 interactions) were removed based on log-likelihood ratio tests.

100

101 Results

102 Differences in nest defence score between dispersing and non-dispersing individuals
103 depended on the supplementation treatment (interaction between dispersal status and
104 supplementation: $X^2_1 = 3.86$, $P = 0.049$, Figure 1). Dispersing birds had a higher score in
105 supplemented nests compared to controls (estimate \pm SE for supplemented compared to

106 controls = 2.04 ± 0.71 , $X^2_1 = 7.94$, $P = 0.005$) whereas the scores of philopatric birds did not
107 significantly differ according to the treatment ($X^2_1 = 0.95$, $P = 0.33$). Differences in nest
108 defence between dispersing and non-dispersing individuals also depended on breeding
109 density (interaction between dispersal status and density: $X^2_1 = 5.37$, $P = 0.021$; Figure 2).
110 Among dispersing individuals, nest defence decreased with increasing density (estimate \pm
111 SE: -3.73 ± 1.84 , $X^2_1 = 4.25$, $P = 0.043$), while no relation was observed in non-dispersing
112 birds ($X^2_1 = 2.19$, $P = 0.14$). Individual's age and sex, either alone or in interaction with
113 treatment, had no significant effect on nest defence (all $P > 0.27$, Table S2). There was no
114 evidence for biases in the sample of tested breeders with respect to dispersal and food
115 supplementation due to unbalanced breeding failure (Supplementary information S2).

116

117 Discussion

118 Positive links between food abundance and nest defence behaviour are well known in
119 birds (e.g. [15,16]). Accordingly, higher levels of nest defence were observed in dispersing
120 parents in supplemented compared to control nests. Non-dispersing individuals however
121 showed high levels of nest defence behaviour independently of the food supplementation
122 experiment. We observed no change in the composition of our sample with respect to
123 dispersal status due to early breeding failure, and the effect of supplementation was not due
124 to the higher brood value of supplemented nests. Our results thus strongly suggest that
125 differences in nest defence between dispersing and non-dispersing individuals are not fixed
126 but driven by intra-individual variation in response to environmental conditions.

127 The observed difference in nest defence response of dispersing and non-dispersing
128 individuals to the supplementation treatment can result either from a constraint on dispersers
129 or from an adaptive adjustment by dispersers. In control conditions, dispersing individuals
130 may not be able to invest as much time and energy in nest defence as non-dispersing
131 individuals. Dispersers may exploit their habitat less efficiently and/or breed in lower quality

132 territories due to unfamiliarity with the environment [17], and thus need to allocate more time
133 and energy to nestling provisioning. Consistently, the decrease in nest defence behaviour of
134 dispersing individuals with increasing breeding density might reflect increased allocation of
135 time and/or energy to competitive interactions. When such constraint was released, here via
136 food supplementation, dispersing individuals could increase their investment in other parental
137 behaviours. Under this scenario, the reduced nest defence in control nests would reflect a
138 cost to dispersers in terms of increased risk of nest predation [18]. Alternatively, our results
139 could suggest the existence of different investment strategies, with dispersing individuals
140 adjusting their level of parental care depending on resource availability while non-dispersing
141 ones show a constantly high investment in nest defence. Under this scenario, the reduced
142 nest defence in control nests would reflect a beneficial adjustment by dispersing individuals
143 [19]. In line with this idea, dispersing individuals reared heavier nestlings than non-dispersing
144 ones independently from the supplementation treatment (Supplementary information S2),
145 and thus seemed to benefit from adjusting their investment in parental care. The reason why
146 non-dispersing individuals maintain a high level of nest defence whatever the environmental
147 conditions however remains to be explored.

148 Our experimental study demonstrates that environmental conditions can modulate the
149 association between dispersal and other behaviours, potentially defining context-dependent
150 personalities [20]. Hence, to better understand the processes at play on the evolution of
151 dispersal strategies, future studies should integrate measures of variation in habitat quality or
152 manipulate this quality when studying dispersal syndromes, and more generally differences
153 in life-histories associated to dispersal.

154

155 **Ethics statement.** Permission for catching and ringing adult and young birds was granted by
156 the Ringing Centre from the Museum of Natural History in Stockholm (licence number
157 471:M009 to CR).

158 **Data accessibility.** Data are available from the Dryad Digital Repository:
159 <http://dx.doi.org/10.5061/dryad.n3k7f> [21].

160 **Authors' contributions.** CR, GD, BD and PB designed the study; CR, JT and GD carried
161 out the field work; JT extracted the data from the tests recordings; CR and JT analysed the
162 data; CR, JT, GD, PB and BD drafted the manuscript or revised it critically. All authors gave
163 final approval of the version to be published and agree to be accountable for its content. The
164 authors hereby declare that they have no competing interests.

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178

179 **References**

- 180 1. Greenwood, P. J. & Harvey, P. H. 1982 The natal and breeding dispersal of birds.
181 *Annu. Rev. Ecol. Syst.* **13**, 1–21.
- 182 2. Clobert, J., Danchin, E., Dhondt, A. A. & Nichols, J. D., editors 2001 *Dispersal*. New
183 York: Oxford University Press.
- 184 3. Clobert, J., Le Galliard, J.-F., Cote, J., Meylan, S. & Massot, M. 2009 Informed
185 dispersal, heterogeneity in animal dispersal syndromes and the dynamics of spatially

- 186 structured populations. *Ecol. Lett.* **12**, 197–209. (doi:10.1111/j.1461-
187 0248.2008.01267.x)
- 188 4. Clobert, J., Baguette, M., Benton, T. G. & Bullock, J. M., editors 2012 *Dispersal*
189 *ecology and evolution*. New York: Oxford University Press.
- 190 5. Meylan, S., De Fraipont, M., Aragon, P., Vercken, E. & Clobert, J. 2009 Are dispersal-
191 dependent behavioral traits produced by phenotypic plasticity? *J. Exp. Zool. Part A*
192 *Ecol. Genet. Physiol.* **311**, 377–388. (doi:10.1002/jez.533)
- 193 6. Duckworth, R. A. & Kruuk, L. E. B. 2009 Evolution of genetic integration between
194 dispersal and colonization ability in a bird. *Evolution (N. Y.)*. **63**, 968–977.
195 (doi:10.1111/j.1558-5646.2009.00625.x)
- 196 7. Pennekamp, F., Mitchell, K. a., Chaine, A. & Schtickzelle, N. 2014 Dispersal
197 propensity in *Tetrahymena thermophila* ciliates-a reaction norm perspective. *Evolution*
198 *(N. Y.)*. **68**, 2319–2330. (doi:10.1111/evo.12428)
- 199 8. Svensson, L. 1992 *Identification guide to European passerines*. London: British Trust
200 for Ornithology.
- 201 9. Doligez, B., Danchin, E., Clobert, J. & Gustafsson, L. 1999 The use of conspecific
202 reproductive success for breeding habitat selection in a non-colonial, hole-nesting
203 species, the collared flycatcher. *J. Anim. Ecol.* **68**, 1193–1206. (doi:10.1046/j.1365-
204 2656.1999.00362.x)
- 205 10. Duckworth, R. A. 2006 Behavioral correlations across breeding contexts provide a
206 mechanism for a cost of aggression. *Behav. Ecol.* **17**, 1011–1019.
207 (doi:10.1093/beheco/arl035)
- 208 11. Hakkarainen, H. & Korpimäki, E. 1994 Nest defense of Tengmalms owls reflects
209 offspring survival prospects under fluctuating food conditions. *Anim. Behav.* **48**, 843–
210 849. (doi:10.1006/anbe.1994.1308)
- 211 12. Agresti, A. 2010 *Analysis of ordinal categorical data*. 2nd editio. Wiley, New York.
- 212 13. Christensen, R. H. B. 2015 ordinal - Regression Models for Ordinal Data. R package
213 version 2015.6-28.
- 214 14. Doligez, B., Pärt, T., Danchin, E., Clobert, J. & Gustafsson, L. 2004 Availability and
215 use of public information and conspecific density for settlement decisions in the
216 collared flycatcher. *J. Anim. Ecol.* **73**, 75–87.
- 217 15. Rytönen, S. 2002 Nest defence in great tits *Parus major*: support for parental
218 investment theory. *Behav. Ecol. Sociobiol.* **52**, 379–384. (doi:10.1007/s00265-002-
219 0530-y)
- 220 16. Kontiainen, P., Pietiäinen, H., Huttunen, K., Karell, P., Kolunen, H. & Brommer, J. E.
221 2009 Aggressive ural owl mothers recruit more offspring. *Behav. Ecol.* **20**, 789–796.
222 (doi:10.1093/beheco/arp062)
- 223 17. Bonte, D. et al. 2012 Costs of dispersal. *Biol. Rev.* **87**, 290–312. (doi:10.1111/j.1469-
224 185X.2011.00201.x)
- 225 18. Weidinger, K. 2002 Interactive effects of concealment, parental behaviour and
226 predators on the survival of open passerine nests. *J. Anim. Ecol.* **71**, 424–437.
227 (doi:10.1046/j.1365-2656.2002.00611.x)

- 228 19. Martin, T. E. 1992 Interaction of nest predation and food limitation in reproductive
229 strategies. In *Current Ornithology* (ed D. M. Power), pp. 163–197. Boston, MA:
230 Springer US.(doi:10.1007/978-1-4757-9921-7_5)
- 231 20. van Oers, K., Klunder, M. & Drent, P. J. 2005 Context dependence of personalities:
232 Risk-taking behavior in a social and a nonsocial situation. *Behav. Ecol.* **16**, 716–723.
233 (doi:10.1093/beheco/ari045)
- 234 21. Récapet, C., Daniel, G., Taroni, J., Bize, P. & Doligez, B. 2016 Data from: Food
235 supplementation mitigates dispersal-dependent differences in nest defence in a
236 passerine bird. Dryad Digital Repository. (doi:10.5061/dryad.n3k7f)
- 237

For Review Only

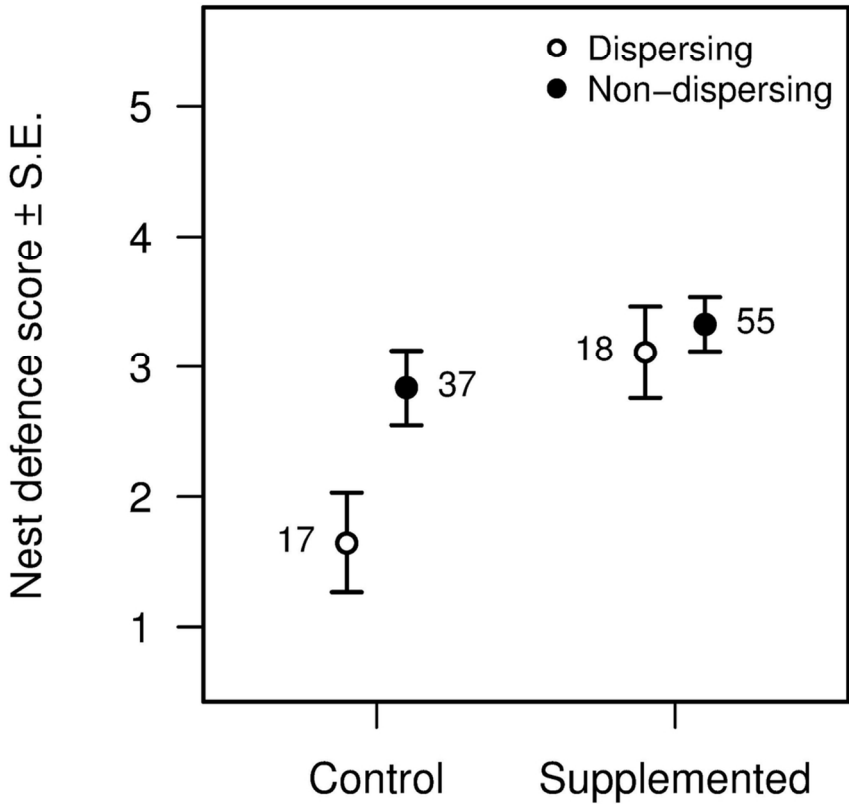
Figure 1: Average nest defence score according to the food supplementation treatment and the dispersal status of collared flycatchers.

Figure 2: Nest defence score according to breeding density and dispersal status in collared flycatchers. The size of the dots is proportional to the number of individuals. The lines represent model predictions, with their 95% CIs (in grey) calculated from a bootstrap with 10000 re-sampling.

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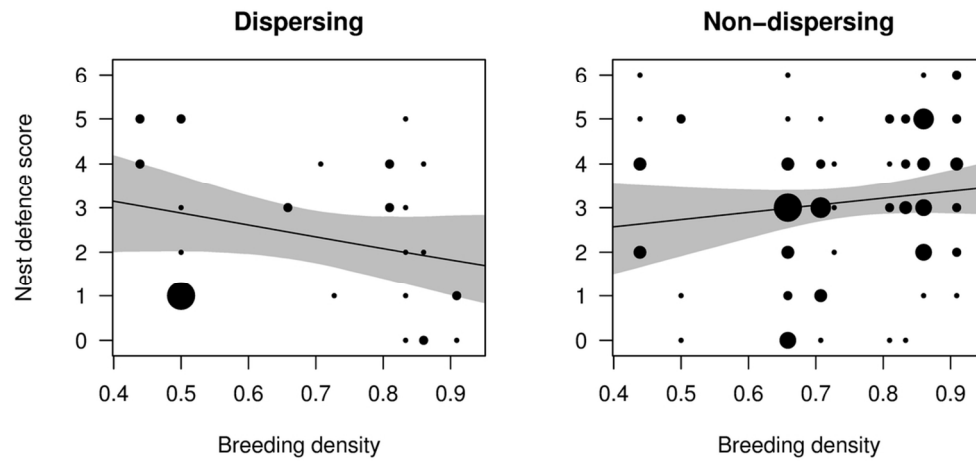
Table 1: Construction of the nest defence score. Tertiles of the distribution for the whole population were used as cut-off values. The score was set to zero for individuals that were not seen during the test and for one individual that arrived 16s before the end of the test. If individuals attacked the dummy, their score was increased by one. Thus the final score varied between zero and six.

		Time spent within 2m of the nestbox		
		≤ 29.9%	29.9% to 81.1%	> 81.1%
Number of movements	≤ 14	1	2	3
	14 to 26	2	3	4
	> 26	3	4	5



100x100mm (300 x 300 DPI)





104x52mm (300 x 300 DPI)