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► **To cite this version:**

Charlotte Récapet, Grégory Daniel, Joëlle Taroni, Pierre Bize, Blandine Doligez. Food supplementation mitigates dispersal-dependent differences in nest defence in a passerine bird. *Biology Letters*, 2016, 12 (5), 10.1098/rsbl.2016.0097 . hal-01802611

**HAL Id: hal-01802611**

**<https://hal.science/hal-01802611v1>**

Submitted on 6 May 2024

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# BIOLOGY LETTERS

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

Journal:	<i>Biology Letters</i>
Manuscript ID	RSBL-2016-0097.R2
Article Type:	Research
Date Submitted by the Author:	n/a
Complete List of Authors:	Récapet, Charlotte; Université de Lyon-Université Claude Bernard Lyon 1- CNRS, Laboratoire de Biométrie et Biologie Evolutive UMR 5558; Université de Lausanne, Département d'Ecologie et d'Evolution Daniel, Grégory; Université de Lyon-Université Claude Bernard Lyon 1- CNRS, Laboratoire de Biométrie et Biologie Evolutive UMR 5558; University of Uppsala, Evolutionary Biology Centre Taroni, Joëlle; Université de Lausanne, Département d'Ecologie et d'Evolution Bize, Pierre; University of Aberdeen, School of BIological Sciences Doligez, Blandine; Université de Lyon-Université Claude Bernard Lyon 1- CNRS, Laboratoire de Biométrie et Biologie Evolutive UMR 5558
Subject:	Behaviour < BIOLOGY, Ecology < BIOLOGY, Evolution < BIOLOGY
Categories:	Animal Behaviour
Keywords:	dispersal, personality, parental care, <i>Ficedula albicollis</i> , anti-predator behaviour, habitat quality



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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 =  $0.674 \pm 0.030$  and  $0.737 \pm 0.015$   
94 respectively;  $t_{51} = 1.92$ ,  $P = 0.061$ ) or body mass (mean  $\pm$  SE =  $13.0 \pm 0.1$ 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 =  $2.04 \pm 0.71$ ,  $X^2_1 = 7.94$ ,  $P = 0.005$ ) 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:  $-3.73 \pm 1.84$ ,  $X^2_1 = 4.25$ ,  $P = 0.043$ ), 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.

165 **Acknowledgements.** Many thanks to Jukka Forsman and the landowners of Gotland for  
166 access to the study sites; Lars Gustafsson for field logistics; Myriane Chalopin, Arthur Colliot,  
167 Justine Le Vaillant, Pierre-Lou Marion, and Murielle Vergniol for their help on the field; and  
168 Nicolas Morellet and an anonymous referee for constructive comments on an earlier version  
169 of the manuscript.

170 **Funding statement.** This work was supported by the Centre National de la Recherche  
171 Scientifique (PICS France-Switzerland to BD), the Ministère de l'Enseignement Supérieur et  
172 de la Recherche (PhD fellowship to CR), the University of Aberdeen (stipend to CR), the  
173 Uppsala Universitet (stipend to GD), the Université de Lausanne (grant to JT), the Région  
174 Rhône-Alpes (Programme Cible PhD fellowship to GD and Explora'doc mobility grants to CR  
175 and GD), the L'Oréal Foundation-UNESCO "For Women in Science" program (fellowship to  
176 CR), the Rectors' Conference of the Swiss Universities and the Fondation pour l'Université  
177 de Lausanne (grants to CR).

178

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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

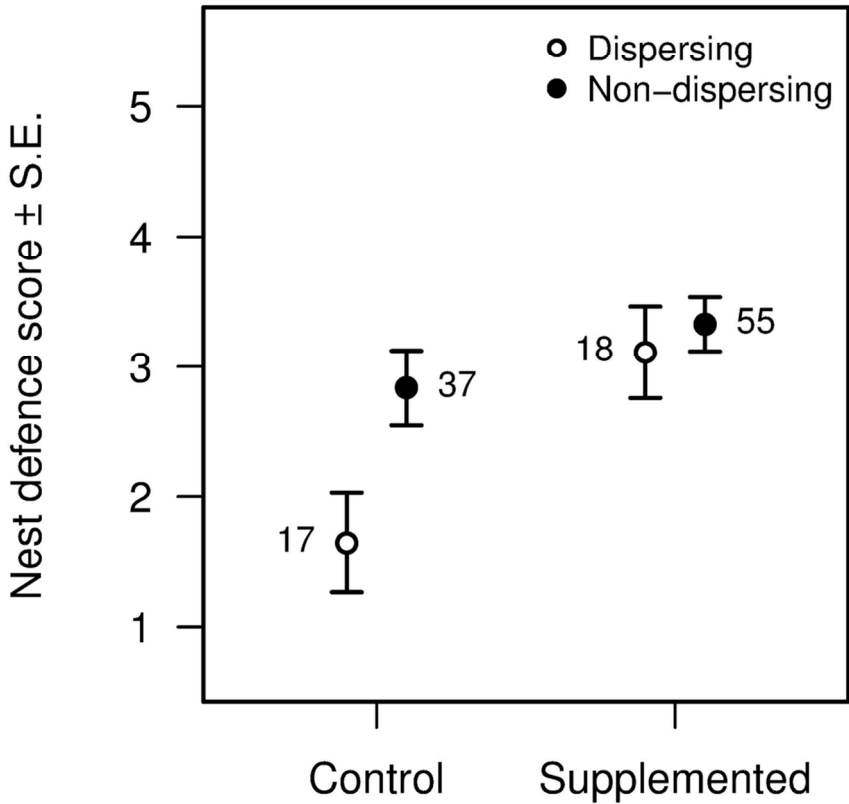
Figure 1: Average nest defence score according to the food supplementation treatment and the dispersal status of collared flycatchers.

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.

For Review Only

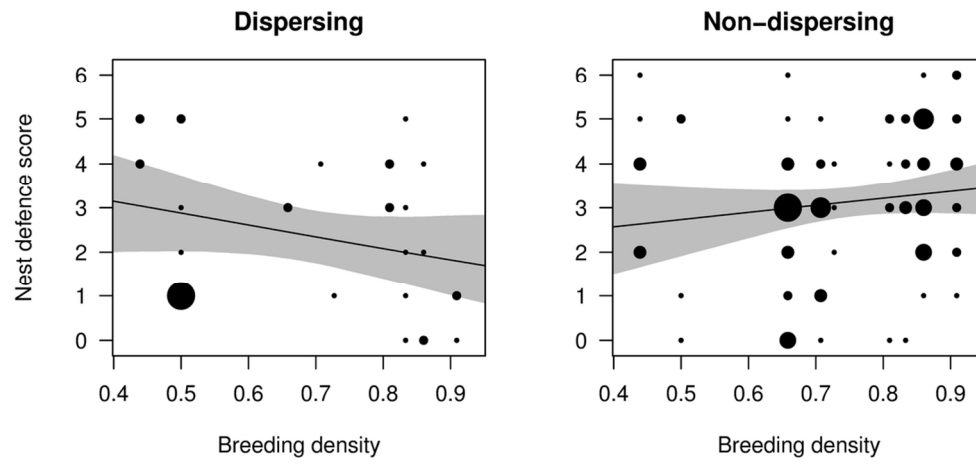
Table 1: Construction of the nest defence score. Tertiles of the distribution for the whole population were used as cut-off values. The score was set to zero for individuals that were not seen during the test and for one individual that arrived 16s before the end of the test. If individuals attacked 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)