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#### nest defence in a passerine bird. 2

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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.

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

47

#### 48 Material and methods

The study was conducted in spring 2014 on a population of collared flycatchers breeding on the island of Gotland, Sweden (57°07'N, 18°20'E). Nest boxes were monitored regularly in eight study patches to record breeding data and weigh and measure (tarsus length) 12-day old nestlings. Parents were caught when chicks were 6 to 12 days old, aged (yearlings vs. older adults) based on plumage characteristics [8] (age uncertain for one individual), and weighed. Dispersal was defined as a change of patch between birth and the first capture as a breeder (natal dispersal) or between successive captures as a breeder (breeding dispersal). Non-dispersing individuals did not change plot between successive captures (see [9] for a discussion of this definition of dispersal in this population). We excluded previously unringed adults (N = 94), which were of uncertain dispersal status because a fraction of local breeders are missed every year and breeding dispersal is frequent in flycatchers.

Food availability was manipulated by providing 30g live maggots daily to half of our nests (N = 86 supplemented nests) from 2 to 12 days post-hatching in transparent containers attached to nest boxes. Control nests (N = 82) received no food, but were also visited daily. Treatments were assigned to nests homogeneously in space and according to hatching date within study plot. Food supplementation had positive effects on nestling survival (and in turn 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

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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 dispersing and philopatric individuals: 25:10 and 42:51 respectively,  $X_{1}^{2} = 6.02$ , P = 0.010; 86 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 ± SE = 13.0 ± 0.1g 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**

Differences in nest defence score between dispersing and non-dispersing individuals depended on the supplementation treatment (interaction between dispersal status and supplementation:  $X_{1}^{2} = 3.86$ , P = 0.049, Figure 1). Dispersing birds had a higher score in supplemented nests compared to controls (estimate ± SE for supplemented compared to

106 controls =  $2.04 \pm 0.71$ ,  $X_{1}^{2} = 7.94$ , P = 0.005) whereas the scores of philopatric birds did not significantly differ according to the treatment ( $X_{1}^{2} = 0.95$ , P = 0.33). Differences in nest 107 108 defence between dispersing and non-dispersing individuals also depended on breeding 109 density (interaction between dispersal status and density:  $X_{1}^{2} = 5.37$ , P = 0.021; Figure 2). 110 Among dispersing individuals, nest defence decreased with increasing density (estimate ± 111 SE:  $-3.73 \pm 1.84$ ,  $X_{1}^{2} = 4.25$ , P = 0.043), while no relation was observed in non-dispersing 112 birds ( $X_{1}^{2}$  = 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

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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.

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

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Ethics statement. Permission for catching and ringing adult and young birds was granted by
the Ringing Centre from the Museum of Natural History in Stockholm (licence number
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].

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

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- 237

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.

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	≤ 14	1	2	3			
movements	14 to 26	2	3	4			
movemento	> 26	3	4	5			

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