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

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

1. Introduction

Dispersal, defined as the movement of individuals between breeding sites or between birth site and first breeding site [1], is a fundamental process in ecology. Dispersal decisions are frequently driven by interactions between environmental factors and individuals’ phenotype [2], and natural selection might favour the functional integration of dispersal with phenotypic traits that reduce dispersal costs [3]. In particular, aggressiveness is often associated with dispersal in vertebrates [4]. Thus, dispersal is predicted to be associated with fixed differences in phenotype defining a dispersal syndrome [5,6]. However, natural selection is also expected to favour flexibility, allowing individuals to adjust decisions to environmental conditions. In this case, dispersing individuals may differ in their response to environmental conditions, and the variation observed between dispersing and non-dispersing individuals would be conditional on the environment rather than fixed [7]. Because most studies on dispersal syndromes so far did not manipulate environmental conditions after individuals’ settlement, whether phenotypic differences between dispersing and non-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 tenacity of the breeders depending on their between-patch dispersal status in the context of defence against nest predators just before fledging.

2. 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 weight and to measure (tarsus length) 12 day old nestlings. Parents were caught when chicks were 6–12 days old, aged (yearlings versus 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 patch 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 is missed every year, and breeding dispersal is frequent in flycatchers.

Food availability was manipulated by providing 30 g live maggots daily to about 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 nesting survival (and in turn brood size) but did not alter nestling body mass (electronic supplementary material, S1).

Adult nest defence was measured when chicks were 13 days old by placing a stuffed nest predator (European red squirrel, Sciurus vulgaris) on the entrance hole. To avoid premature fledging, the nest-box entrance was closed during the test. The stuffed squirrel was left for no longer than 5 min from the arrival of the second parent and no longer than 15 min from the observer’s arrival. If no adult was seen, then the squirrel was removed after 10 min. An observer hidden under a camouflage net at least 8 m from the nest-box recorded the behaviour of the breeding pair (electronic supplementary material, table S1). Behavioural responses during the 4.5 min following an individual first sighting were available for all, but three individuals and were thus used in the analyses. Based on a multivariate analysis of the data (electronic supplementary material, S2), a nest-defence score was computed using the behaviours that best described the intensity of the response: (i) time spent within 2 m of the box, (ii) number of movements around the box and (iii) whether the individual attacked the dummy (table 1). Similar scoring procedures have been used in other studies of nest defence [10,11]. Nest defence was measured for 128 individuals from 91 nests. The supplemented (n = 51) and control nests (n = 40) had similar laying dates (Wilcoxon rank-sum test: W = 903, p = 0.350) and brood sizes (W = 886, p = 0.257) at the start of the supplementation treatment.

The effect of individuals’ dispersal status in interaction with the supplementation treatment on nest-defence score (ordinal variable) was analysed using a cumulative-link mixed-effects model [12] with package ‘ordinal’ in R [13]. As in many bird species, females 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^2 = 6.02, p = 0.010; ratio of yearlings to older adults: 7:28 and 2:90, respectively, Fisher’s exact test: p = 0.002). Therefore, we included sex and age, as well as interaction with supplementation. Breeding density in the patch, measured as the fraction of available nest-boxes occupied by flycatchers, is likely to reflect natural variability in local competition and/or habitat quality as denoted by its positive association with breeding success [14]. We thus controlled for it by adding the interaction of dispersal with breeding density. Dispersers did not differ from philopatric individuals in patch density (mean ± s.e. = 0.674 ± 0.030 and 0.737 ± 0.015, respectively; t_51 = 1.92, p = 0.061) or body mass (mean ± s.e. = 13.0 ± 0.1 g in both groups; t_53 = −0.52, p = 0.60). Time of the day was included as a fixed covariate. Nest and observer were included as random effects. Adding the interactions of dispersal status with either brood size or average nestling body mass to correct for a potential confounding effect of brood value yielded similar results (not detailed here). Non-significant effects (starting with interactions) were removed based on log-likelihood ratio tests.

3. Results

Differences in nest-defence score between dispersing and non-dispersing individuals depended on the supplementation treatment (interaction between dispersal status and supplementation: X^2 = 3.86, p = 0.049, figure 1). Dispersing birds had a higher score in supplemented nests compared with controls (estimate ± s.e. for supplemented compared with controls = 2.04 ± 0.71, X^2 = 7.94, p = 0.005), whereas the scores of philopatric birds did not significantly differ according to the treatment (X^2 = 0.95, p = 0.33). Differences in nest defence between dispersing and non-dispersing

![Figure 1. Average nest-defence score according to the food supplementation treatment and the dispersal status of collared flycatchers.](https://rsbl.royalsocietypublishing.org/Downloaded from http://rsbl.royalsocietypublishing.org/ on October 11, 2017)

<table>
<thead>
<tr>
<th>time spent within 2 m of the nest-box</th>
<th>≤29.9%</th>
<th>29.9–81.1%</th>
<th>&gt;81.1%</th>
</tr>
</thead>
<tbody>
<tr>
<td>number of movements</td>
<td>≤14</td>
<td>1</td>
<td>2</td>
</tr>
<tr>
<td></td>
<td>14–26</td>
<td>2</td>
<td>3</td>
</tr>
<tr>
<td></td>
<td>≥26</td>
<td>3</td>
<td>4</td>
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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 16 s 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.
individuals also depended on breeding density (interaction between dispersal status and density: $\chi^2 = 5.37$, $p = 0.021$; figure 2). Among dispersing individuals, nest defence decreased with increasing density (estimate ± s.e.: $-3.73 ± 1.84$, $\chi^2 = 4.25$, $p = 0.043$), whereas no relation was observed in non-dispersing birds ($\chi^2 = 2.19$, $p = 0.14$). Individuals’ age and sex, either alone or in interaction with treatment, had no significant effect on nest defence (all $p > 0.27$, electronic supplementary material, table S2). There was no evidence for biases in the sample of tested breeders with respect to dispersal and food supplementation owing to unbalanced breeding failure (electronic supplementary material, S1).

4. Discussion

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

The observed difference in nest-defence response of dispersing and non-dispersing individuals to the supplementation treatment can result either from a constraint on dispersers or from an adaptive adjustment by dispersers. In control conditions, dispersing individuals may not be able to invest as much time and energy in nest defence as non-dispersing individuals. Dispersers may exploit their habitat less efficiently and/or breed in lower-quality territories owing to unfamiliarity with the environment [17], and thus need to allocate more time and energy to nestling provisioning. Consistently, the decrease in nest defence behaviour of dispersing individuals with increasing breeding density might reflect increased allocation of time and/or energy to competitive interactions. When such constraint was released, here via food supplementation, dispersing individuals could increase their investment in other parental behaviours. Under this scenario, the reduced nest defence in control nests would reflect a cost to dispersers in terms of increased risk of nest predation [18]. Alternatively, our results could suggest the existence of different investment strategies, with dispersing individuals adjusting their level of parental care depending on resource availability, whereas non-dispersing ones show a constantly high investment in nest defence. Under this scenario, the reduced nest defence in control nests would reflect a beneficial adjustment by dispersing individuals [19]. In line with this idea, dispersing individuals reared heavier nestlings than non-dispersing ones independently of the supplementation treatment (electronic supplementary material, S1), and thus seemed to benefit from adjusting their investment in parental care. The reason why non-dispersing individuals maintain a high level of nest defence whatever the environmental 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 with dispersal.

Ethics. Permission for catching and ringing adult and young birds was granted by the Ringer’s Centre from the Museum of Natural History in Stockholm (licence number 471: M009 to C.R.).

Data accessibility. Data are available from the Dryad digital repository: http://dx.doi.org/10.5061/dryad.rkJ7f.

Authors’ contributions. C.R., G.D., B.D. and P.B. designed the study; C.R., J.T. and G.D. carried out the fieldwork; J.T. extracted the data from the tests recordings; C.R. and J.T. analysed the data; C.R., J.T., G.D., P.B. and B.D. 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.

Competing interests. The authors declare that they have no competing interests.

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