

Research



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Animal behaviour

Negative phenotypic and genetic correlation between natal dispersal propensity and nest-defence behaviour in a wild bird

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Natural selection is expected to favour the integration of dispersal and phenotypic traits allowing individuals to reduce dispersal costs. Accordingly, associations have been found between dispersal and personality traits such as aggressiveness and exploration, which may facilitate settlement in a novel environment. However, the determinism of these associations has only rarely been explored. Here, we highlight the functional integration of individual personality in nest-defence behaviour and natal dispersal propensity in a long-lived colonial bird, the Alpine swift (*Apus melba*), providing insights into genetic constraints shaping the coevolution of these two traits. We report a negative association between natal dispersal and nest-defence (i.e. risk taking) behaviour at both the phenotypic and genetic level. This negative association may result from direct selection if risk-averseness benefits natal dispersers by reducing the costs of settlement in an unfamiliar environment, or from indirect selection if individuals with lower levels of nest defence also show lower levels of aggressiveness, reducing costs of settlement among unfamiliar neighbours in a colony. In both cases, these results highlight that risk taking is an important behavioural trait to consider in the study of dispersal evolution.

1. Introduction

Natal dispersal, the movement of individuals from their birth to first breeding site, is a fundamental process affecting population dynamics and evolution [1]. Because dispersal entails costs [2], natural selection may favour the functional integration of dispersal with phenotypic traits allowing individuals to reduce these costs [1,3]. In particular, personality traits, defined as consistent behavioural differences in aggressiveness, exploratory behaviour, boldness, activity and/or sociability [4] between individuals over time and across contexts, may affect the success of dispersing individuals when settling and breeding in novel habitats [3,5,6]. For instance, natal dispersal can be linked to aggressiveness towards conspecifics or exploratory behaviour if it facilitates breeding territory establishment [3] or acquiring knowledge on the novel habitat for the exploitation of food patches [7], respectively. Moreover, the fitness returns of different life-history strategies, in particular associated with dispersal, are suggested to favour the evolution of animal personalities [8].

Table 1. Description of the nest-defence behaviour scores used in this study and how the 3092 observations were distributed among the 5 scores between locally born individuals and natal dispersers.

score	description	no. observations	
		locally born	natal dispersers
0	individuals flush from the nest immediately upon first detection of observer	327	351
0.5	individuals remain on the nest during observer approach but flush before capture	473	362
1	individuals remain motionless during approach and capture	885	434
1.5	individuals remain motionless during approach but subsequently move towards observer when extending hand for capture	58	41
2	individuals move immediately towards observer during both approach and capture (move towards observer hand, flap wings and claw on approaching hand)	105	56

Consistently, studies in various taxa have reported associations between dispersal and personality traits [3,6,7,9]. However, the determinism of these associations (genetic and environmental covariation) has only rarely been investigated although this is critical to understand how phenotypic associations evolve. Because natal dispersal and personality traits can be heritable [6,10–12], a genetic correlation between these traits can arise through linkage disequilibrium or pleiotropy [13]. Whereas linkage disequilibrium is likely to be an important source of genetic correlation in newly established populations, selection is expected to favour pleiotropy over the long term [11,13]. On the other hand, genetic correlations do not always result in phenotypic correlations (e.g. natal dispersal distance and exploratory behaviour [6]) if genetic and environmental influences on a trait go in opposite directions [13]. Insights on the determinism of associations between natal dispersal propensity and personality traits is thus central in understanding how dispersal by a non-random sample of genotypes and phenotypes may shape population-level processes, such as the distribution and range expansion of a species [3,6,11,14].

Here, working both at a phenotypic and genetic level, we report significant covariance between individual personality in nest-defence behaviour and natal dispersal propensity in a long-lived colonial bird, the Alpine swift (*Apus melba*), providing insights into genetic constraints shaping the coevolution of personality and dispersal traits.

2. Material and methods

Since 1999, we have monitored Alpine swifts in two Swiss colonies located 21 km apart, in the clock towers of Bienne (ca. 100 breeding pairs) and Solothurn (ca. 50 breeding pairs). Details on the study system are provided in the electronic supplementary material. Each year, adults were captured for identification and measurements. Natal dispersal status was defined for 522 individuals ringed as nestlings by a change of colony between birth and first breeding (i.e. change/no change; 74 natal dispersers/448 locally born). Because adult Alpine swifts do not disperse once settled (no breeding dispersal event observed out of 2064 breeding events in those two close-by colonies since 1999 despite almost perfect individual detection) and because all nestlings are ringed each year in the two study colonies, we assumed that all the individuals ringed as adults ($N = 237$) in the two study colonies were immigrants from other unmonitored colonies (see electronic supplementary material, table S1 and figure S1) and thus included

them as natal dispersers into the analyses. Thus, altogether natal dispersal status was known for 759 birds.

Between 2003 and 2014, breeders' nest-defence behaviour was estimated by a single observer (PB) as a 5-level score based on birds' reaction to a human approach and hand-capture (table 1) [12]. Nest defence was scored in 3092 occasions on the 759 individuals with known natal dispersal status over the study period, averaging 4.1 ± 3.3 (s.d.) observations per individual.

At a phenotypic level, we tested whether nest-defence score (ordinal trait) differed between natal dispersers and locally born individuals using a linear mixed model in 'ordinal' R package. In addition to natal dispersal status, the model included breeding colony, sex and the interaction between natal dispersal status and sex as factors, and bird identity and year of observation as random effects.

To estimate the genetic correlation between natal dispersal and nest-defence behaviour, we used a quantitative genetic approach, a bivariate 'animal model' [13,15], allowing us not only to partition the phenotypic variance of each trait (V_P) into its additive genetic (V_A) and environmental (V_E) components but also to estimate the genetic correlation (r_A) between two traits (see [6]). The model fitted natal dispersal status and nest-defence behaviour as response variables with a binomial and an ordinal distribution, respectively. Sex and breeding colony were included as fixed effects because of their known effects on both traits [1,12]. The additive genetic (co)variance for the traits of interest was estimated using the matrix of relatedness between individuals obtained from the pedigree by fitting individual identity linked to the pedigree as a random effect. Our social pedigree included 826 informative individuals (see also electronic supplementary material, table S2). Since nest-defence behaviour had repeated measures, a permanent environment (i.e. individual identity not linked to the pedigree) and the year of observation were also fitted as random effects [12,15]. Given the structure of the data (ordinal trait with repeated measures and binary trait with a single measure per individual) it was not possible to estimate the residual and phenotypic covariance within the bivariate model. The model was fitted using a Bayesian approach in 'MCMCglmm' R package [15] (see electronic supplementary material for details).

3. Results

Natal dispersal status and nest-defence behaviour were phenotypically negatively linked in Alpine swifts ($p < 0.001$), after accounting for sex and colony effects (electronic supplementary material, table S3). The nest-defence behaviour was lower for natal dispersers (least square mean behavioural

Table 2. Estimates of fixed effects, variance components, heritability and genetic correlation for natal dispersal status and nest-defence behaviour in the Alpine swift study colonies, obtained from the bivariate animal model. The table gives the mean posterior distribution and its 95% credible interval (CI). 95% CIs that do not cross zero are considered significant.

variable	natal dispersal			nest-defence behaviour		
	estimate	95% CI		estimate	95% CI	
fixed effects						
intercept	−1.087	−1.662	−0.533	1.785	1.534	2.023
sex [male]	0.658	0.014	1.257	−0.311	−0.537	−0.080
colony [Solothurn]	2.076	1.171	2.949	−0.819	−1.087	−0.553
variance components						
additive genetic variance, V_A	7.608	2.486	14.726	0.847	0.341	1.399
residual variance, V_R	1	—	—	1	—	—
permanent environment effect variance, V_{PE}	—	—	—	0.914	0.447	1.392
year effect variance, V_{year}	—	—	—	0.0452	0.007	0.104
variance ratio						
h^2	0.598	0.440	0.801	0.235	0.089	0.346
pe^2	—	—	—	0.260	0.123	0.357
$year^2$	—	—	—	0.008	0.002	0.027
ordinal cut points (first fixed to zero)						
2	—	—	—	1.444	1.354	1.531
3	—	—	—	4.157	3.991	4.312
4	—	—	—	4.671	4.488	4.862
trait covariation: dispersal – nest defence						
genetic covariance, Cov_A		−0.214	−0.359	−0.084		
genetic correlation, r_A		−0.361	−0.590	−0.140		

score \pm s.e. = 0.60 ± 0.03) compared with locally born individuals (0.71 ± 0.02).

The bivariate animal model revealed heritability for both traits and a negative genetic correlation between them (table 2). For natal dispersal, the additive genetic variance [95% CI] was 7.608 [2.486; 14.726] (with residual variance fixed to 1 for a binary variable; table 2), corresponding to a heritability value of 0.598 [0.440; 0.801]. The additive genetic and permanent environment effect variances relative to the overall phenotypic variance for nest-defence behaviour were respectively 0.847 [0.341; 1.399] and 0.914 [0.447; 1.392] (table 2), accounting altogether for a repeatability of nest-defence behaviour of 0.457 [0.413; 0.509]. The heritability of nest-defence behaviour was low but significantly different from zero: 0.235 [0.089; 0.346]. The genetic correlation between natal dispersal status and nest-defence behaviour was estimated to be -0.361 [-0.590 ; -0.140].

4. Discussion

Using 12 years of data on natal dispersal and nest-defence behaviour in two colonies of Alpine swifts, we found that natal dispersers were less prone than locally born individuals to defend their nest (i.e. took fewer risks) against a human intruder. The negative association between natal dispersal and nest defence occurred both at the phenotypic and genetic levels, suggesting the integration of those two low to

moderately heritable traits in a dispersal behavioural syndrome [9,16]. These findings strongly support the idea that dispersing individuals are not a random subset of the population, with potentially important consequences on the dynamics of spatially structured populations [5,9,14]. The mechanisms (linkage disequilibrium, pleiotropic gene effects, maternal effects) [11,13,16] accounting for the integration of natal dispersal with nest-defence behaviour remain however to be uncovered. Linkage disequilibrium can play an important role over the short term [13] and may arise in association with a recent range expansion that favours integration of dispersal with other behavioural traits [3]. The Alpine swift population in Switzerland was established at least 200 years ago [17], and thus the described link between dispersal and nest-defence is probably not of recent origin. Research on genes and hormones with pleiotropic effects on dispersal and nest-defence behaviour may be insightful.

Because the three natal dispersal stages (departure from the natal patch, movement between patches and settlement in a novel patch) entail different costs [2], selection may favour a stage-specific functional integration of dispersal with specific phenotypic traits in order to reduce costs [9]. In this study, nest-defence behaviour was expressed after natal dispersal and breeding settlement. Hence, the negative integration of nest-defence behaviour with natal dispersal suggests that prudent natal dispersers may be favoured by selection if risk-averseness reduces costs of settling in an unfamiliar

environment (e.g. exposure to predators [17]). Variation in nest-defence behaviour may also be tightly linked to other behavioural axes (behavioural syndromes), such as sociability, aggressiveness or exploration [16]. Thus, an alternative hypothesis is that the association between natal dispersal and nest-defence behaviour may have been indirectly selected, for instance if individuals with lower levels of nest defence (i.e. risk taking) also show lower levels of aggressiveness, allowing them to settle more easily in a colony, among unfamiliar neighbours. Evidence for direct selection favouring the integration of dispersal with exploratory behaviour [6] or aggressiveness [3] has been reported. Our study highlights that risk taking is another important behavioural trait to consider in the study of dispersal evolution. Much remains to be done to tease apart the contribution of direct and indirect selection linking natal dispersal to personality traits.

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Data accessibility. Data are provided as electronic supplementary material.

Authors' contributions. P.B. and B.D. designed the study; P.B. performed the fieldwork; G.D., J.G.A.M. and P.B. carried out the statistical analyses and all authors interpreted the results; P.B., V.A.V. and B.D. drafted the manuscript and G.D. and J.G.A.M. revised it for significant intellectual content. All authors approved the final version of the manuscript and agree to be held accountable for the content therein.

Competing interests. We declare we have no competing interests.

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