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

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

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17 **Key-words:** behavioural syndrome, heritability, personality trait, dispersal costs, settlement,
18 *Apus melba*

19

20 **Running head:** Dispersal and nest defence behaviour

21 **Abstract**

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

37 **Introduction**

38 Natal dispersal, the movement of individuals from their birth to first breeding site, is a
39 fundamental process affecting population dynamics and evolution [1]. Because dispersal
40 entails costs [2], natural selection may favour the functional integration of dispersal with
41 phenotypic traits allowing individuals to reduce these costs [1,3]. In particular, personality
42 traits, defined as consistent behavioural differences in aggressiveness, exploratory behaviour,
43 boldness, activity and/or sociability [4] between individuals over time and across contexts,
44 may affect the success of dispersing individuals when settling and breeding in novel habitats
45 [3,5,6]. For instance, natal dispersal can be linked to aggressiveness towards conspecifics or
46 exploratory behaviour if it facilitates breeding territory establishment [3] or acquiring
47 knowledge on the novel habitat for the exploitation of food patches [7], respectively.
48 Moreover, the fitness returns of different life-history strategies, in particular associated with
49 dispersal, are suggested to favour the evolution of animal personalities [8].

50 Consistently, studies in various taxa have reported associations between dispersal and
51 personality traits [3,6,7,9]. However, the determinism of these associations (genetic and
52 environmental co-variation) has only rarely been investigated although this is critical to
53 understand how phenotypic associations evolve. Because natal dispersal and personality traits
54 can be heritable [6,10-12], a genetic correlation between these traits can arise through linkage
55 disequilibrium or pleiotropy [13]. Whereas linkage disequilibrium is likely to be an important
56 source of genetic correlation in newly established populations, selection is expected to favour
57 pleiotropy over the long term [11,13]. On the other hand, genetic correlations do not always
58 result in phenotypic correlations (e.g. natal dispersal distance and exploratory behaviour [6])
59 if genetic and environmental influences on a trait go in opposite directions [13]. Insights on
60 the determinism of associations between natal dispersal propensity and personality traits is
61 thus central in understanding how dispersal by a non-random sample of genotypes and

62 phenotypes may shape population-level processes, such as the distribution and range
63 expansion of a species [3,6,11,15].

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

68

69 **Material and Methods**

70 Since 1999, we have monitored Alpine swifts in two Swiss colonies located 21 km apart, in
71 the clock towers of Bienne (*ca.* 100 breeding pairs) and Solothurn (*ca.* 50 breeding pairs).
72 Details on the study system are provided in the Electronic Supplementary Materials (ESM).
73 Each year, adults were captured for identification and measurements. Natal dispersal status
74 was defined for 522 individuals ringed as nestlings by a change of colony between birth and
75 first breeding (i.e. change / no change; 74 natal dispersers / 448 locally-born). Because adult
76 Alpine swifts do not disperse once settled (no breeding dispersal event observed out of 2,064
77 breeding events in those two close-by colonies since 1999 despite almost perfect individual
78 detection) and because all nestlings are ringed each year in the two study colonies, we
79 assumed that all the individuals ringed as adults (N = 237) in the two study colonies were
80 immigrants from other unmonitored colonies (see Figure S1 in ESM) and thus included them
81 as natal dispersers into the analyses. Thus, altogether natal dispersal status was known for 759
82 birds.

83 Between 2003 and 2014, breeders' nest-defence behaviour was estimated by a single
84 observer (PB) as a 5-level score based on birds' reaction to a human approach and hand-
85 capture (Table 1) [12]. Nest-defence was scored in 3,092 occasions on the 759 individuals
86 with known natal dispersal status over the study period, averaging 4.1 ± 3.3 (SD) observations

87 per individual.

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

93 To estimate the genetic correlation between natal dispersal and nest-defence
94 behaviour, we used a quantitative genetic approach, a bivariate ‘animal model’ [13,16],
95 allowing not only to partition the phenotypic variance of each trait (V_P) into its additive
96 genetic (V_A) and environmental (V_E) components but also to estimate the genetic correlation
97 (r_A) between two traits (see [6]). The model fitted natal dispersal status and nest-defence
98 behaviour as response variables with a binomial and an ordinal distribution, respectively. Sex
99 and breeding colony were included as fixed effects because of their known effects on both
100 traits [1, 12]. The additive genetic (co)variance for the traits of interest was estimated using
101 the matrix of relatedness between individuals obtained from the pedigree by fitting individual
102 identity linked to the pedigree as a random effect. Our social pedigree included 826
103 informative individuals (see also Table S3 in ESM). Since nest-defence behaviour had
104 repeated measures, a permanent environment (i.e. individual identity not linked to the
105 pedigree) and the year of observation were also fitted as random effects [12,16]. Given the
106 structure of the data (ordinal trait with repeated measures and binary trait with a single
107 measure per individual) it was not possible to estimate the residual and phenotypic covariance
108 within the bivariate model. The model was fitted using a Bayesian approach in
109 ‘MCMCglmm’ R package [16] (see ESM for details).

110

111 **Results**

112 Natal dispersal status and nest-defence behaviour were phenotypically negatively linked in
113 Alpine swifts ($P < 0.001$), after accounting for sex and colony effects (Table S2 in ESM). The
114 nest defence behaviour was lower for natal dispersers (least square mean behavioural score \pm
115 SE = 0.60 ± 0.03) compared to locally-born individuals (0.71 ± 0.02).

116 The bivariate animal model revealed heritability for both traits and a negative genetic
117 correlation between them (Table 2). For natal dispersal, the additive genetic variance [95%
118 CI] was 7.608 [2.486; 14.726] (with residual variance fixed to 1 for a binary variable; Table
119 2), corresponding to a heritability value of 0.598 [0.440; 0.801]. The relative additive genetic
120 and permanent environment effect variances to the overall phenotypic variance for nest-
121 defence behaviour were respectively 0.847 [0.341; 1.399] and 0.914 [0.447; 1.392] (Table 2),
122 accounting altogether for a repeatability of nest-defence behaviour of 0.457 [0.413; 0.509].
123 The heritability of nest-defence behaviour was low but significantly different from zero:
124 0.235 [0.089; 0.346]. The genetic correlation between natal dispersal status and nest-defence
125 behaviour was estimated to -0.361 [-0.590; -0.140].

126

127 Discussion

128 Using 12 years of data on natal dispersal and nest defence behaviour in two colonies of
129 Alpine swifts, we found that natal dispersers were less prone than locally-born individuals to
130 defend their nest (i.e. took fewer risks) against a human intruder. The negative association
131 between natal dispersal and nest defence occurred both at the phenotypic and genetic levels,
132 suggesting the integration of those two low to moderately heritable traits in a dispersal
133 behavioural syndrome [9,18]. These findings strongly support the idea that dispersing
134 individuals are not a random subset of the population, with potentially important
135 consequences on the dynamics of spatially structured populations [5,9,15]. The mechanisms
136 (linkage disequilibrium, pleiotropic gene effects, maternal effects) [11,13,18] accounting for

137 the integration of natal dispersal with nest defence behaviour remain however to be
138 uncovered. Linkage disequilibrium can play an important role over the short term [13] and
139 may arise in association with a recent range expansion that favours integration of dispersal
140 with other behavioural traits [3]. The Alpine swift population in Switzerland was established
141 at least 200 years ago [17], and thus the described link between dispersal and nest-defence is
142 probably not of recent origin. Research on genes and hormones with pleiotropic effects on
143 dispersal and nest-defence behavior may be insightful.

144 Because the three natal dispersal stages (departure from the natal patch, movement
145 between patches and settlement in a novel patch) entail different costs [2], selection may
146 favour a stage-specific functional integration of dispersal with specific phenotypic traits in
147 order to reduce costs [9]. In this study, nest defence behaviour was expressed after natal
148 dispersal and breeding settlement. Hence, the negative integration of nest defence behaviour
149 with natal dispersal suggests that prudent natal dispersers may be favoured by selection if
150 risk-averseness reduces costs of settling in an unfamiliar environment (e.g. exposure to
151 predators [17]). Variation in nest-defence behaviour may also be tightly linked to other
152 behavioural axes (behavioural syndromes), such as sociability, aggressiveness or exploration
153 [18]. Thus, an alternative hypothesis is that the association between natal dispersal and nest-
154 defence behaviour may have been indirectly selected, for instance if individuals with lower
155 levels of nest-defence (i.e. risk taking) also show lower levels of aggressiveness, allowing
156 them to settle more easily in a colony, among unfamiliar neighbours. Evidence for direct
157 selection favouring the integration of dispersal with exploratory behaviour [6] or
158 aggressiveness [3] has been reported. Our study highlights that risk-taking is another
159 important behavioural trait to consider in the study of dispersal evolution. Much remains to be
160 done to tease apart the contribution of direct and indirect selection linking natal dispersal to
161 personality traits.

162

163 **Ethics.** The data were collected under permission from the Swiss Federal Agency for
164 Environment, Forests and Landscapes.

165 **Data accessibility.** Data are provided as supplementary material.

166 **Authors' contributions.** PB and BD designed the study, PB performed the fieldwork; GD,
167 JM and PB carried out the statistical analyses and all authors interpreted the results; PB, VAV
168 and BD drafted the manuscript and GD and JM revised it for significant intellectual content.
169 All authors agree to be held accountable for the content therein and approve the final version
170 of the manuscript.

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

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178 **References.**

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224

225 **Table 1.** Description of the nest defence behaviour scores used in this study and how the
 226 3,092 observations were distributed among the 5 scores between locally-born individuals and
 227 natal dispersers.

Score	Description	N. 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

228

229

230 **Table 2.** Estimates of fixed effects, variance components, heritability and genetic correlation
 231 for natal dispersal status and nest defence behaviour in the Alpine swift study colonies,
 232 obtained from the bivariate animal model. The table gives the mean posterior distribution and
 233 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	
<i>Fixed effects</i>						
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
<i>Variance components</i>						
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
<i>Variance ratio</i>						
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
<i>Ordinal cut points (first fixed to zero)</i>						
2	-	-	-	1.444	1.354	1.531
3	-	-	-	4.157	3.991	4.312
4	-	-	-	4.671	4.488	4.862
<i>Trait covariation: Dispersal - Nest defence</i>			Estimate	95% CI		
Genetic covariance, Cov_A			-0.214	-0.359	-0.084	
Genetic correlation, r_A			-0.361	-0.590	-0.140	

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235