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Unravelling the causes and consequences of dispersal syndromes in a wild passerine

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Evidence accumulates that dispersal is correlated with individual behavioural phenotype (dispersal syndrome). The evolutionary causes and consequences of such covariation depend on the degree of plasticity versus inheritance of the traits, which requires challenging experiments to implement in mobile organisms. Here, we combine a forced dispersal experiment, natural colonization and longitudinal data to establish if dispersal and aggression levels are integrated and to test their adaptive nature in pied flycatchers (*Ficedula hypoleuca*). We found that (forced) dispersers behaved more aggressively in their first breeding year after dispersal and decreased their aggression in following years. Strength of dispersal syndrome and direction of fecundity selection on aggression in newly colonized areas varied between years. We propose that the net benefits of aggression for dispersers increase under harsh conditions (e.g. low food abundance). This hypothesis now warrants further testing. Overall, this study provides unprecedented experimental evidence that dispersal syndromes can be remodelled via adaptive plasticity depending on the individuals' local breeding experience and/or year-specific ecological conditions. It highlights the importance of individual behavioural variation in population dynamics.

1. Introduction

Dispersal, broadly defined as the movement of an individual from site of birth/breeding to another breeding site, is a key-behaviour affecting ecological and evolutionary processes [1]. Such movements can greatly impact population dynamics, range expansion, species invasion, gene flow and thereby local adaptation processes. Dispersal was long considered as being random with respect to genotypes, implying that the homogenizing effect of gene flow could commonly limit adaptation by natural selection in nature [2–5]. However, dispersal can be non-random [6] and in fact, dispersive and less-dispersive individuals of the same population often differ consistently in suites of morphological, behavioural and/or life-history correlated traits [6–10]. Covariation of such traits with dispersal, also termed 'dispersal syndromes', are important to study because it implies that individual movements, and thus gene flow, could be directional and, therefore, spread rates, colonization success, population genetic structure, evolvability or evolutionary stability strongly depend on populations' phenotypic composition [9,11–14].

Many studies on dispersal syndromes focus on the covariation between dispersal tendencies and individual repeatable differences in behaviours (so-called animal personality) [7,9,15]. For example, in numerous vertebrate taxa, dispersing individuals are on average more aggressive, more exploratory and/or less social compared to philopatric individuals (birds [16–18]; reptiles [19,20]; fish [21–23]; mammals [24,25]). Such behavioural dispersal syndromes are often assumed to be adaptive with correlational selection leading to the functional integration of traits that mitigate the costs of dispersal and/or increase settlement success in new areas [26]. However, because most of the literature is

descriptive and based on successful settlers [15], it remains unclear to what extent selection is causing the observed covariation or whether other mechanisms are involved. For example, trait covariation may arise through adaptive plasticity occurring within generations when individuals adjust their behaviour upon dispersal [27] or across generations when parents remodel offspring dispersive phenotype depending on the environment [28,29]. In such cases, adaptive plasticity will lead to phenotypic differentiation among individuals or populations without affecting genetic composition. Establishing the mechanisms giving rise to dispersal syndromes is thus essential to understand the evolutionary and ecological implications of dispersal.

This study aims to establish the existence of a correlation between individual aggressive and dispersal tendencies, unravel the underlying mechanism of trait covariation during settlement and test its adaptive nature in a wild pied flycatcher (*Ficedula hypoleuca*) population. Pied flycatchers are migratory and mandatory secondary nest cavity breeders that use the presence of resident heterospecific competitors as a means to localize suitable breeding areas [30] despite intense competition for access to nest sites [31]. Increasing northwards dispersal is one of the expected responses to climate change [32] and in our study population, dispersal syndromes have been established with respect to life-history, morphology and plumage coloration [33]. Yet the link to behaviour is still unknown. We aim to fill that gap as behaviour directly mediates how individuals interact with their environment and thus can influence population dynamics. To that end, we performed a colonization experiment for 2 consecutive years where 12 new nest-box areas (plots) were created in the vicinity of a long established population. We allowed natural colonization to happen in addition to forced dispersal events of pairs of known aggressive phenotype. Manipulating individual dispersal decisions enables us to formally test if high aggression level is the cause or the consequence of having dispersed. We subsequently monitored individual aggressive phenotype before and/or after forced dispersal and birds' local performance in old established and new areas. We tested the hypotheses that (i) initial colonization will be performed by the most aggressive individuals that can better compete with prior resident species. Hence mean aggression level in new areas will be higher than in old established populations [34], (ii) aggression-dispersal covariation is fixed across contexts (before/after dispersal within the same year) if the aggression-dispersal syndrome arises through correlational selection, whereas birds will upregulate level of aggression after dispersal if trait covariation arises through adaptive plasticity [35], (iii) the functional integration of dispersal and aggression is adaptive and the performance of aggressive phenotypes is density dependent [36–38].

2. Material and methods

(a) Study species

The pied flycatcher is a long-distance insectivorous migratory passerine, wintering in sub-Saharan Western Africa and breeding in temperate and boreal forests across Europe. Flycatchers readily accept nest-boxes for breeding and are found in habitat types ranging from deciduous forests to coniferous habitats. Flycatchers are usually single-brooded, monogamous and provide biparental care although polygyny occurs [39].

(b) Study sites

Our study was carried out in the pied flycatcher population of the National Park Dwingelderveld (52°49′5″ N, 6°25′41″ E) in the Netherlands (see [40] for details). This population consists of 12 spatially distinct study plots established in 2007 (old plots) in three larger forested areas, carrying 50 or 100 nest-boxes each (1050 boxes in total) and of seven plots established in 2017 or 2018 (new plots) carrying 15 or 20 nest-boxes each (160 boxes in total, see map in electronic supplementary material, information S1). Plots in our area are heterogeneous regarding vegetation and vary from totally deciduous to totally coniferous (range: 18–99% of deciduous trees) [41].

(c) General field procedure

From the beginning of April onwards, arrival of males and females was monitored daily [42]. After observed pair formation, targeted pairs were visited daily to determine the onset of nest building and egg laying. In a subset of seven-old plots and in all new plots, pairs were screened repeatedly for their aggressive behaviour during the nest building and egg laying phase (see aggression tests). On day 7 (hatch date = day 0), parents were caught using a spring trap, measured and ringed (if unringed) and the nestlings weighted and ringed. On day 12, nestlings were measured again and later checks informed us on their fledging success. During the study period (2016–2018) and in the studied old plots, flycatchers in our population laid eggs around May 6 (36.3 April date ± 5.3 s.d.; $n = 405$ nests), produced on average 6.3 eggs (±0.8 s.d.; $n = 405$ nests) and fledged 5.5 young (±1.5 s.d.; $n = 323$ nests with at least one young fledged) weighing 13.8 gram (±0.9 s.d., $n = 323$ nests). The major reason for nests failing was predation of clutches and/or the incubating females by martens. Young fledge after about 15 days.

(d) Aggression tests

Individual level of aggression was measured by simulating territory intrusions by a heterospecific dominant competitor [31]. For triggering aggressive responses of the focal pair, we placed a taxidermic mount of a great tit male (*Parus major*) protected by mesh wire on top of the focal nest-box together with a broadcasted song. Each pied flycatcher pair was subjected to four aggression tests; two during nest building and two during egg laying (1 and 3 days after the first egg was laid). Tests were conducted between 07.00 and 12.00. We used 10 different mounts and 12 playback songs (recorded from Dutch and German populations) to minimize potential undesired effects of individual great tit physical or vocal characteristics. Songs were broadcast with an Intenso MP3 player connected to a X-mini Uno speaker. Mounts, songs and observers were all randomly assigned among nests and, as a result, they explained none to relatively little amount of behavioural variation (electronic supplementary material, information S2).

After the start of a test and once one of the members of the focal pair entered a 15 m radius around the box, an observer (sitting at 15 m from the nest-box) recorded the behaviours of the focal bird(s) for 3 min. Focal individuals were identified based on the highly variable plumage coloration in males, the presence of metal and/or colour rings for returning birds, observation of nest building for females and/or the assumption that birds approaching belong to the nest-box. Individual characteristics were noted each time, allowing confirmation of birds' identity when individuals were later caught during incubation (females) or chick feeding (males). We are thus confident that birds associated with the nest-box are indeed members of the focal pair (see [42] for a more detailed description). The observer counted the number of aggression calls, the number of swoops and attacks to the mount (i.e. actual landing) and estimated the minimum distance to the mount. If the partner of the focal bird

showed up later during the test, its behaviour was also scored for the remaining period (i.e. for 3 min minus its arrival time). For example, if the focal bird was the male and its female arrived 1 min later, the male would be scored for 3 min and the female for 2 min. To check if duration of scoring affected the results, all analyses presented in the study were also performed with individuals that were scored for a minimum of 90 s (i.e. with a presumably more accurate estimate of aggressiveness). Results and conclusions were not affected (see e.g. electronic supplementary material, Information S2) and hence we kept all individuals in the following analyses. Subjects that did not arrive within 15 min after the onset of a test were scored as non-responsive (35.72% of all observations). We have previously shown that call rate (the number of aggression calls per minute) was the best proxy of aggressiveness, as it correlated with all other scored behaviours, while exhibiting the highest repeatability [41]. We have also shown that call rate increased between nest stages (nest building versus egg laying) [41]. Repeatability of call rate adjusted for such effect of nest stage was higher within-year than across years and varied between years (within-year adjusted R (95% CrI) = 0.27 (0.26, 0.29); across-year adjusted R (95% CrI) = 0.14 (0.13, 0.16), $n = 2424$ observations from 681 individuals, electronic supplementary material, Information S2). Population mean call rate increased directionally over the study years (mean 2016 = 48.9 ± 55.1 s.d., $n = 830$ obs. of 321 ind.; mean 2017 = 54.5 ± 59.0 s.d., $n = 661$ obs. of 244 ind; mean 2018 = 60.8 ± 61.1 s.d., $n = 533$ obs. of 215 ind.; overall effect of year = $F_{2,2034} = 6.91$, $p = 0.001$).

(e) Colonization and translocation experiments

In 2017, we created eight new plots (fitted with 20 nest-boxes) and, in 2018, four new plots (fitted with 15 nest-boxes), thereby allowing 12 independent colonization opportunities over 2 years. Five of the 2017 new plots were left in place to monitor the new populations over time (2018 and 2019) and the remaining three were removed. The four new plots of 2018 were left and monitored in 2019 as well. Bottoms of approximately 40% of the nest-boxes were removed until the first flycatcher males arrived to prevent tit species from monopolizing the newly available boxes. New plots were heterogeneous regarding vegetation (range: 12–95% of deciduous trees) and comparable to the old plots. The distances between new plots and old plots ranged from 0.4 to 18.4 km (electronic supplementary material, information S1). From the beginning of April onwards, new plots were visited every 3 days to monitor pair formation and determine the onset of nest building and egg laying.

In 2017 and 2018, we performed a translocation experiment following a known procedure [43]. We introduced pairs from old plots to one of the 12 new plots. Targeted pairs were first screened for their aggressive behaviour during nest building (see aggression tests). If both pair members responded to the test, they were caught via mist netting in the following morning (8.00–12.00). Caught individuals were kept in dark small transport cages provided with mealworms. Caught pairs were randomly assigned to and released into outdoor aviaries (2 × 2 × 2 m) in one of the new plots on the same day (10.00–13.00). In case we failed to capture one of the pair members, the caught bird was released inside the aviary and we made a second attempt to capture its partner the next day. If unsuccessful, we released the bird. Aviaries were built around a tree and fitted with a nest-box. Birds in the aviaries were provided with *ad libitum* water and food (waxmoth larvae, crickets and *ad libitum* mealworms) on a feeding table, nesting material, and large bushes and branches for perching and shelter. Aviaries were covered in double netting to prevent predator attacks. After a period of 3 days, the aviaries were opened to release the birds. In 2017 aviaries and food were removed the same day, in 2018, this was done 1 day later. For control pairs, the same

procedure was followed with the difference that birds were released into an aviary built around their original nest-box (for more details see [43,44]). This resulted in a sample size of 23 translocations and 6 controls. We chose to have a higher number of translocated birds than controls because we have previously shown that translocated birds were less likely to stay after forced dispersal [43], and this set-up allowed replicates within the 12 new plots. Settlement success after translocation to a new plot was higher in 2018 than in 2017 (2017 = 38.5% (10 birds out of 26) versus 2018 = 75% (15 out of 20)) and higher for females than males (females = 65.2% (15 out of 23) versus males = 43.5% (10 out of 23)). All control birds settled after local translocation to their own box. Control and translocated male and female flycatchers did not differ in their mean aggression call rate prior to the experiment (*Mann–Whitney-U* test: control versus translocated birds: $W = 202$, $p = 0.406$, $n = 12$ versus 46). Settlement probability was independent of an individual's aggression call rate before translocation (*Mann–Whitney-U* test: settled versus unsettled birds: 2017: $W = 81$, $p = 0.860$, $n = 10$ versus 16; 2018: $W = 35$, $p = 0.866$, $n = 15$ versus 5).

(f) Statistical analyses
(i) Dispersal syndrome
First, we analysed if variation in aggression call rate generally differed between old and new plots in general linear mixed models (GLMM) with Gaussian errors where plot type (old versus new plot) and year (2017 versus 2018) were fitted as fixed factors ('old plot' and year '2017' were used as reference categories). Subsequently, we added information on bird's dispersal status because old plots also harbour a substantial proportion of new immigrants each year that may differ in behaviour. In this model, bird status (experienced breeder in old plots versus naïve breeder in old plots (i.e. immigrant) versus naïve breeder in new plots (i.e. colonizer)), year (2017 versus 2018) and status × year interaction were fitted as fixed factors in a GLMM ('experienced breeder in old plots' and year '2017' were used as reference categories). In all GLMMs, individual$_{ID}$ and pair$_{ID}$_year combination were included as random effects. Sample size was 1046 observations of 361 individuals. The analyses only included the first colonization year of the new plots.

(ii) Underlying mechanisms of dispersal syndrome
To unravel the main mechanisms underlying dispersal syndromes (selection and/or plasticity), we first used longitudinal descriptive data (old plots, 2016–2019). We tested whether difference between naïve (first time breeders whether they were locally born or not) and experienced breeders was caused by between-individual (indicating selection) or within-individual (indicating plasticity) effects. To that end, variation in call rate was analysed in a GLMM where between-individual and within-individual effects of status were fitted as covariates (see below), nest stage and year were fitted as fixed factors and individual$_{ID}$ and pair$_{ID}$_year combination as random effects. We separated the effect of status (naïve versus experienced breeder) into within- and between-year effects using a centring technique [45]. For each individual, we calculated its mean status value ('mean status'; between-individual effect) and for each observation the deviation from its mean status ('change in status'; within-individuals effect indicating plasticity) and we fitted these as covariates. Sample size was 1573 observations of 500 individuals (electronic supplementary material, information S3).

Second, using data from the translocation experiment, we tested whether individuals would adjust their aggression call rate after forced dispersal to a new environment in the same year ($n = 42$ individuals). To control for effects of nest stage and between-year effects on aggressiveness [41], we mean-centred

call rate within nest stage and year before calculating the average score per individual before and after forced dispersal. Then, we analysed variation in the change in aggressiveness (call rate after minus call rate before) in relation to the treatment (translocation versus control, the latter being used a reference category) while controlling for status (experienced versus naïve breeder, the former being used as reference category) and a ceiling effect (centred call rate before) in a GLMM with Gaussian error. Interactions between the treatment and the other fixed effects were initially tested but were removed as they were not significant and made the model more complex. Pair_ID and plot of origin were fitted as random effects.

(iii) Fitness consequences of dispersal syndromes

We first quantified the fitness consequences of the translocation experiment in relation to individual aggressive phenotype. Variation in the number of fledglings (excluding zeros) and in female and male survival probability to the next breeding season was analysed in generalized linear models (GLMs) in relation to female and male mean aggression call rate (mean centred within nest stage and year), the experiment (translocation versus control, the latter being used as reference category), year (2017 versus 2018, the former being used as reference category) and the interactions between female and male phenotype and the experiment (electronic supplementary material, Information S4). GLMs were fitted with a Poisson error for the number of fledglings and with binomial error for adult survival probability. We limited our analysis on the number of fledglings to nests where both parents stayed in the plot after forced dispersal (i.e. nests where one of the parents returned to its original plot or dispersed elsewhere were excluded) to avoid confounding effects of unmanipulated parents. This conservative selection resulted in a sample size of 15 nests (6 control + 9 translocated) but results were very similar if 'mixed pairs' (composed of one manipulated parent that stayed and one unmanipulated parent, $n = 6$ pairs) were included (not shown). For the survival analyses, we only included parents that stayed in the plot after forced dispersal resulting in a sample size of 21 females and 15 males.

Using descriptive data (2017–2018), we then quantified the strength of linear selection acting on mean parents' call rate in old and new plots and in different years. This was achieved by analysing variation in the relative number of fledglings in a GLM in relation to parents' standardized call rate (to obtain linear selection gradient β), plot type (old versus new) and year (2017 versus 2018) fitted as factors, their three-way interactions (stz alarm × plot type × year) and underlying terms. Relative number of fledglings was calculated as the number of fledglings alive at day 12 in a nest divided by the annual mean of the population (excluding failed nests). Parent call rate was calculated as the behavioural mean of the two parents (corrected for effects of nest stage) and was standardized (by subtracting the annual population mean from each parent's observation and dividing it by the annual population's standard deviation). Results were qualitatively similar if data were scaled relative to the plot specific annual mean and if standardized mother's and father's call rate were used (not shown). This implies that our findings did not hinge on how the data were standardized. The phenotypic selection analysis only included the first colonization year of the new plots. Sample size was 178 nests (old versus new plots = 143 versus 35 nests).

All GLMMs and GLMs were constructed in R v. 3.4.3 (R Development Core Team 2017) using the glmer-function of the lme4-package [46]. We used the confint-function to obtain 95% confidence interval (CI) around the estimates. The statistical significance of fixed effects was assessed based on these 95% CI. We consider an effect to be significant in the frequentist's sense when its associated 95% CI does not overlap with 0.

Table 1. Model summary examining whether the level of aggression (call rate) differs between naïve and experienced birds breeding in old versus newly established plots. Estimated effect sizes (β) are reported with their 95% CI. Significant effects are denoted in italics. Sample size is 1046 observations of 361 individuals.

fixed effects	β (95% CI)
intercept	*20.93 (10.66, 35.32)*
nest stage[a]	*24.26 (18.75, 31.23)*
status[b]	
naïve in old plots	*17.79 (5.19, 32.30)*
naïve in new plots	*25.12 (11.35, 45.55)*
year[c]	14.33 (−0.83, 30.16)
year × status	
2018 × naïve in old plots	−5.29 (−25.15, 14.06)
2018 × naïve in new plots	*−35.89 (−60.71, −3.92)*
random effects	**σ^2 (95% CI)**
individual_ID	1003.18 (864.57, 1140.76)
pair_ID–year	158.04 (123.58, 186.26)
residual	2397.71 (2207.90, 2570.04)

[a] 'nest building' is used as reference category.
[b] 'experienced breeder' in old plots is used as reference category.
[c] '2017' is used as reference category.

3. Results

(a) Dispersal syndrome

We found that the overall level of aggression tended to be higher in newly established plots (CI are skewed towards positive values: effect of plot type ('old plot is used as reference category): β (95% CI) = 12.34 (−1.44, 24.98)) especially in 2017 compared to 2018 (effect of year ('2017' is used as reference category): β (95% CI) = 8.68 (0.29, 18.99); effect of year × plot type: β (95% CI) = −19.44 (−46.11, −0.07)). Further analyses that include bird status (experienced versus naïve breeder) reveal that the effect of bird status on call rate differs between the years (significant year × status interaction; table 1 and figure 1). In 2017, as expected, naïve breeders in new plots (i.e. colonizers) were significantly more aggressive than experienced breeders in old plots, with naïve breeders in old plots exhibiting intermediate aggression level (table 1 and figure 1). By contrast in 2018, no significant differences were found between these three groups (table 1 and figure 1). These patterns were confirmed when years were analysed independently (not shown). Individual_ID explained a substantial amount of variation in call rate, confirming that aggression is repeatable in this population (electronic supplementary material, Information S2). Call rate in newly established plots did not significantly change in years following initial colonization (effect of 'year since last colonization' (controlled for year differences and nest stage): β (95% CI) = 8.96 (−20.27, 25.56)).

(b) Underlying mechanisms of dispersal syndrome

Behavioural plasticity (within-individual effects) explained the higher level of aggression of naïve breeders (table 1 and figure 1): naïve breeders that returned to the study area
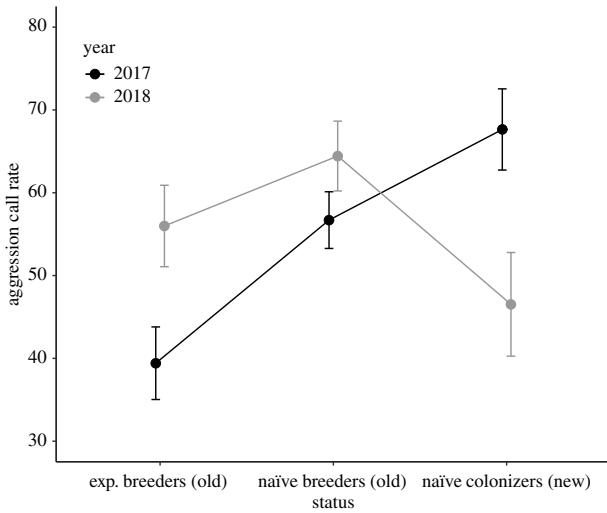
Figure 1. The relationship between individual aggression call rate (number per minute) and bird status (experienced breeder in old established plots, naïve breeder in old established plots and naïve breeders in newly established plots (colonizers)) differs between the years in a Dutch pied flycatcher population. Raw means are shown with their standard error.

Figure 2. Experimental effect of dispersal on aggressive phenotype (aggression call rate). Raw means of two years are shown for with their standard error for translocated (black) and control (grey) birds. Sample size (number of sampled birds) before and after dispersal is indicated in brackets. Raw means are shown with their standard error; $x = y$ line is depicted.

Table 2. Model summary examining the effect of 2 years of translocation on the change of individual aggressive phenotype (call rate). Estimated effect sizes (β) are reported with their 95% CI. Significant effects are denoted in italics. Sample size is 46 translocated and 12 control birds before translocation and 32 translocated and 10 control birds after translocation.

fixed effects	β (95% CrI)
intercept	−28.63 (−63.53, 13.27)
aggression before	*−0.92 (−1.12, −0.69)*
status[a]	*−34.33 (−54.78, −11.32)*
translocation[b]	*43.79 (3.99, 87.74)*
random effects	σ^2 **(95% CI)**
pair$_{ID}$	1711.57 (1013.79, 2457.90)
plot of origin	16.92 (0.37, 94.85)
residuals	474.34 (312.38, 751.88)

[a] 'experienced breeder' is used as reference category.
[b] 'control' group is used as reference category.

decreased their call rate in the following breeding seasons (effect of 'change in status' on aggression: β (95% CI) = −18.02 (−31.68, −6.54)) versus effect of 'mean status' on aggression: β (95% CI) = −4.18 (−14.59, 2.84), electronic supplementary material, Information S3). This result supports the finding that repeatability of call rate is larger within a season than across years (electronic supplementary material, Information S2).

Furthermore, the translocation experiment revealed that, compared to control birds that became less aggressive over time (negative intercept, table 2), individuals moved to a new environment maintained higher levels of aggression, implying behavioural plasticity (positive significant effect of 'translocation', table 2 and figure 2). Behavioural change was less pronounced for individuals that had higher levels of aggression before translocation (table 2). Results further show that naïve breeders were more plastic than experienced breeders (negative significant effect of 'status', table 2) but that all
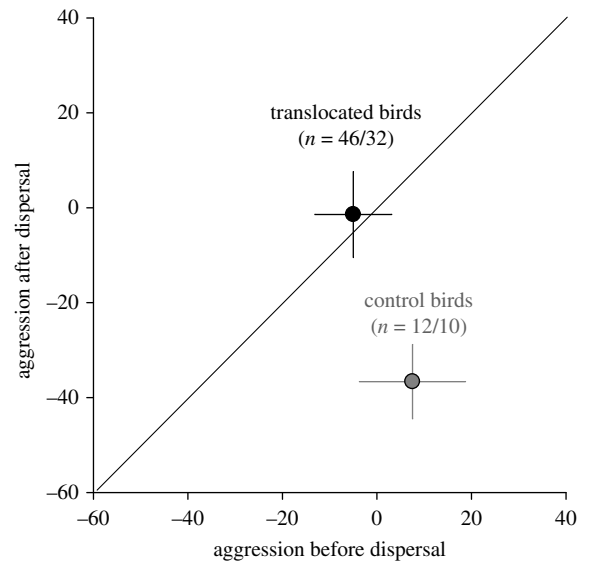
birds were affected similarly by the experiment (no significant 'status' × 'translocation' interaction: β (95% CI) = −27.71 (−84.49, 29.31)).

(c) Fitness consequences of dispersal syndromes
Overall the translocation experiment did not affect fitness, also not in a phenotype-dependent manner (no significant effects of 'translocation', or 'translocation × phenotype' on variation in fitness, electronic supplementary material, Information S4). Interestingly, the phenotypic selection analysis on descriptive data showed that the strength and direction of fecundity selection on parents' aggression call rate differed between years and plot types. Indeed, while selection on aggression was rather weak in old established plots, in new plots more aggressive parents were first favoured by selection in 2017 (most aggressive parents fledged relatively more young) and this pattern reversed in 2018 (most aggressive parents fledged relatively less young) (significant three-way interactions, table 3 and figure 3).

4. Discussion
Testing the nature and the adaptiveness of dispersal syndromes is intrinsically challenging in wild mobile organisms, yet crucial to evaluate its ecological and evolutionary consequences. Using a unique combination of natural colonization, translocation experiments and longitudinal data, we established that successful initial settlement was associated with higher levels of aggression, that the strength of dispersal syndrome was context-dependent and that adaptive plasticity was the major cause of the aggression-dispersal correlation in this population.

(a) Context-dependent dispersal syndrome
Higher levels of aggression are expected to benefit individuals that need to colonize new areas as it increases their settlement success, for example, through the displacement of pre-established hetero- or conspecifics [38]. Here, we found
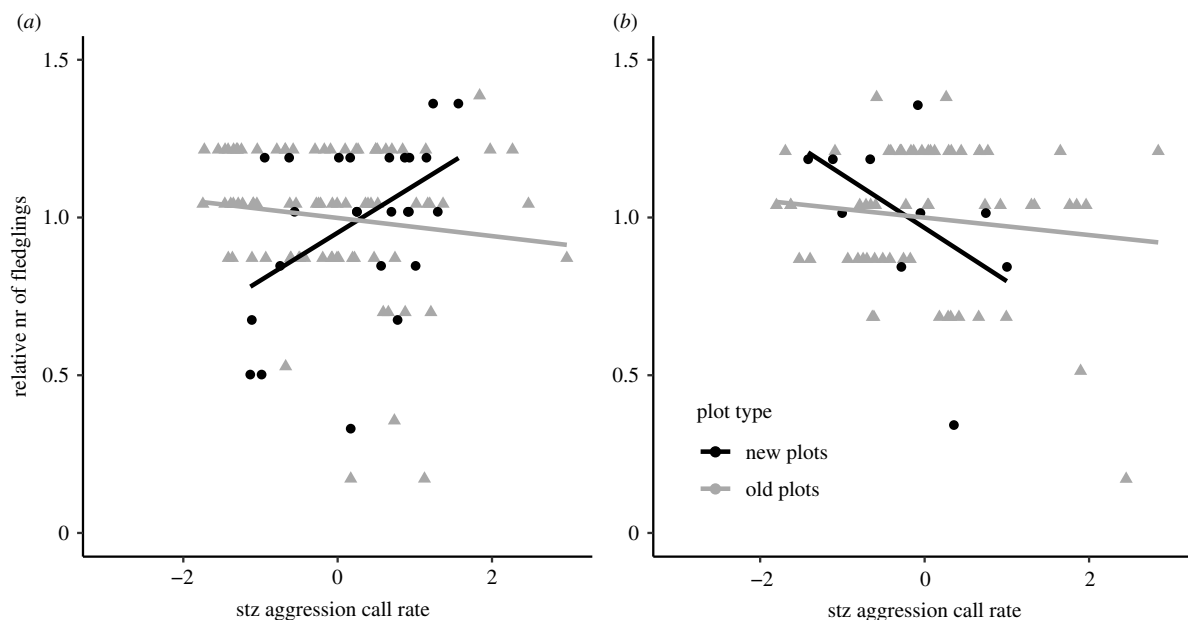
Figure 3. Strength and direction of fecundity selection on aggression call rate of pied flycatchers vary between years and between old and newly established populations (plots). (*a*) 2017; (*b*) 2018. Only the first year of colonization of each plot is included in the analyses. Regressions through raw data are depicted.

Table 3. Year-specific phenotypic selection on parent standardized aggressive phenotype (stz call rate) in old versus newly established plots in a Dutch pied flycatcher population (*n* = 178 nests). Estimated effect sizes (*β*) are reported with their 95% CI. Significant selection gradients are denoted in italics.

	r nr. fledglings	
	β	95% CI
intercept	1.00	(0.95, 1.05)
plot type[a]	−0.05	(−0.15, 0.06)
year[b]	0.00	(−0.08, 0.08)
plot type × year	0.01	(−018, 0.21)
stz call rate	−0.03	(−0.08, 0.02)
stz call rate × plot type	*0.18*	*(0.06, 0.30)*
stz call rate × year	0.00	(−0.07, 0.08)
stz call rate × plot type × year	*−0.32*	*(−0.55, −0.09)*

[a]'old' established plots is used as reference category.
[b]year '2017' is used as reference category.

that successful colonizers in new plots and new incomers in old plots were indeed more aggressive than philopatric individuals. The association between aggression and dispersal was more pronounced in 2017 than in 2018, implying that the strength of dispersal syndrome in this population was context-dependent. In Collared flycatchers (*Ficedula albicollis*), the strength and direction of aggression-behavioural syndromes also varied among age-classes [47] and among years [48]. It was proposed that such heterogeneous variation in the strength and structure of behavioural syndromes is mediated by the annual fluctuations in demographic factors (age composition and relative density) that alter levels of competition for breeding opportunities [48]. An obvious candidate in our study would be density of great tits, but densities were very similar between 2017 and 2018. However, during our study years, caterpillar peak abundance (estimated via frass mass collected under 8–10 reference oak trees) that is a major food source for flycatchers during breeding [49,50], increased from 0.95 to 2.3 to 13.3 g caterpillars m^{-2} between 2016 and 2018 (Both unpublished) and mean population aggression level increased in concert. These observations imply that different ecological conditions may affect dispersal syndromes differently: covariation was detected in the 'bad' years (2016: [41], 2017: this study) but not in the 'good' year (2018: this study). We thus propose that in 'bad' years, net benefits of aggressive behaviour are higher for colonizers or immigrants without prior residency advantage [51].

(b) Behavioural plasticity or hard wired correlations?

Most descriptive studies on passerines proposed that the covariation between dispersal and (proxies of) aggression is rather fixed and maintained by genetic, parental or early environmental effects [16–18,28,52]. By contrast, in our population, such a correlation was modulated via phenotypic plasticity, i.e. high aggression level was the consequence rather than the cause of dispersal. Indeed, dispersers exhibited their highest level of aggression in their first breeding year but decreased it in the following years and birds translocated to unfamiliar areas maintain a higher level of aggression compared to control birds. These findings demonstrate that the covariation between dispersal and aggression can be remodelled depending on individuals' local breeding experience and/or year-specific ecological conditions [48]. Aggression is thus not necessarily genetically integrated to other behavioural traits [53]. Counterintuitively, the level of aggression in newly established plots did not decrease in years following initial colonization. This may be explained by few colonizers returning in the new plots in consecutive years, i.e. most of the birds breeding in each year were naïve to the area.

(c) Fitness consequences and eco-evolutionary implications of dispersal syndromes

Using a translocation experiment, we formally show that individuals forced to settle into a new plot maintain a

higher level of aggression and enjoy similar fitness as control individuals. We are aware that we may have underestimated fitness costs of forced dispersal because of our small sample size. However, assuming that these costs are at least not large, our interpretation is that individuals adaptively adjust their aggression level to their environment. Intraspecific competition for mates and interspecific competition for breeding cavities are two important processes that influence the breeding performance of pied flycatchers [39]. In our population, experimental removals of breeding flycatchers revealed a large surplus of non-breeding individuals [40] and 35.7% of the translocated and settled females mated with another local male (some being courted during their stay in the aviary). Moreover, in the new plots, tits were able to build a nest and lay eggs within a few days once the bottom of the nest-boxes was placed back (personal observation). By modulating their aggression level to the local social environment, flycatchers may thus buffer temporal and/or spatial variation in hetero- and conspecific competition levels and maximize fitness.

Phenotypic selection analyses conducted on 2 years of descriptive data revealed that in newly established areas higher levels of aggression are favoured in the 'bad' year (2017) and lower levels of aggression in the 'good' year (2018). Viewed from a reaction norm perspective, results suggest the existence of a behavioural reaction norm favoured by selection (individuals should decrease aggression level in 'good' years and increase it in 'bad' years) and that individuals that do not adjust their behaviour suffer reduced fitness. Because this study was limited to 2 years, a next step should aim to acquire more longitudinal data to identify the main ecological drivers of such heterogeneous selection. By contrast, in old established plots, variation in aggression was not associated with fitness variation. This may be due to the fact that we did not distinguish between immigrants and locally born birds, which could obscure patterns if these groups are under different selection pressures.

The detection of adaptive plasticity raises the intriguing question of how repeatable variation in aggression is maintained in this population. In fact, the existence of behavioural plasticity does not preclude the existence of repeatable variation upon which selection can act. Indeed, phenotypic plasticity is inherently costly [54,55] and consequently individuals are limited in the range of behaviours they can express [56]. In our population, repeatability of aggression varies from 0.27 within years to 0.14 among years which is in the range of most studied personality traits [57] (i.e. it has the potential to evolve under selection). Our study thus adds to the accumulating evidence that heterogeneous selection is one important mechanism maintaining personality variation in wild animal populations (e.g. [58–60]).

The existence of repeatable behavioural variation and the fact that dispersal tendencies covary with other heritable phenotypic traits in this population (Nicolaus *et al.* submitted [33]) further imply that individual movements and settlement success likely can affect the genetic composition of the newly colonized or invaded populations. There is also growing evidence that behavioural types can differ in the degree of plasticity (e.g. [61–64]) that can be the target of selection [65]. A promising future avenue will be to test whether dispersive phenotypes differ in behavioural plasticity and quantify the contribution of

dispersers/colonizers to the genetic structure of the populations and the rate of microevolution (e.g. in the context of adaptation to climate change). This knowledge may not only be important for our understanding of evolutionary processes but also for conservation studies that often use reintroduction or translocation methods for threatened fauna recovery programmes [66]. Establishing if some behavioural types are more likely to survive and reproduce after forced dispersal may contribute to improved conservation success (e.g. [67,68]).

5. Conclusion

Causes and consequences of dispersal syndromes are rarely investigated experimentally. By using forced translocation in combination with natural colonization, we were able to show that (i) colonizers exhibited higher levels of aggression but that such a dispersal syndrome was context-dependent, (ii) dispersal syndromes were caused by behavioural plasticity (both shown experimentally and longitudinally) and (iii) heterogeneous selection likely maintains variation in aggression. This study illustrates that our understanding of animal personality evolution requires replications across ecological contexts. It further confirms that behaviour is a key first response to environmental changes that helps individuals with initial settlement in new sites [69]. Coupling of dispersal and aggression can thus play a role in population dynamics as found in western bluebirds (*Sialia mexicana*) [38]. Here, the causes and consequences of dispersal syndromes were studied using an experiment in the same study area. It will be thus important to establish in future studies if such trait covariation facilitates settlement on a much larger spatial scale and among more contrasted habitat types as longitudinal dispersal to later phenology habitats may be a powerful mechanism for many organisms to adapt to fast climate-induced changes [32].

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