




## RESEARCH PAPER

# A behavioural trait displayed in an artificial novel environment correlates with dispersal in a wild bird

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**Abstract**

Behaviour shown in a novel environment has important consequences for fitness in many animals. It is widely studied with standard tests by placing the individuals into an unfamiliar experimental area, that is the so-called open-field or novel environment test. The biological relevance of traits measured under such artificial conditions is questionable and could be validated by establishing a link with variables that truly reflect exploration in the wild. Our aim in this field study was to characterize behaviours measured in an artificial novel environment (an aviary) and assess the biological relevance of them in the collared flycatcher (*Ficedula albicollis*). Therefore, we measured the repeatability and the association of multiple behavioural traits, as well as their relationship with breeding dispersal (that reflects exploration in the wild). We found evidence for non-zero repeatability for number of crosses between the quarters, number of hops and perching latency in the aviary, and these repeatabilities were high when assessed at shorter time windows. Additionally, birds with short perching latency in the novel environment were more likely residents and bred closer to their breeding nest box in the previous year, which may suggest that latency to perch is connected to dispersal in the wild. In sum, our results indicate that behaviours assessed in an artificial environment are individual-specific at least on smaller timescales, and at least, one component of these behaviours is correlated with an ecologically relevant trait.

**KEYWORDS**

activity, consistency, passerine, personality, philopatry, risk-taking

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## 1 | INTRODUCTION

Most animals frequently encounter unfamiliar environments during their life; thus, behaviour in a novel environment could have great importance for fitness. The successful exploration of novel environments may make new sources of food, mates and refuges available, but it may also incur some costs due to increased risk of predation or parasitism. Behaviour in a novel environment, usually termed as “exploration,” is a complex trait (Carter, Feeney, Marshall, Cowlshaw, & Heinsohn, 2013; Perals, Griffin, Bartomeus, & Sol, 2017). It reflects general activity, but may also reflect risk-taking, that is the tendency of the individual to take the unknown risks for the potential benefits (Cote, Fogarty, Fogarty, Weinersmith, Brodin, & Sih, 2010; Martin & Réale, 2008; Réale, Reader, Sol, McDougall, & Dingemanse, 2007; Verbeek, Drent, & Wiepkema, 1994). Accordingly, a positive relationship was found between behaviour in a novel environment and activity in a familiar environment (David, Auclair, & Cézilly, 2011; Siwak, Murphey, Muggenburg, & Milgram, 2002), as well as the former and risk-taking behaviour (David et al., 2011; van Oers, Drent, Goede, & Noordwijk, 2004), indicating that behaviour in novel environment is connected to activity and risk-taking behaviour in other contexts. However, not every study found such relationships (Nyqvist, Gozlan, Cucherousset, & Britton, 2013; Ruuskanen & Laaksonen, 2010; Vanden Broecke et al., 2018). Behaviour in novel environment is apparently also related to the stress response, as slow exploring birds generally had higher stress responses (Baugh et al., 2012; Bousquet, Petit, Arrivé, Robin, & Sueur, 2015; Carere, Groothuis, Mostl, Daan, & Koolhaas, 2003), but an opposite relationship was found in rodents (Crino, Larkin, & Phelps, 2010).

Behaviour in a novel environment is notoriously hard to study in the wild, because researchers can hardly create a truly new and standard environment for all individuals without causing unusual disturbance to the wild subjects. A common way to characterize these behaviours in many taxa from arthropods to mammals (d'Ettorre et al., 2017; Montiglio, Garant, Thomas, & Réale, 2010), including birds (Verbeek et al., 1994) is to place individuals into an unfamiliar experimental room/cage/arena, where they are supposed to display behaviours specific to the novelty situation (Kluen, Kuhn, Kempnaers, & Brommer, 2012; Rowe, Pierson, & McGraw, 2015; Verbeek et al., 1994). This test is usually called an open-field or novel environment test (Hall & Ballachey, 1932; Verbeek, Boon, & Drent, 1996). The benefit of this method is that novelty can be simulated and behaviour measured under standardized conditions, as each individual is tested in exactly the same environment so the environment-driven variability of behaviour can be minimized (Niemelä & Dingemanse, 2017). Behaviour in novel environment assessed in this way has been found repeatable (Dingemanse et al., 2012; Montiglio et al., 2010; Mutzel, Kempnaers, Laucht, Dingemanse, & Dale, 2011) and heritable (Chervet, Zottl, Schurch, Taborsky, & Heg, 2011; Dingemanse, Both, Drent, Oers, & Noordwijk, 2002; Edwards, Burke, & Dugdale, 2017). Furthermore, its correlation with other

behavioural traits, such as aggression and sociality, as well as with fitness was also frequently shown (Dingemanse, Both, Drent, & Tinbergen, 2004; McCowan, Mainwaring, Prior, & Griffith, 2015; Verbeek et al., 1996).

However, the biological relevance of such behaviour can often be unclear as the experimental situation frequently includes artificial stress stimuli that the animals rarely encounter in the wild. Therefore, it remains plausible that the behavioural patterns that are displayed in the exploration assay reflect the extremes of the natural range of exploratory behaviour, as the study species could not adapt to these artificial conditions through natural selection (McCowan et al., 2015; Niemelä & Dingemanse, 2014). To make the picture more complex, the link between exploratory behaviour as observed in the experimental room and the exploratory behaviour with true biological relevance may be species-specific. This species-specificity may arise because differences in habitat preference and/or foraging ecology may make the biological meaning of similarly measured behavioural traits (i.e. the number of movements/activity) remarkably different for different species. For example, in great tits (*Parus major*) the number of visited trees or branches (number of hops and flights) seems to be a relevant measure of behaviour in novel environment, as they typically search for food by hopping across trees and branches (Dingemanse et al., 2002; Nicolaus et al., 2015; Riyahi, Björklund, Mateos-Gonzalez, & Senar, 2017). On the other hand, it has less relevance for the behaviour of, for example, zebra finches (*Taeniopygia guttata*), which mainly consume grass seeds; thus, movement on the ground may more adequately describe their behaviour in a novel environment.

To assess the biological relevance of the measured traits, it is crucial to ascertain whether the behaviour that we quantify in the test and its putative corresponding behaviour in the wild reflect the same biological phenomenon. One way to achieve this is to establish a link between the measured exploratory behaviour and analogous variables from the wild, that is proxies for exploration in the wild. For example, dispersal may be an ecologically relevant and measurable manifestation of how individuals generally behave in novel environmental situations. Indeed, behaviour of blue tits measured in a small, novel cage has been found to correlate with the tendency to find newly established feeders during winter in the wild (Herborn et al., 2010). Other studies characterizing behaviour in larger spaces (test rooms) in great tits and house sparrows (*Passer domesticus*) found positive relationship between such behaviour in novel environments and natal dispersal and range expansion (Dingemanse, Both, Noordwijk, Rutten, & Drent, 2003; Korsten, Overveld, Adriaensen, & Matthysen, 2013; Liebl & Martin, 2012). Additionally, fast explorers, switched to new feeding sites from a previously frequented one faster (but see also Verbeek et al., 1994), had greater home ranges and tended to gather at the periphery of the flock (Aplin, Farine, Mann, & Sheldon, 2014; van Overveld, Adriaensen, & Matthysen, 2011; van Overveld & Matthysen, 2010). This line of evidence indicates a general link between behaviour in a novel environment and exploration of the environment in an ecologically relevant sense. Birds displaying more explorative behaviour may have a chance

to get in contact with a greater part of their environment, thereby finding new suitable habitats and ultimately dispersing further away than individuals with less explorative behaviour. Alternatively, exploration could be connected to dominance (Verbeek et al., 1996; Verbeek, Goede, Drent, & Wiepkema, 1999) and dominance may influence dispersal (Cote, Clobert, Clobert, Brodin, Fogarty, & Sih, 2010), creating relationship between exploration of a novel environment and dispersal.

In this study, our aim was to establish the biological relevance of behaviours measured in an artificial novel environment in the collared flycatcher (*Ficedula albicollis*), a long-distance migratory passerine bird that feeds mainly on flying insects. Adaptive behavioural strategies in novel environment may have particular importance in migratory species, because these are frequently exposed to such unknown environments during migration stopovers and also when arriving to the breeding/wintering grounds (Mettke-Hofmann & Gwinner, 2004; Mettke-Hofmann, Lorentzen, Schlicht, Schneider, & Werner, 2009). However, migratory species have rarely been studied in this respect. Therefore, we first characterized the different components of exploratory behaviour in an outdoor aviary, assessed the repeatability of the assayed traits along different temporal windows and investigated their interrelations to explore the degree to which they represent different behavioural axes. We then characterized the relationship of the investigated behavioural traits with dispersal distance, which was assessed along two scales: dispersal status, that is differentiating local and immigrant individuals (larger scale), and breeding dispersal distance within the population (smaller scale). Our predictions were that i) behaviours in a novel environment would be repeatable and ii) more explorative individuals would disperse farther away.

## 2 | METHODS

### 2.1 | Study site and study species

The study was performed in an oak-dominated forest area in the Pilis-Visegrádi Mountains, close to Budapest, Hungary (47°43'N, 19°01'E). The research area belongs to the Duna-Ipoly National Park and contains about 800 nest boxes, in which our model organism, the collared flycatcher commonly breeds. Since the establishment of our research area, reproductive investment has been regularly and intensively monitored via standard capturing and ringing protocols, as well as regular nest box checks during the breeding season (Török & Tóth, 1988). Since 2003, behaviour has also been monitored for a subset of birds with standardized tests (Garamszegi et al., 2006).

Collared flycatcher males arrive at the breeding site earlier than females around the middle of April to establish their territories. Males probably prefer nest boxes (if available) over natural holes (Lundberg, Alatalo, Carlson, & Ulfstrand, 1981). During the reproductive period, males can be distinguished from females based on their predominantly black and white plumage. Females lay 4–8 (mainly 6–7) eggs which they incubate for 12–13 days. After hatching, both parents feed the chicks, until they leave the nest at the age of 14–15 days.

Our study species is highly philopatric, as even the movements between the study plots are infrequent (at least in females) and between-year dispersal is low (Garamszegi, Török, Michl, & Møller, 2004; Könczey, Török, & Tóth, 1992). A previous study in our population found that males breed only 128 m and females 358 m away on average from their nest box in the previous year (Könczey et al., 1992). This short breeding dispersal distance may also be associated with fitness benefits in this species (Pärt, 1990, 1991, 1994). The most important determinants of dispersal distance that have been identified are sex, age and previous reproductive success, as females, yearlings and unsuccessful breeders disperse farther (Könczey et al., 1992; Pärt & Gustafsson, 1989).

### 2.2 | Capturing and morphological measurements

We captured birds during courtship and/or during nestling care in their nest boxes using spring traps, and we recorded their morphological data only after the behavioural tests. We measured body mass using a Pesola spring balance (with a precision of 0.1 g) and tarsus length reflecting body size using a calliper (with a precision of 0.1 mm). We could also determine the age of each male based on their plumage, since 1-year-old birds bear brown remiges and smaller white patches on their wings, while the remiges of older males are black and their wing patches are larger (Mullarney, Svensson, Zetterström, & Grant, 1999). The determination of the age of females is unrealistic based on morphological characters; thus, we could only determine their minimum age based on our long-term ringing records. After the measurements, birds without rings were marked with individually numbered rings for long-term identification. The reproductive output of all birds was monitored throughout the breeding season based on systematic nest box checks. We used the number of 8- to 10-day-old ringed chicks as a proxy for reproductive success, as it is highly correlated with the number of fledglings and has much greater sample size (Jablonsky et al., 2017).

All applicable international, national and/or institutional guidelines for the care and use of animals were followed. Permissions for the fieldwork have been provided by the Middle-Danube-Valley Inspectorate for Environmental Protection, Nature Conservation and Water Management, Ref. no's: KTVF 30871-1/2008, KTVF 43355-1/2008, KTVF 45116-2/2011, KTVF 21664-3/2011, KTVF 12677-4/2012, KTVF 10949-8/2013, PE/EA/101-8/2018, PE-06/KTF/8550-4/2018, PE-06/KTF/8550-5/2018 and was approved by the ethical committee of the Eötvös Loránd University (Ref. no. TTK/2203/3).

### 2.3 | Behaviour in novel environment

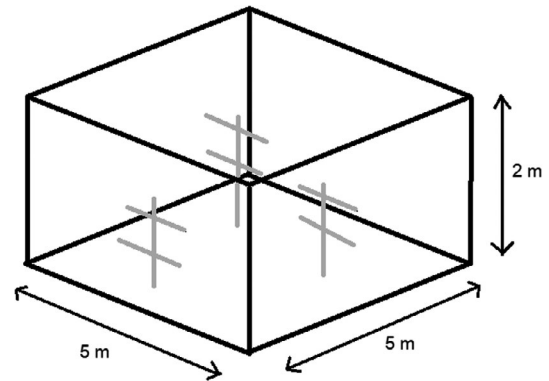
Standardized measurement of behaviour in novel environment with open-field or novel environment tests is widespread in the literature, but the traits measured are defined and interpreted differently in different studies (Jones & Godin, 2010; Montiglio et

al., 2010; Thompson, Evans, Parsons, & Morand-Ferron, 2018). In birds, the variables that are typically recorded in such behavioural assays include the number of short flights between landmark objects, the number of crosses between areas, the time to reach some or all locations and the time spent displaying a certain behaviour, and these are interchangeably used to reflect exploration, activity, boldness or other phenomena (Erasmus & Swanson, 2014; Quinn, Patrick, Bouwhuis, Wilkin, & Sheldon, 2009; Verbeek et al., 1994). However, the different measures may represent different underlying functional axes. To handle this phenomenon, we characterized multiple behavioural traits in the same unfamiliar environment and investigated the correlations between them. We only sought further association with dispersal in the case of variables that we found independent and repeatable.

We used data from 337 (99 female and 238 male) collared flycatchers from 2010 and 2012–2017 (Table 1). Nine females were measured twice, and 91 repeated measurements were taken from 70 males (2 times: 54, 3 times: 12, 4 times: 3 and 5 times: 1 individual). Behavioural data from males could be taken from different phases of the breeding season, during the courtship (between April 13 and May 8) and the chick-feeding period (between May 3 and June 22). Females could be tested during the latter period only, because they cannot be captured efficiently in large numbers during the former period. All behavioural tests were conducted between 07:30 and 13:30.

We assayed the behaviour of the birds in a  $5 \times 5 \times 2$  m aviary we built in the study area and covered with a net. Within the enclosure, we provided three perching trees, each with two horizontal branches (Figure 1). The experimental area, where the enclosure was set up, was remote from the territory of the assayed individuals enabling us to control for the confounding effect of environment on behaviour (Pärt, 1994), as all birds were tested in the same standard arena. Thus, the measuring environment was standard, but we could not control for the long-term effect of territory quality (e.g. the effect of better condition due to the possession of a good territory). Another advantage of this setup was that during the chick-feeding period, the parents could be tested separately.

We measured behaviour in the following way for a subset of birds breeding in our study site due to ethical reasons and logistical constraints (see sample sizes above and in Table 1). After catching the birds (during either the courtship or the chick-feeding period), we transferred them into the aviary in standard bird bags (transportation time was between 10 and 103 min, with an average of 37 min) and released them therein by hand lifting up one



**FIGURE 1** Schematic figure of the aviary used for the measurement of behaviour in a novel environment

corner of the net. We left the area for at least 6 min, during which we video-recorded the individuals remotely to derive behavioural traits in a subsequent laboratory analysis. From the video records, the evaluation of the behaviour started when it was evident that the experimenter left the observation area (i.e. at least 1 min has elapsed since the start of the video record) and included a sample of 5 min. We characterized 4 variables: number of crosses between the quarters of the aviary, latency to perch on one of the trees (sec) (hereafter latency to perch), number of landings on the different trees/perches (number of hops) and general behaviour of the birds during the analysed period. For the evaluation of number of crosses, the aviary was divided into four equal quadrants, and a cross was made when the bird flew through any of the borders of the quadrants. We classified the general behaviour of the birds into three categories. The birds were categorized as i) freezing if they remained in one spot of the aviary without any sign of movement during the test; ii) panicking if they flew to and fro in a disoriented way within a small part of the aviary (i.e. smaller than its quarter); and iii) normal if the individuals showed signs of normal behaviour in the enclosure according to the observer's judgement (i.e. perched on the trees, frequently visited different parts of the aviary). Number of crosses and number of hops may represent some measures of activity, but these could also be influenced by the stress tolerance of the birds. On the other hand, latency to perch may reflect risk-taking if seen as the willingness to calm down and begin the exploration of a novel environment after perceived predation threat induced by the capture of the bird. However, latency to perch may involve elements of activity (active birds may perch later), as well as stress tolerance.

**TABLE 1** Sample sizes of behavioural measurements in the aviary according to year and general behaviour with the respective percentages

	2010	2012	2013	2014	2015	2016	2017
Normal	86 (81.13%)	3 (60%)	47 (79.66%)	71 (78.89%)	65 (83.33%)	71 (93.42%)	21 (91.30%)
Freezing	10 (9.43%)	2 (40%)	7 (11.86%)	5 (5.56%)	4 (5.13%)	1 (1.32%)	1 (4.35%)
Panicking	10 (9.43%)	0	5 (8.47%)	14 (15.56%)	9 (11.54%)	4 (5.26%)	1 (4.35%)
Total	106	5	59	90	78	76	23

As two researchers were engaged in the analysis of the video records (GM in 2010, MJ in the other years), in 2010, 10 randomly chosen videos were independently analysed by both analysers and the consistency of the measured variables was investigated with Spearman correlation to detect interobserver error. Based on the high correlations (number of crosses  $r_{sp} = .948$ ,  $p < .001$ , latency to perch:  $r_{sp} = .997$ ,  $p < .001$ , relative number of hops:  $r_{sp} = .719$ ,  $p = .019$ ), we concluded that observer effect is small and did not consider this confounding variable in the further analysis. The classification into general behavioural categories was carried out by only one observer (JM).

## 2.4 | Dispersal

Dispersal was assessed with different measures on two different scales. On the larger scale, we compared immigrants (caught in our study area for the first time) and local breeders or recruits (ringed previously in our study site), and this reflects dispersal status across populations. Thus, we used ringing status as a proxy for dispersal status. This approximation could be erroneous, because some birds could not be ringed when breeding in our study area, if they nested in natural cavities or successfully avoided capture in our nest boxes in previous years. The extent of these biases could not be assessed, but it is not expected to be large, as only few flycatchers choose natural cavities for breeding in areas with nest boxes (Lundberg et al., 1981), and we made an effort to capture all breeding birds (80%–90% of the birds rearing at least one ringed chick were captured).

On a smaller scale, we determined breeding dispersal distance for the birds that had bred in our study plots in the previous year or in the subsequent year ( $N = 225$ ) relative to the year of behavioural measurements. Breeding dispersal distance is defined as the distance between the former breeding area and a new breeding site of the animal (Belliere, Sorci, Moller, & Clobert, 2000; Végvári et al., 2018), and it is also commonly used in migratory species (Paradis, Baillie, Sutherland, & Gregory, 1998; Pärt, 1990). To estimate breeding dispersal distance, we used the GPS coordinates of the respective nest boxes and calculated their aerial distance. Additional analyses for the validation of the dispersal data are provided in the electronic supplementary material (the potential effect of the period in which the reference nest box was occupied (during courtship or chick-feeding), repeatability estimate). Additionally, the measured behavioural traits in the novel environment did not differ significantly between birds that had or had not breeding dispersal data (number of crosses, unpaired  $t$  test:  $t = 0.34254$ ,  $df = 177.64$ ,  $p$ -value = .7323; latency to perch, chi-squared test:  $\chi^2 = 2.9165$ ,  $df = 1$ ,  $p$ -value = .08768).

## 2.5 | Statistical analysis

The number of crosses was  $\log_{10}$  transformed to achieve normal distribution on model residuals. Latency to perch was binarized (values below the median of 17 s was scored as 0, while the rest as 1), as its

distribution was heavily skewed and truncated (the maximum value of this variable was an arbitrary value, 301 s, and 8.72% of the measurements had to be truncated). According to video recordings and distribution of the variable, there was no biologically relevant cut-off point between birds with short and long perching latency; thus, we used the median that yielded a balanced binary variable. However, via such binarization some biologically relevant information may be lost, so we repeated our analyses for latency by using truncated normal distribution and present these results in the electronic supplementary material (S3, Tables S1–S3). The number of hops fulfilled the criteria of the Poisson distribution, but was dependent on the latency to perch (it could be evaluated only after the first landing on a tree). Therefore, we used the relative number of hops; specifically, we used 300 s minus the estimated latency to perch as an offset in the further models, or in analyses when offset could not be used (for example when calculating correlations) we calculated relative number of hops as:

$$\text{relative}N_{\text{hops}} = \frac{N_{\text{hops}}}{300 - \text{Lat}_{\text{perch}}}$$

(where  $N_{\text{hops}}$  is number of hops and  $\text{Lat}_{\text{perch}}$  is latency to perch). General behaviour yielded very unbalanced distribution (freezing  $N = 30$ , panicking  $N = 43$  and normal  $N = 364$ , Table 1); thus, we calculated repeatability (see below), but did not analyse this variable further, and included only birds that were considered to display normal behaviour in the analysis of the other variables measured in the aviary. We excluded freezing and panicking birds because they probably did not display biologically meaningful exploration. Furthermore, birds were used only if there was no external disturbance during their behavioural measurements (e.g. by other bird, human or predator) and if there were no missing data (either for behavioural or for control variables) in their record.

For the majority of the analyses, we used linear mixed models (LMM) and generalized linear mixed models (GLMM). In case of LMM, the models were fitted using maximum likelihood instead of restricted maximum likelihood method (Bolker et al., 2009). Prior to the analyses and the interpretation of model outputs, the distribution of the variables, as well as model residuals, was checked visually by inspecting histograms and q-q plots. Furthermore, homogeneity and homoscedasticity of the residuals, the stability of models against influential data points, as well as presence of collinearity with variance inflation factor (VIF; Freckleton, 2011; O'Brien, 2007) were also verified before the interpretation of the model outputs. We extracted results from the full models.  $p$ -values for fixed predictors were calculated with likelihood ratio tests (LRT) comparing models with and without the focal predictor. We did not derive significance estimates for random factors, but we provide the variance explained by them. In the case of GLMM, we inspected the stability of models against influential data points, and the presence of collinearity, similarly as above.  $p$ -values were extracted from the model output; otherwise, the process was the same as in LMM.



Repeatability for the number of crosses, the binarized latency to perch and the relative number of hops were calculated by dividing their between-individual variance with the total variance (Lessells & Boag, 1987). Variance components were derived from the appropriate LMMs and GLMMs (Nakagawa & Schielzeth, 2010) including the focal variables one by one as the response variables, and individual and year as random factors. Therefore, the obtained estimate is formally consistency repeatability and not agreement repeatability, as we controlled for the potential differences between the measurement sessions (Nakagawa & Schielzeth, 2010). For males, repeatability was calculated separately for three intervals, that is for the within-day, within-year and between-year scenarios. In the within-day scenario, we assessed repeatability also for the two periods (courtship and chick-feeding) separately. Period was also added to the model if the data originated from different periods, but we avoided including other variables because of the limited sample size that was available in the repeated measurement design (see also Jablonsky et al., 2017). For females, data were available only for the calculation of repeatability on the across-year level (see also Table 2). *p*-values and confidence intervals for repeatability values were computed with randomization and parametric bootstrap approaches, respectively, according to Nakagawa and Schielzeth (2010). Repeatability of the multinomial general behaviour variable was assessed with Cohen's kappa (Cohen, 1960).

The independence of the behavioural variables measured in the novel environment in birds showing normal behaviour was estimated in a form of correlation effect size based on Spearman rank correlations and *t* tests, after which *t*-values were converted to correlations (in the case of latency to perch). Based on these correlations, we decided to retain two variables (latency to perch and crosses between the quarters), because relative number of hops was highly correlated with number of crosses ( $r_{sp} = .614$ ), thereby probably representing a common activity factor with that variable. On the other hand, the

latency to perch and number of crosses between the quarters were independent ( $r = .004$ ), while the correlation between latency to perch and relative number of hops was  $r = .303$ . We chose number of crosses instead of number of hops because of its very low correlation with latency to perch and because it may be biologically more relevant for the collared flycatcher that does not often forage by searching among branches. However, because the relative number of hops resembles a widely used measure of behaviour in novel environment (Dingemanse et al., 2012; McCowan, Rollins, & Griffith, 2014; Riyahi et al., 2017), we repeated the analysis also with this variable and present these results in the electronic supplementary material (Tables S4 and S5).

We also investigated the relationship of the number of crosses and the latency to perch with the dispersal status (immigrant or local recruit/breeder), while controlling for additional morphological and other proximate variables. Because of the different distribution of the response variables, LMM (for number of crosses) and GLMM (for binarized latency to perch) with binomial distribution were used, respectively. Because females were measured only in the chick-feeding period, we only used data from this period. The control variables were condition (residuals from mass-tarsus regression calculated separately for years), sex and date of measurement, while we also considered the interaction between dispersal status and sex. The random effects were bird identity (as we included all measurements across years from an individual) and year (see also Table 3). Date of observation was standardized across years by re-coding it relative to the date of the first behavioural measurements during the chick-feeding period in the given year. The effect of age was evaluated in a separate model excluding dispersal status, because the age of newly captured, immigrant females could not be reliably determined; thus, nearly all immigrant females were categorized as juveniles.

Finally, the relationship between number of crosses and latency to perch with breeding dispersal distance was investigated. In these

**TABLE 2** Repeatability of the behavioural variables measured in the aviary across different timescales and in the within-day scenario also separately for the data obtained during courtship or the chick-feeding period

Sex	Interval	N (individual)	R or r (confidence interval)			Cohen's Kappa
			Number of crosses	Latency to perch	Relative number of hops	General behaviour
Females	Between-year	15 (8)	0.321 (0–0.925)	0 (0–0.996)	0.359 (0–0.898)	0
Males	Between-year	34 (15)	0.166 (0–0.587)	0.095 (0–0.716)	<0.001 (0–0.445)	0
	Within-year	88 (48)	<b>0.331</b> (0.017–0.553)	0.118 (0–0.378)	0.021, (0–0.303)	–0.077
	Within-day	103 (46)	<b>0.444</b> (0.199–0.632)	<b>0.400</b> (0.041–0.661)	<b>0.608</b> (0.435–0.783)	0.161
	Within-day, courtship	76 (42)	<b>0.489</b> (0.170–0.698)	<b>0.349</b> (<0.001–0.594)	<b>0.718</b> (0.506–0.884)	0.176
	Within-day, chick-feeding	27 (14)	<b>0.686</b> (0.226–0.889)	<b>0.554</b> (0–0.991)	<b>0.453</b> (0.0259–0.829)	0

Note: Significant values are in bold. N: number of observations.

**TABLE 3** Results from the mixed models investigating the relationship of the number of crosses or binarized latency to perch with dispersal status and control variables, including data from the chick-feeding period for both sexes

Predictor variables	Crosses				Latency to perch		
	$\beta$ (SE)	<i>t</i>	LRT $\chi^2$	<i>p</i>	$\beta$ (SE)	<i>z</i>	<i>p</i>
Standardized mass	-0.005 (0.005)	-1.025	1.014	.314	-0.027 (0.029)	-0.923	.356
Date	-0.003 (0.006)	-0.456	0.202	.653	0.081 (0.039)	2.085	<b>.037</b>
Sex	-0.122 (0.062)	-1.976	3.691	.055	-1.009 (0.543)	-1.858	.063
Dispersal status	0.092 (0.061)	1.510	2.239	.135	-1.323 (0.504)	-2.624	<b>.009</b>
Sex:dispersal status	-	-	-	-	1.197 (0.700)	1.711	.087
Random effects	<b>Variance</b>				<b>Variance</b>		
Identity	0.019				0.096		
Year	0.005				0.062		
Residual	0.134						

Note: Significant values are in bold.

Estimates ( $\beta$ ) are displayed together with standard errors (SE), *t*-values and chi-squared statistics from likelihood ratio tests (LRT) or *z*-values and *p*-values. *N* = 183.

models, we selected few variables with assumed importance based on previous evidence (sex, interaction of sex and breeding distance and reproductive success before the dispersal event sensu; Pärt & Gustafsson, 1989; Könczey et al., 1992) as control variables beside the above-mentioned control variables (age, standardized mass and date of measurement). The random structure was similar to the models above (bird identity and year), with further inclusion of nest (pair) identity (see also Table 4).

An additional analysis investigating the effect of experience with the behavioural measurements on the measured behavioural variables is also presented in the electronic supplementary material (S2).

All statistical analyses were performed in the R 3.4.3 statistical environment (R Development Core Team, 2015). Linear mixed models and GLMMs were fitted with the “lme4” package (Bates, Maechler, & Bolker, 2011). Variance inflation factor was calculated by the “vif” function from the “car” package (Fox & Weisberg, 2011). Repeatability for number of hops with Poisson distribution was calculated with “rptPoisson” from the “rptR” package (Stoffel, Nakagawa, & Schielzeth, 2017).

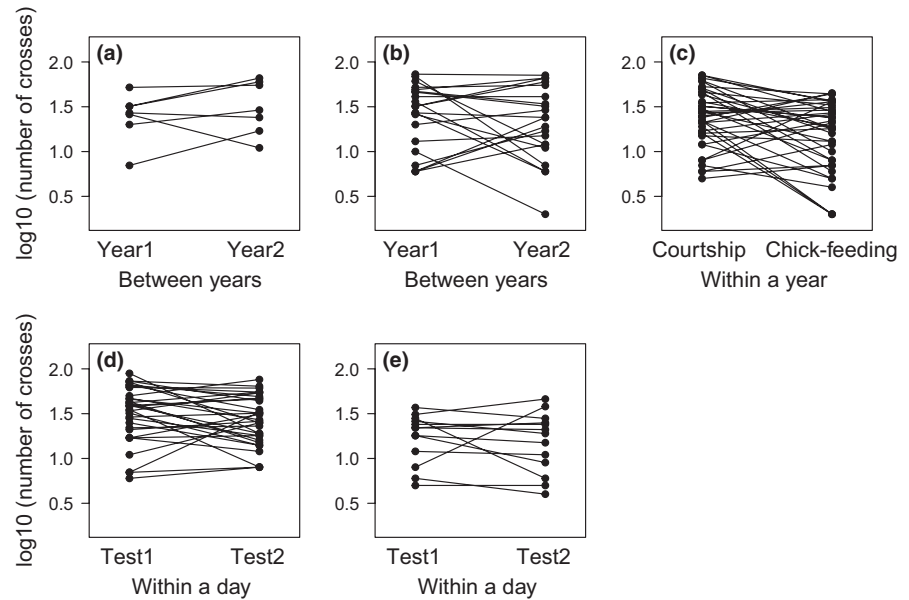
**TABLE 4** Results from the mixed models investigating the relationship between the number of crosses or binarized latency to perch and breeding dispersal distance and control variables

Predictor variables	Log10 (number of crosses)				Latency to perch		
	$\beta$ (SE)	<i>t</i>	LRT $\chi^2$	<i>p</i>	$\beta$ (SE)	<i>z</i>	<i>p</i>
Breeding dispersal	0.021 (0.072)	0.287	0.082	.775	1.355 (0.620)	2.186	<b>.029</b>
Sex	-0.149 (0.086)	-1.742	2.959	.085	0.219 (0.530)	0.413	.680
Chicks before the Dispersal event	0.030 (0.020)	1.500	2.196	.138	0.151 (0.130)	1.163	.245
Age	-0.018 (0.082)	-0.221	0.049	.825	0.320 (0.528)	0.606	.545
Standardized mass	-0.005 (0.007)	-0.747	0.557	.456	-0.050 (0.044)	-1.119	.263
Date	-0.005 (0.009)	-0.568	0.322	.571	0.018 (0.056)	0.324	.746
Random effects	<b>Variance</b>				<b>Variance</b>		
Identity	0				<0.001		
Nest identity	0				0.077		
Year	0				0.670		
Residual	0.143						

Note: Significant values are in bold.

Estimates ( $\beta$ ) are displayed together with standard errors (SE), *t*-values and chi-squared statistics from likelihood ratio tests (LRT) or *z*-values and *p*-values. *N* = 96.

**FIGURE 2** Individual changes of number of crosses measured for females (a) during chick-feeding between years and for males (b) between years, (c) between the two periods of the breeding season, (d) during courtship within a day and (e) during chick-feeding within a day



### 3 | RESULTS

#### 3.1 | Repeatability

Number of crosses (Figure 2), relative number of hops and binarized latency to perch in the novel environment, had generally low repeatability in males between years, higher repeatability between periods and high and significant repeatability within a day (Table 2). For females, the repeatability between years was higher but not significant for number of crosses and relative number of hops, and very low for latency to perch and general behaviour. Cohen's kappa for general behaviour was close to zero in every case.

The models for repeatability also including period as a control variable revealed that the number of crosses decreased from courtship to the chick-feeding period (between-year model: period (chick-feeding) estimate  $\pm$  SE =  $-0.399 \pm 0.128$ ,  $p = .004$ , within-year model:  $-0.202 \pm 0.063$ ,  $p = .003$ , within-day model:  $-0.272 \pm 0.063$ ,  $p < .001$ ), but there was no significant relationship between period and latency to perch (between-year model: estimate  $\pm$  SE =  $-0.482 \pm 1.016$ ,  $p = .635$ , within-year model:  $-0.227 \pm 0.480$ ,  $p = .636$ , within-day model:  $0.180 \pm 0.643$ ,  $p = .779$ ).

#### 3.2 | Behaviours in novel environment and dispersal status

In the models including the number of crosses as response variable, none of the investigated predictors were significantly related to the response variable (Table 3). For better interpretation, in Table 3 the results are displayed from the model excluding the non-significant interaction between dispersal status and sex ( $\beta \pm$  SE =  $-0.118 \pm 0.121$ ;  $p = .356$ ). In the latency to perch model, however, dispersal status had a significant relationship with latency to perch in the aviary, as

immigrant birds had longer perching latency than already ringed, resident birds (Table 3). The date of measurement was significantly and positively associated with latency to perch, while sex had also a notable tendency (males tended to perch sooner than females). Using minimum age instead of dispersal status in the models (as these two variables could not be included in the same model) yielded similar results, except that age was not related to either of the response variables (number of crosses: estimate  $\pm$  SE =  $-0.049 \pm 0.064$ ,  $p = .457$ , latency to perch: estimate  $\pm$  SE =  $0.593 \pm 0.384$ ,  $p = .122$ ).

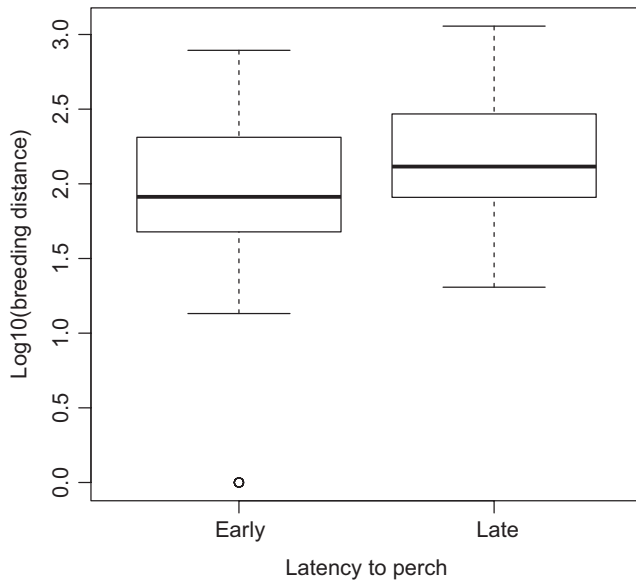
#### 3.3 | Behaviours in novel environment and breeding dispersal distance

Due to the relatively low sample size, results from models excluding the non-significant interaction term between dispersal distance and sex (number of crosses:  $\beta \pm$  SE =  $0.110 \pm 0.149$ ;  $p = .465$ ; latency to perch:  $0.273 \pm 1.031$ ;  $p = .791$ ) are displayed in Table 4. In the model for the number of crosses, only sex had a marginally significant relationship with the response variable, with males performing relatively fewer crosses than females (Table 4). However, in the model for latency to perch, the relationship with breeding dispersal distance was significant and positive, that is birds with a short perching latency in the aviary had lower breeding distance (Table 4, Figure 3). On the original scale, the range of breeding dispersal distance for birds perching earlier in the aviary was 0–782 m, with an average of 70 m, while the range for those perching later was 19–1137 m, with an average of 143 m.

### 4 | DISCUSSION

We found that the behavioural variables measured in an artificial novel environment had low repeatability between years, but the





**FIGURE 3** Relationship between binarized latency to perch and  $\log_{10}$  transformed breeding distance (m)

majority of them showed moderate repeatability within a season and high repeatability within a day. The number of crosses in the enclosure probably reflecting the activity of the birds in a novel environment decreased between courtship and the chick-feeding period, but was unrelated to dispersal status or breeding dispersal. The binarized latency to perch in the novel environment was associated with dispersal on two different scales and also with date of measurement. Short latency to perch may reflect high risk-taking tendency, low activity or high stress tolerance, but in any case birds with short perching latency in the novel environment seemed to be more philopatric.

Our variables describing the behaviour in novel environment were more repeatable on shorter timescales, which is in line with the findings of several other studies (Dingemanse et al., 2012; Michelangeli, Chapple, & Wong, 2016; Riyahi et al., 2017). The repeatability of general behaviour was close to zero and not significant, but due to the low sample size for birds with freezing or panicking behaviour this result should be considered with caution. Generally, our results further confirm other findings showing that repeatability of plastic traits like behaviours decreases with time elapsed between measurements (Arvidsson, Adriaensen, Dongen, Stobbeleere, & Matthysen, 2017; Bell, Hankison, & Laskowski, 2009; Wexler, Subach, Pruitt, & Scharf, 2016; Zsebök et al., 2017). Some studies found high and significant repeatability between years for certain behavioural traits (Expósito-Granados et al., 2016; Krause, Krüger, & Schielzeth, 2017; Thys et al., 2017), but in our study population we systematically detected reduced repeatability between breeding seasons for several behavioural traits, such as aggression, novelty avoidance, predator avoidance, escape ability and several song variables (Garamszegi et al., 2015; Jablonsky et al., 2017; Zsebök et al., 2017). The generally moderate repeatability on larger time scales suggests that although birds may apply a more or less consistent tactic to explore novel environments, it still involves some degree of plasticity allowing individuals to adjust their behaviours

to environmental changes over longer periods. Thus, it seems that in the collared flycatcher plasticity has an important role in shaping behavioural variance, especially over longer periods.

Both dispersal status and breeding dispersal were related to latency to perch in the aviary; thus, a component of the exploratory behaviour in an artificial novel environment seems to be associated with ecologically relevant variables on different spatial scales. Those birds that had been ringed in our study site in the previous years were more likely to perch early than those that can be considered as immigrants based on their ringing history. The results in association with breeding dispersal distance indicate the same trend: birds that perch early realize shorter breeding dispersal distance than individuals with longer latency to perch. Note that the causality of these relationships could not be fully resolved based on correlational data. However, we infer that it is unlikely that local birds behaved less cautiously because they were accustomed to the behavioural testing protocol as experience with the aviary did not have an effect on the behaviours (see electronic supplementary material). Nonetheless, the experience with the ringing protocol and human presence may still affect the behaviours of the resident birds and we could not control for this confounding effect.

As we could not ascertain what underlying mechanism influences the latency to perch, we offer different interpretations. If latency to perch is determined by risk-taking tendency, because the birds perceive the capture as a predation attempt, the positive association between perching latency and breeding dispersal distance may suggest that birds taking higher risk in a novel environmental context could be more philopatric to their natal population than birds with lower risk-taking tendency. However, our results are in contrast with other findings that suggest that taking higher risk behaviourally is associated with greater dispersal tendency (Møller & Garamszegi, 2012; Myles-Gonzalez, Burness, Yavno, Rooke, & Fox, 2015). But latency to perch could reflect also activity or stress tolerance, so these aspects could also be connected to dispersal. Based on our results, more active individuals that perch later also disperse further and similar relationship was also found in mammals and fish (Haughland & Larsen, 2004; Závorka, Aldvén, Näslund, Höjesjö, & Johnsson, 2015). However, latency to perch had low correlation with our other variables more likely representing activity (number of crosses and number of hops); therefore, we assume that this variable rather reflects some sort of acceptance of the perches than activity. Finally, capture and release in the aviary inflict stress on the birds, so it is also possible that increased stress tolerance is connected with philopatry.

There is accumulating evidence that dispersal is coupled with certain consistent behavioural traits that facilitate dispersal, thus creating a “dispersal syndrome” (Cote, Clobert, et al., 2010). These behaviours are, for example, aggression and foraging in birds or sociability in lizards (Cote & Clobert, 2007; Duckworth & Badyaev, 2007; Nicolaus, Barrault, & Both, 2018). According to our results, latency to perch in an unknown environment may take part in the dispersal syndrome in collared flycatchers. As mentioned earlier, we could not exactly determine the biological meaning of latency

to perch, so its exact role in the dispersal syndrome require further investigation.

Studies on the great tit also found a relationship between dispersal distance and behaviour in novel environment, specifically immigrants and birds dispersing farther explored the novel environment faster (Dingemanse et al., 2003; Quinn, Cole, Patrick, & Sheldon, 2011), and this link was also found at the genetic level (Korsten et al., 2013). Similar relationship was also reported in fish and in mammals (Cooper et al., 2017; Rasmussen & Belk, 2012). It is difficult to compare these results with ours, because there are remarkable differences in the underlying study designs and the ecology of the focal species, which should also be considered. For example, the studies on great tits investigated natal dispersal and all studies measured behaviours in different ways than the protocols we followed in the present study. Thus, our results with latency to perch are difficult to interpret; however, the number of hops (see results in the Supplementary Material) was measured similarly to the other studies and it had a negative relationship with dispersal distance. A possible explanation for the qualitative differences among our findings and that of studies on other species may be that philopatry is advantageous in the collared flycatcher in both sexes. This may occur due to the benefits of information on resources such as good breeding sites (Pärt, 1990, 1991, 1994; Pärt & Gustafsson, 1989), while in other species the exploration of new, unexploited areas may offer relatively greater benefit. Although philopatry seems to have advantages in great tits as well (van Overveld, Adriaensen, & Matthysen, 2015), the magnitude of the benefit may be greater in the collared flycatcher, as the shorter breeding season of this migratory species may increase the value of fast and successful settlement in the breeding grounds. And competition for the nest boxes may also be higher in the collared flycatcher, leading to an advantage of more active birds that are apparently better competitors (Both, Dingemanse, Drent, & Tinbergen, 2005; Cole & Quinn, 2012; Colléter & Brown, 2011) in settlement at better nest boxes (that are nearer to their territory in the previous year). Such major differences among species highlight that the variables measured in similar test situations may have species-specific ecological relevance.

While there was no effect of period on latency to perch, the number of crosses was lower during the chick-feeding period than during courtship. A possible explanation to this result is that the increased work load due to the provisioning of the chicks led to worse condition, thereby reducing general activity. We found in another study in this population that the impairment of condition throughout the breeding season is associated with a decrease in escape ability (Jablonszky et al., 2017), and a similar mechanism is suggested by our present findings for number of crosses. However, a number of hops and flights in novel environment were found to be lower at the beginning than at the end of the breeding season in great tits (Dingemanse et al., 2002) and total number of visited objects and flights were comparable between two measurements in spring in starlings (*Sturnus vulgaris*) (Thys et al., 2017). A potential explanation to this discrepancy may again be the different ecology of the species (e.g. greater effort invested by flycatchers into reproduction during

the shorter breeding season due to migration) and that the starlings were kept captive during the study.

In summary, we found evidence for the biological relevance of behaviours measured in artificial novel environment. Non-zero repeatability was found for multiple behavioural traits, and some of these repeatabilities were remarkably high when assessed over shorter time windows. Dispersal on two different spatial scales was also related to one of the measured behavioural variables, indicating that a component of behaviour of the collared flycatcher assessed in an unnatural spatial enclosure represents an ecologically relevant trait.

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## CONFLICT OF INTEREST

The authors declare that they have no conflict of interest.

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## SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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