

Male and female identity and environmental contexts influence courtship behaviour in a songbird

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Behavioural variation in courtship has become a central theme in the study of sexual selection. Courtship behaviour can vary consistently between males (between-individual variation) due to inherent characteristics of individuals, but males may also plastically adjust their courtship (within-individual variation) in response to the characteristics of the potential breeding mate or the environmental contexts. However, the relative importance of these components in courtship behaviour remains poorly understood. Here, we exposed male collared flycatchers, *Ficedula albicollis*, to different stimulus females simulating a female's visit to the male's territory during mate choice. We measured the male's latency to explicitly invite the female to visit the nestbox (hereafter, invitation latency), as a proxy of the male's motivation to mate. Repeated measurements of focal males (exposed to different stimulus females) and stimulus females (presented to different males) allowed us to assess the relative importance of male and female identity in male courtship, while also assessing the importance of their phenotype and other environmental sources of within-individual variation in invitation latency. We found that invitation latency was determined by male and, to a lesser extent, female identity, with the latter suggesting the existence of male mate choice in the species. We failed to identify specific traits of males and females that influenced courtship behaviour, although male responsiveness to stimulus females increased as the season advanced, possibly due to the costs of delaying breeding in temperate breeding areas. Overall, these results suggest that invitation latency is a consistent courtship attribute in males that can be adjusted plastically according to perceived female quality and environmental conditions. We emphasize that understanding within- and between-individual sources of courtship variation is essential for assessing its evolutionary potential, as plasticity in the expression of sexual signals may affect their reliability and the strength of sexual selection on them.

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Sexual selection and the evolution of secondary sexual traits are a backbone of evolutionary biology (Andersson, 1994; Jennions et al., 2012; Kokko et al., 2003; Kuijper et al., 2012). Traditionally, studies have mainly focused on extravagant male structures or colours which, either through production and/or maintenance costs or through their association with the individual's condition, act as honest signals to allow assessment of mate quality (e.g.

immune capacity, parental effort; Andersson, 1994; Kokko et al., 2003; Kuijper et al., 2012; Møller & Jennions, 2001; e.g. Zahavi, 1975). In recent years, however, the study of behaviour in the context of sexual selection has become prevalent, and it is now widely accepted that behaviours, as consistent individual characteristics, can be reliable indicators of quality and, therefore, that between-male behavioural variation could affect mate choice decisions and reproductive success (Bell et al., 2009; Dingemanse & Réale, 2005; Dougherty, 2021; Husak & Fox, 2008; Kappeler,

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2010; Réale et al., 2007; Schuett et al., 2010; Wolf & Weissing, 2012).

Although behaviours often vary consistently between individuals, they also vary plastically within individuals over time or in response to environmental contexts (Dingemanse et al., 2010; Dingemanse & Réale, 2005; Dingemanse & Wolf, 2013; Dougherty, 2021). Within-individual variation in behaviour may be related to individuals' intrinsic properties such as sex (Krenhardt et al., 2021), age (Delaney et al., 2020; Dingemanse et al., 2020), breeding stage (Araya-Ajoy & Dingemanse, 2017) and immune status (Garamszegi et al., 2015; Horváth et al., 2019) or to environmental conditions (reviewed in Dougherty, 2021) shaped by abiotic factors (Briffa et al., 2013), predation risk (Brown et al., 2005) or social context (Bierbach et al., 2015; Briffa et al., 2013; Brown et al., 2005; Jablonszky et al., 2021; Magellan & Magurran, 2007). Social contexts may be particularly important during courtship as courtship displays are used as signals to conspecifics. For example, males may modify their courtship behaviour, displaying more intensively, in response to intense intrasexual competition (Araya-Ajoy & Dingemanse, 2017; Magellan & Magurran, 2007). Female characteristics could also affect the males' motivation for courtship, especially when female availability and/or variation in female quality are high (Edward & Chapman, 2011; Kokko & Johnstone, 2002). In this regard, increasing evidence shows functional roles of female traits by reflecting, among other factors, future maternal investment, body condition, immunological capacity, dominance or fighting ability (Amundsen, 2000; Clutton-Brock, 2007, 2009; Edward & Chapman, 2011; Morales et al., 2014; Potti et al., 2013; Potti & Merino, 1996). If certain traits of females signal their phenotypic or genetic quality, males are expected to exercise mate choice and adjust their courtship activity accordingly, as this would increase the chances of mating with females of high reproductive potential (Amundsen, 2000; Edward & Chapman, 2011; Kokko & Johnstone, 2002; Kraaijeveld et al., 2007). Given that plasticity in the expression of sexual signals may affect signal reliability and the strength of sexual selection on them, understanding within- and between-individual sources of courtship variation is essential for assessing its evolutionary potential (Griffith & Sheldon, 2001; Réale et al., 2007; Wolf & Weissing, 2012).

Here, we empirically investigated the within- and between-individual variation in male courtship using the collared flycatcher, *Ficedula albicollis*, as a model species. We performed a set of behavioural tests in which different stimulus females were presented to focal males, thus simulating female visits to the male's territory during mate choice. Our focal behaviour was invitation latency, that is, the time elapsed between the focal male detecting the stimulus female in his territory and explicitly inviting her to visit the nestbox by landing on the entrance hole (see *Methods*). Invitation latency was thus used as a proxy for a male's motivation to mate. Repeated measures of males (exposed to different stimulus females) and stimulus females (presented to different males) allowed us to investigate the relative importance of both male and female identity and their phenotype on invitation latency as well as other potential sources of within-individual variation in this behaviour (e.g. the effect of the season advance). Based on previous work on other species examining the role of male and female identity as well as the context dependence in courtship behaviour (Dougherty, 2021; Godin & Auld, 2013; e.g.; Lehtonen et al., 2011) and studies on the collared flycatcher (see *Study species*), we formulated the following predictions. First, we predicted significant between-individual variation in invitation latency, suggesting that this courtship behaviour is an individual-specific attribute. To test the behavioural consistency of invitation latency, we estimated its repeatability, that is, the fraction of behavioural variation due to differences between individuals (Bell et al., 2009; Nakagawa &

Schielzeth, 2010). Second, we predicted that high-quality males (e.g. with more elaborate sexually selected traits) would consistently show higher levels of courtship in comparison to poor-quality males. However, two other scenarios are possible. As several females often visit male collared flycatchers during the pairing period, high-quality males could display consistently low levels of courtship if they perceive that their attraction ability is superior and courtship activity constrains other behaviours and/or activities. Alternatively, low-quality males, whose probability of mating is lower, might consistently express a more determined courtship strategy. Third, we expected the expression of courtship behaviour to be sensitive to female identity and affected by traits indicative of female quality (see below), so that high-quality females will elicit a higher response from courting males compared to low-quality females. Finally, we also expected temporal (due to the advance of the breeding season) and environmental (due to breeding territory replacement) variation to influence the expression of courtship behaviours by affecting available resources and/or patterns of resource allocation. In particular, we expected males to invest more effort in courtship as the season progresses due to the increased risk of failing to mate. We also predicted that males that lose/change the territory will have to engage in further disputes to acquire a new territory, negatively affecting their investment in courtship.

METHODS

Study Species

The collared flycatcher is a small (ca. 13 g), insectivorous passerine which is sexually dichromatic (males show a predominantly black and white plumage during the reproductive period compared to greyish-brown females). It exhibits long-distance migrations and breeds in deciduous forests in Central Europe (Cramp & Perrins, 1994). After spring migration (mid-April), males establish a territory around a nest hole (Cramp & Perrins, 1994). Males defend their nesting site by aggressive interactions against intruding individuals (Garamszegi et al., 2006) and try to attract females by singing. When a prospecting female visits the surroundings of an unpaired male's nestbox, the male stops singing and performs conspicuous courtship displays involving calls and excited flights around the nestbox with repeated landings on its top and entrance hole. Females arrive at the breeding area about a week later than males and usually visit several nesting sites that males have occupied before mating (Cramp & Perrins, 1994).

Several phenotypic traits, including body size, age, white wing patch size (WPS) and white forehead patch size (FPS; only expressed in males) are indicative of individual quality and influence success in mating and intrasexual contexts in the collared flycatcher (e.g. Björklund & Gustafsson, 2017; Garamszegi et al., 2006; Gustafsson et al., 1995; Hegyi, Garamszegi, et al., 2008; Hegyi, Rosivall, et al., 2008; Laczi et al., 2013; Mitrus, 2005; Qvarnström, 1997; Qvarnström et al., 2006; Török et al., 2003). These aspects make the collared flycatcher a suitable model species to empirically investigate intrinsic and extrinsic determinants of courtship variation within and between males.

Study Population and Experimental Procedures

Data were obtained between 2007 and 2019 from a population of collared flycatchers breeding in the Pilis Mountains (47°43'N, 19°01'E), Hungary. The study population is located in an unmanaged, oak-dominated forest within the protected area of the Duna-Ipoly National Park and consists of ca. 800 nestboxes, mainly occupied by collared flycatchers. Each breeding season (April–June), the

reproductive performance of collared flycatchers is intensively monitored as part of a long-term study initiated in 1982 (Török & Tóth, 1988).

During the breeding season, we conducted intensive daily monitoring of the study area (returning to the same location several times a day) to ascertain the arrival date of males from their wintering site. When a male was located holding a nestbox (i.e. settled and singing in its immediate vicinity), we measured his courtship behaviour by presenting a live stimulus female placed in a wire cage (20 × 15 cm and 15 cm high) on top of the nestbox. In this species, singing activity ceases (almost) completely after mating, so we were sure that focal males were unpaired. When we placed the cage with the stimulus female on the nestbox, males typically stopped singing and flew away. When they returned a few (<5) minutes later to the vicinity of the nestbox, they immediately noticed the presence of the female. Our focal behavioural trait was the time elapsed between the moment the focal male detected the stimulus female (when the male perched on a nearby branch and stared at the female) and the first landing on the entrance hole of the nestbox (invitation latency), which constitutes an explicit invitation for the female to visit the nestbox (see Garamszegi et al., 2012). It is reasonable to assume that our ability to detect the focal male within the territory and start the measurements is not related to the phenotypic traits of either the focal male or the stimulus female; therefore, we are confident that our procedures prevented any substantial bias in the results. We recorded the behaviour of males for 5 min, beyond which male interest in the stimulus female was assumed to be low, and invitation latency was assigned 301 s. This threshold was based on previous work in the study population (Garamszegi et al., 2006, 2012), in which males not responding aggressively to stimulus males or a novel object in the first 5 min did not show any response thereafter.

Stimulus females ($N = 65$) were captured when building their nests in plots far away from the experimental plots and were therefore likely to be unfamiliar with the focal males. Females were randomly assigned to the focal males during the behavioural tests in such a way that (1) the same female was used in several tests (mean $\pm$ SD = 9.2 ± 7) as a stimulus individual for different males and (2) different stimulus females were assigned to repeated tests of the same focal male (see Results). As a result, stimulus females were kept in captivity for several days (mean $\pm$ SD = 4.4 ± 3.8) and, during that period, were supplied with mealworms and drinking water ad libitum. Before releasing the birds at the site of capture, we verified that they were in optimal condition. It is possible that the natural behaviour of females was somewhat altered by being caged. However, this issue is unlikely to affect the main conclusions of this work, as (1) females could acclimatize to the situation as they were kept in captivity for a few hours to a few days, (2) the same standard protocol was used for all behavioural tests and (3) sample size was high ($N = 65$ females) and potential confounding factors (e.g. time in captivity and date of the first trial) were considered in the models (or in preliminary analyses confirming their lack of effect).

Males were caught after the behavioural test and individually marked on their belly with unique combinations of three colours using waterproof pens. If an already measured male was identified singing in a territory a few days after the first behavioural test, we conducted a new behavioural test (using a different stimulus female) to obtain repeated measurements for the courtship behaviour. Behavioural tests were conducted in good weather conditions during the most active period of individuals (between 0500 and 1200 hours) and the observers hid 25–30 m from the focal nestbox. In total, we conducted 633 behavioural tests on 434 different males, of which 140 were tested repeatedly (mean $\pm$ SD = 2.68 ± 0.99).

Standardized ringing protocols and measurements were carried out for all captured individuals. Body mass was measured with a spring balance (± 0.1 g) and tarsus length (as a proxy of body size) was measured with a calliper (± 0.1 mm). FPS in males (the trait was not measured in females as a large fraction of individuals does not express this patch in the study population; Hegyi et al., 2002) was estimated as the product of the largest width and the largest height of the patch (measured with a calliper; ± 0.1 mm). In both sexes, WPS was the sum of the length of white bars between the fourth and eighth primaries, measured from the tip of the coverts. Given that the expression of WPS changes from yearling to adult plumage in males (Török et al., 2003), we standardized WPS across age categories (first year old, hereafter yearling or older) bringing the age classes to a common mean of 0 and standard deviation of 1. The exact age of many individuals was known because all nestlings were ringed before fledging and because of the high natal philopatry of the species (Kónczy et al., 1992; e.g. Pärt, 1990, 1991). Unringed individuals first captured as adults were aged (all males and, when possible, females) as yearlings or older based on plumage traits (Svensson, 1992).

Statistical Analyses

We were able to repeatedly measure the behaviour of some males within the same breeding season. Thus, during analyses, we used two different data sets: one containing only the information of the subset of individuals with repeated data on invitation latency (repeated individual data set, hereafter) as well as one containing the first (if several) behavioural tests of each individual (first test data set, hereafter). The latter data set thus contains the information of individuals tested only once and the first test of individuals with repeated measures of invitation latency.

Before investigating the determinants of latency (s) to land on the nestbox entrance during the courtship, we first checked whether latency differed between the group of males tested once and the group of males tested multiple times within a breeding season. We fitted a linear mixed model (LMM; using the first test data set) including invitation latency as the dependent variable, while as fixed effects, we included the following traits relative to males: whether the male had been tested several times (yes/no) as well as age (two-level class variable: yearling versus older), WPS (standardized by age; see above), FPS, mass, tarsus length and the year of the behavioural test (to account for environmental heterogeneity). In addition, the identity of the stimulus females was included as a random effect. This model yielded no significant differences between the two male groups (i.e. tested once and tested multiple times; $\chi^2 = 3.07$, $P = 0.08$), indicating that individuals with repeated data were not a skewed subset of individuals in respect of the focal behaviour, i.e. between-individual differences in detectability are not strongly associated with differences in invitation latency, and, therefore, further analyses are not biased.

To investigate the factors affecting male willingness to court females, we used LMMs and the repeated individual data set (i.e. including males repeatedly exposed to different females, which in turn were used as a stimulus several times for different males; see above). As a response variable, we included invitation latency, while we considered age (yearling versus older), body mass, tarsus length and WPS of both focal males and stimulus females as well as the male FPS (as only a small fraction of females expresses this trait; see above) as fixed effects. In the model, we also included the year of the behavioural test, the order number of the test (standardized by year; to account for behavioural changes over time due to, for example, acclimation and/or learning) as well as the date of the first

behavioural test for each individual (standardized by year) as covariates. The latter variable was included because the number of unpaired females decreases throughout the season and breeding date is a strong determinant of reproductive success in the species (e.g. Garamszegi et al., 2004; Qvarnström et al., 2005). Thus, male invitation latency is expected to decrease over the season. As random effects, we included the identity of the male and of the stimulus female to account for repeated measures of individuals. The inclusion of the male ID allowed us to investigate the repeatability (R) of the response of the same males to different females. Similarly, the inclusion of female ID allowed us to investigate the variance in invitation latency explained by females, i.e. to quantify the repeatability of the response of different males induced by the same female, which potentially represents the degree of male preference for certain females. When estimating the repeatability of the response of different males to the same females (random effect: female ID), we repeated the model above using the data set containing only the first test of each individual (therefore, male ID was not included as a random effect), but results remained qualitatively unchanged (see Table A1).

Some males ($N = 52$) with multiple measurements within the same year successively changed nestboxes across behavioural tests during the study. Thus, we investigated whether the repeatability of the response of males to different females (random effect: male ID) as well as the repeatability of the different males' response caused by the same female (random effect: female ID) differed between those focal males that changed or those that retained their territory across tests. To this end, we fitted two additional models on invitation latency, but the data were restricted to contain only either those males that remained in the same territory during all behavioural tests ($N_{\text{obs}} = 129$; $N_{\text{Males}} = 62$; $N_{\text{Females}} = 38$) or those males that changed the territory across behavioural tests ($N_{\text{obs}} = 105$; $N_{\text{Males}} = 52$; $N_{\text{Females}} = 33$; results were qualitatively similar when considering males that did not always change/remain in the territory between tests; not shown). Specifically, these two models contained invitation latency as a response variable, while as fixed effects, we included age, mass, tarsus length and WPS of both focal males and stimulus females, the male FPS as well as the year of the behavioural test, the trial number and the date of the first behavioural test for each individual. In addition, male and female identities were included as random factors. Exploratory analyses showed that individuals that changed territory or retained territory did not differ in their phenotypic traits reflecting individual quality (all $P > 0.3$). This result suggests that possible differences in their courtship behaviour are not driven by innate differences between males, but rather the changes in their socioecological environment.

Before interpreting any model outcome, we systematically performed several model diagnostic statistics (e.g. checking the distribution of residuals, effect of influential data points, existence of multicollinearity) to avoid misleading results due to statistical artefacts. Based on these diagnostics, invitation latency was log transformed. After transformation, although invitation latency was truncated (301 s; see above), diagnostic statistics did not indicate obvious deviation from the assumptions of linear models.

Statistical analyses were performed in R version 3.6.2 (R Core Team, 2019). For the mixed modelling, we used the package lme4 (Bates et al., 2014). Significance of the fixed effects in the models was calculated with Type II tests using the function Anova in the car package (Fox & Weisberg, 2011). In LMMs, significance of fixed effects was calculated on maximum likelihood models, while parameter estimates were extracted from restricted maximum likelihood models (as suggested by Zuur et al., 2009, pp. 101–139). Repeatabilities (R) of invitation latency were analysed with the rpt function in the package rptR (Nakagawa & Schielzeth, 2010). We estimated adjusted repeatability (by including control variables

and effects of interests in the models; Nakagawa & Schielzeth, 2010), quantified its uncertainty (84% confidence intervals; as suggested by Julious, 2004; Payton et al., 2003) through parametric bootstrapping (1000 runs), and tested its statistical significance through likelihood ratio tests. The packages HLMdiag (Loy & Hofmann, 2014), and car (VIF function) were used for model diagnostics, and graphical figures were obtained using the sjPlot package (Lüdtke, 2020).

Ethical Note

All applicable international, national and/or institutional guidelines for the care and use of animals were followed and the study was approved by the ethical committee of the Eötvös Loránd University (no. TTK/2203/3). Housing conditions of decoy females, handling and behavioural assays were conducted in a way to minimize the welfare impact on the birds. The time required for these procedures was restricted to a minimum and all of them were carried out as cautiously and efficiently as possible. Permissions for the fieldwork were provided by the Middle-Danube-Valley Inspectorate for Environmental Protection, Nature Conservation and Water Management (numbers: KTVF 16360-2/2007, KTVF 30871-1/2008, KTVF 43355-1/2008, KTVF 45116-2/2011, KTVF 21664-3/2011, KTVF 12677-4/2012, KTVF 10949-8/2013, KTF 11978-5/2015, PEI/001/1053-6/2015, PE/EA/101-8/2018, PE-06/KTF/8550-4/2018 and PE-06/KTF/8550-5/2018).

RESULTS

The invitation latency to females during courtship decreased as the season progressed, indicating that the male willingness to mate increased along the breeding season (Fig. 1, Table 1). Invitation latency, however, was not consistently associated with any of the measured traits of the focal males or the stimulus females (Table 1). Specifically, the latency of invitation increased with male WPS when using the subset of males tested repeatedly (Table 1). However, this relationship disappeared both when we restricted the analysis to those males that either changed or retained their territory across behavioural tests and when we included a single measure of latency per male in the analysis (i.e. first test data set; Appendix Table A1).

Latency of invitation showed moderate repeatability according to male ID ($R = 0.38$; Table 1), whereas female ID explained a low fraction of variance in male courtship behaviour ($R = 0.07$; Table 1). The variance in invitation latency explained by male and female ID

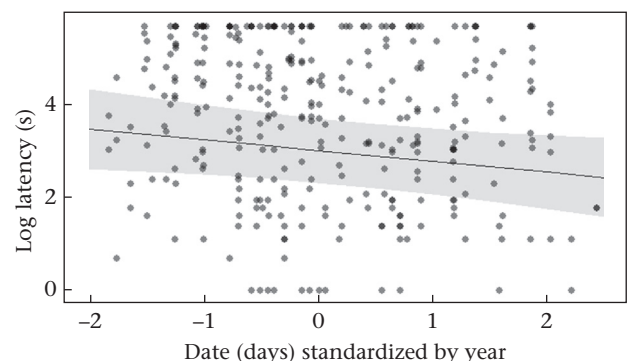


Figure 1. The relationship between log-transformed latency (s) of collared flycatcher males to land on the nestbox entrance hole during a simulated female visit and the calendar date (standardized by year) of the first behavioural test (if multiple tests per male were conducted). Predicted values (line) and confidence intervals (grey area) for latency at each value of the first test date are shown ($N = 148$).

Table 1

Results of a linear mixed model testing the relationship between invitation latency (s) of collared flycatcher males to land on the entrance hole of the nestbox during a simulated female visit and the traits of the focal male and stimulus female

Fixed effects	β	SE	df	Type II Wald χ^2	P
Intercept	11.09	7.036	—	—	—
Year	—	—	8	6.568	0.584
2011	0.573	0.641	—	—	—
2013	0.596	0.497	—	—	—
2014	0.732	0.619	—	—	—
2015	0.739	0.531	—	—	—
2016	0.209	0.508	—	—	—
2017	1.154	0.954	—	—	—
2018	0.967	0.57	—	—	—
2019	0.464	0.626	—	—	—
Date of first test	−0.231	0.126	1	3.993	0.046
Order of test	0.192	0.107	1	2.958	0.085
Male age	0.483	0.28	1	3.536	0.06
Male mass	−0.029	0.024	1	1.45	0.228
Male tarsus	−0.017	0.025	1	0.432	0.511
Male FPS	0.001	0.001	1	0.164	0.686
Male WPS ¹	0.234	0.113	1	4.419	0.036
Female age	0.037	0.298	1	0.062	0.803
Female mass	−0.022	0.016	1	2.231	0.135
Female tarsus	0.004	0.028	1	0.027	0.871
Female WPS	0.001	0.002	1	0.438	0.508
Random effects ^{2,3}	σ^2	R	SE	CI	P
MaleID	1.047	0.382	0.063	0.327–0.507	<0.001
FemaleID	0.194	0.071	0.047	0.015–0.149	0.04
Residual	1.5				

The model was fitted using the data set containing individuals with repeated measures of latency and stimulus females were used several times in different behavioural tests ($N_{\text{obs}} = 330$; $N_{\text{Males}} = 148$; $N_{\text{Females}} = 43$). Parameter estimates and SE were calculated using REML models. Repeatabilities (estimated according to Nakagawa & Schielzeth, 2010), their P values (based on 1000 permutations) and 84% confidence intervals (CI) are shown. Forehead patch size (FPS, only males), wing patch size (WPS), age (two-level class variable: yearlings versus adults), date of the first test for each individual standardized by year (date of first test) and the order number of the test (order of test) are considered in the model. See main text for further details.

¹ The significance of the male WPS vanished both when considering a single measure of invitation latency per male and when analysing the behaviour of these males according to whether they changed/ remained in the same territory between behavioural tests. See Table A1 and main text for further details.

² Random effects obtained by restricting the data set to males that remained in the same nestbox (territory) across behavioural tests ($N_{\text{obs}} = 129$; $N_{\text{Males}} = 62$; $N_{\text{Females}} = 38$) were: MaleID: $\sigma^2 = 1.238$, $R = 0.479$, $SE = 0.096$, 84% CI = 0.402–0.676, $P < 0.001$; FemaleID: $\sigma^2 = 0$, $R = 0$, $SE = 0.067$, 84% CI = 0–0.168, $P = 1$; Residual: $\sigma^2 = 1.346$.

³ Random effects obtained by restricting the data set to males that changed nestbox (territory) across behavioural tests ($N_{\text{obs}} = 105$; $N_{\text{Males}} = 52$; $N_{\text{Females}} = 33$) were: MaleID: $\sigma^2 = 0.597$, $R = 0.221$, $SE = 0.128$, 84% CI = 0.158–0.512, $P = 0.061$; FemaleID: $\sigma^2 = 0.474$, $R = 0.176$, $SE = 0.136$, 84% CI = 0.038–0.433, $P = 0.083$; Residual: $\sigma^2 = 1.623$.

differed between males that retained and males that changed their territory, suggesting a role of the territory in the within-individual variation in behaviour during courtship. However, the uncertainty of the repeatability estimates was high, and their confidence intervals overlapped, indicating that none of these estimates differed statistically (Table 1, Fig. 2).

DISCUSSION

We have empirically shown through simulated female visits that courtship, measured as the male's latency to explicitly invite the female to visit the nestbox, varied consistently between males in collared flycatchers. At the same time, males showed certain variation in their invitation latency based on female identity, which is indicative of male mate choice. However, contrary to our predictions, none of the analysed traits in males and females mediated

this variation in courtship. Courtship behaviour was also responsive to environmental contexts as latency to land decreased within males with the advance of the breeding season. The latter is, to our knowledge, the first evidence of seasonal variation in courtship behaviour (Dougherty, 2021).

Invitation latency was consistent within males across behavioural tests, indicating that males display similar levels of courtship to different females (whether or not males were influenced by other potential receivers in the surroundings; Fisher & Rosenthal, 2007). A possible explanation is that invitation latency is directly related to the male's perception of their own quality in the study species. Since several females often visit male collared flycatchers during the breeding season, it is possible that high-quality males consistently express high latency values irrespective of female quality. In contrast, low-quality males for whom the probability of remaining unmated is higher might consistently express a more purposeful courtship strategy (low latency values) than high-quality male. However, contrary to this possibility, we did not find any trait in males that influenced their courtship behaviour (see below). Regardless of the underlying mechanisms, our results suggest that invitation latency is an individual-specific attribute, as is the case for other courtship components in a variety of taxa (Bell et al., 2009; Dougherty, 2021; Godin & Auld, 2013; Lehtonen et al., 2011), and is therefore expected to be subject to selection.

Whereas males behaved similarly in successive behavioural tests, the moderate levels of repeatability indicate that there is within-individual variation in behaviour (due to either intentional plastic adjustment or external causes beyond the male's control; Dougherty, 2021) across different situations. In this regard, female identity is expected to be an important modulator of the within-individual expression of courtship display when there is variation in female quality, when male reproductive investment is relatively high (e.g. associated with the acquisition of territories, mate guarding, parental care) or when the opportunity to mate with additional females is limited (Edward & Chapman, 2011; Kokko & Johnstone, 2002), as occurs in our study species (e.g. Garamszegi et al., 2004; Hegyi, Garamszegi, et al., 2008; Hegyi, Rosivall, et al., 2008; Laczi et al., 2013; Mitrus, 2005; Qvarnström, 1997). Accordingly, we found an effect, albeit small, of female identity on invitation latency, indicating that males adjusted their courtship behaviour based on perceived differences between the females to which they were exposed and, therefore, that male mate preferences may be in effect at some degree in the study species. Male preference for females may be related to body size, ornamentation or age, which can function as signals for direct (e.g. fecundity) and/or indirect (genetic) fitness benefits and thereby incentivize males to increase their courtship intensity for particular females (Amundsen, 2000; Clutton-Brock, 2009; Edward & Chapman, 2011; Potti et al., 2013). However, we did not find any female traits that influenced within-individual variation in courtship (discussed below).

The socioecological conditions of the breeding environment are expected to be another important source of within-individual variation in courtship display. Familiarity with the territory and its neighbourhood may allow efficient foraging and/or reduce agonistic contests (Beletsky & Orans, 1989; Krebs, 1982), with subsequent consequences for energetic costs and behavioural plasticity. This mechanism can be particularly relevant to philopatric, protandrous species like the collared flycatcher. It is also possible that investment asymmetries between males that are able to maintain a single territory and those that need to acquire several territories before breeding generate differences in within-individual consistency in invitation latency via trade-offs (Sterns, 1992). We found that within-individual consistency in latency decreased, while the variance in male behaviour explained by female ID increased for individuals that changed territory between tests. However, the uncertainty estimates

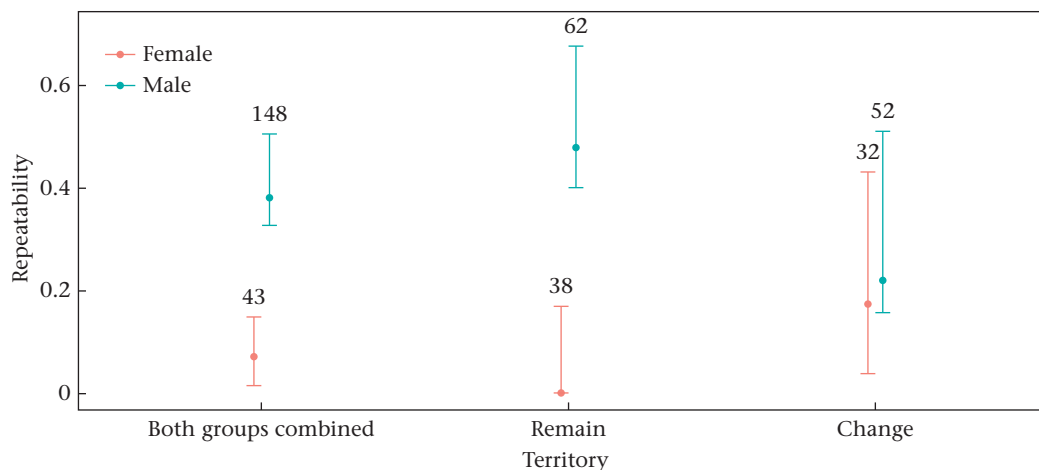


Figure 2. Repeatability of latency of collared flycatcher males to land on the nestbox entrance hole during a simulated female visit in relation to male identity and female identity. Mean estimates are shown for males that remained in the same territory across successive tests, that changed territory across successive tests and for both groups combined (note that the latter group also include males that did not always change/remain in the territory between tests). The 84% confidence intervals are shown; nonoverlapping 84% confidence intervals indicate significant differences between group repeatability estimates (equivalent to *z* tests at the 0.05 level). The numbers above bars are sample sizes.

of the repeatabilities between different contexts (changing/remaining in the territory) overlapped, indicating that they do not differ statistically (Fig. 2). Therefore, we could not find strong evidence for the idea that territory familiarity and/or the costs associated with acquiring several territories before mating affect within-individual consistency in male courtship.

Invitation latency was negatively related to the date of the behavioural test, which suggests that male responsiveness increases as the season advances. While several studies have examined mate choice variation over the breeding season, to our knowledge, this is the first evidence of seasonal variation in courtship response (Dougherty, 2021). In seasonally breeding birds, the number and quality of available females typically decrease and conditions for successful breeding deteriorate (e.g. suboptimal food supply, less time for moult before winter migration) as the season progresses (e.g. Barta et al., 2008; B  ty et al., 2003; Canal et al., 2012; Gr  nst  l et al., 2003; Lozano et al., 1996; Smith & Moore, 2005; Thomas, 2001 and references therein). Consequently, a plausible explanation for the detected seasonal pattern is that males increased their interest in courtship regardless of female quality. This is because, later in the breeding season, the costs of delaying breeding and the risk of missing a breeding opportunity outweigh the costs of pairing with a less ideal female (Ferretti & Winkler, 2009; Rowe et al., 1994; Slagsvold et al., 1988). The quality of courting males could also contribute to this pattern as, in seasonal species including collared flycatchers, males courting (thus breeding) late in the season are usually of lower quality, as indicated by the phenotype (in our study lower mass; see Table A2) compared to early courting (breeding) individuals.

Although male courtship behaviour was repeatable and sensitive to some extent to female ID, none of the male or female traits analysed, which are indicative of individual quality in the study species (e.g. Hegyi, Garamszegi, et al., 2008; Hegyi, Rosivall, et al., 2008; Laczi et al., 2013; Mitrus, 2005), predicted latency to invite the female to visit the nestbox. Our findings, therefore, contrast with other work in a number of taxa showing a relationship between male traits and courtship behaviours (Kraaijeveld et al., 2007) and/or male preference for certain female qualities such as age or plumage characteristics (Edward & Chapman, 2011; Griggio et al., 2005; Kraaijeveld et al., 2007 and references therein). At least three mutually non-exclusive scenarios can explain the lack of relationship between invitation latency and phenotypic traits of either males or females. First,

the effects of the analysed traits may be too small to be detected with the sample sizes used in this study. However, we consider this unlikely, as we used a large data set ($N = 633$ tests on 434 different males and 65 stimulus females) and the parameter estimates for some variables (e.g. body mass or tarsus length) are of opposite sign to that initially expected. Second, courtship may be influenced by other nonmeasured traits, such as song-related characteristics, aggressiveness, parasite load or ultraviolet components of the plumage (e.g. Kraaijeveld et al., 2007; Simpson & McGraw, 2019; Soma & Garamszegi, 2015), acting either independently or complementarily (Candolin, 2003; Mitoyen et al., 2019). Third, mate preferences may be context dependent and vary between individuals (e.g. according to the breeding contexts experienced) and thus fluctuate markedly in space and/or time (Cotton et al., 2006), hampering the identification of traits that affect courtship.

Overall, we have shown that latency to invite the female to visit the nestbox during courtship is an individual-specific attribute. Although repeatable, this courtship behaviour was also sensitive to the identity of the stimulus female, with some females eliciting systematically higher interest among males than others. We also observed that male responsiveness to females increased as the season progressed, but we failed to identify the individual traits that mediate male variation in courtship. Future studies with a broader focus on male and female traits (e.g. including coloration or other behavioural traits, see Siitari et al., 2002) combined with experimental approaches are needed to identify the determinants of courtship behaviour in this and other species.

Author Contributions

D.C. and L.Z.G. designed the study. All authors except D.C. collected the data. D.C. performed statistical analyses with inputs from L.Z.G. drafted the first version of the manuscript. All authors contributed to later versions of the manuscript.

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Appendix

Table A1

Results of a linear mixed model testing the relationship between latency to land on the hole of the nestbox (s) and the traits of the focal male and stimulus female

Fixed effects	β	SE	df	Type II Wald χ^2	P
Intercept	7.8	5.454			
Year			10	15.739	0.107
2009	−0.39	0.547	—	—	—
2010	−0.879	0.58	—	—	—
2011	−0.561	0.572	—	—	—
2013	−0.244	0.508	—	—	—
2014	−0.009	0.53	—	—	—
2015	0.133	0.533	—	—	—
2016	0.238	0.537	—	—	—
2017	0.039	0.768	—	—	—
2018	0.423	0.564	—	—	—
2019	0.15	0.565	—	—	—
Date first test	−0.297	0.098	1	9.694	<0.001
Male age (binary)	0.148	0.214	1	0.477	0.49
Male mass	−0.022	0.017	1	1.938	0.164
Male tarsus length	0.025	0.019	1	2.004	0.157
Male FPS	0	0	1	0.248	0.619
Male WPS	−0.006	0.093	1	0.009	0.926
Female age (binary)	0.307	0.259	1	1.706	0.191
Female mass	−0.006	0.014	1	0.151	0.697
Female tarsus length	−0.027	0.024	1	1.523	0.217
Female WPS	0	0.002	1	0.005	0.946
Random effects	σ^2	R	SE	CI	P
FemaleID	0.06173	0.025	0.043	0–0.147	1
Residual	2.44893				

The model was fitted using the data set containing only the first test (if several) of each male (therefore, male identity is not considered as a random factor). Stimulus females were used several times in different tests ($N_{\text{obs}} = 321$; $N_{\text{females}} = 57$). Parameter estimates and SE were calculated using REML models. Repeatabilities (estimated according to Nakagawa & Schielzeth, 2010), their P values (based on 1000 permutations) and 84% confidence intervals (CI) are shown. FPS = forehead patch size; WPS = wing patch size; age = two-level class variable (yearlings versus adults). See main text for further details.

Table A2

Results of a linear model testing the relationship between the date of the first behavioural test and the traits of the focal male

Fixed effects	β	SE	F	P
Intercept	6.705	1.999		
Year			0.758	0.682
2009	0.000	0.294		
2010	0.252	0.322		
2011	−0.109	0.300		
2012	0.429	0.504		
2013	−0.336	0.292		
2014	−0.243	0.301		
2015	−0.008	0.288		
2016	−0.199	0.303		
2017	−0.319	0.406		
2018	−0.013	0.285		
2019	−0.069	0.297		
Male WPS	0.029	0.056	0.264	0.608
Male age	−0.177	0.129	1.898	0.169
Male mass	−0.025	0.010	5.638	0.018
Male FPS	0.000	0.000	1.490	0.223
Male tarsus	−0.017	0.011	2.387	0.123

The rationale was to test whether males courting early in the season differ in quality, as indicated by their phenotype, relative to males courting late in the season. The model ($N_{\text{obs}} = 332$) was fitted using the data set containing only the first test (if several) of each male (therefore, male identity is not considered as a random factor). Parameter estimates and SE were calculated using REML models. FPS = forehead patch size; WPS = wing patch size; age = two-level class variable (yearlings versus adults). See main text for further details.