

## Sex-dependent risk-taking behaviour towards different predatory stimuli in the collared flycatcher

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### ABSTRACT

Prey animals may react differently to predators, which can thus raise plasticity in risk-taking behaviour. We assessed the behavioural responses of nestling-feeding collared flycatcher (*Ficedula albicollis*) parents towards different avian predator species (Eurasian sparrowhawk, long-eared owl) and a non-threatening songbird (song thrush) by measuring the latency to resume feeding activity. We found that the sexes differed in their responses towards the different stimuli, as males resumed nestling-provisioning sooner after the songbird than after the predator stimuli, while latency of females was not affected by the type of stimulus. Parents breeding later in the season took less risk than early breeders, and mean response also varied across the study years. We detected a considerable repeatability at the within-brood level across stimuli, and a correlation between the latency of parents attending the same nest, implying that they may adjust similarly their risk-taking behaviour to the brood value. Repeated measurements at the same brood suggested that risk-taking behaviour of flycatcher parents is a plastic trait, and sex-specific effects might be the result of sex-specific adjustments of behaviour to the perceived environmental challenge as exerted by different predators. Furthermore, the nest-specific effects highlighted that environmental effects can render consistently similar responses between the parents.

### 1. Introduction

Risk-taking behaviour specifies the way how an individual behaves in a life-threatening or in other risky situations (e.g. risk of parasite or disease transmission, Møller et al., 2013; fighting for resources, Behney et al., 2019; or encountering a threatening prey, Veselý et al., 2017). Similarly to other behavioural traits, risk-taking behaviour can be considered consistent when an individual shows similar behavioural responses in different temporal and environmental situations (Sih et al., 2004, 2012). In various species, a consistently bolder individual (i.e. taking more risk) can have higher reproductive success than its conspecifics, but due to higher risk of predation, it might have a shorter lifespan (Réale et al., 2000; Korhonen et al., 2001). Beside consistency, risk-taking behaviour can be also plastic at the within-individual level (Heynen et al., 2016; Jolles et al., 2019). When environmental conditions change rapidly, or at least over a shorter timescale than a lifetime, individuals that can show a reversible behav-

our change in response to that specific environmental change might incur a selective advantage (Dingemanse et al., 2009).

One common factor triggering plasticity in risk-taking behaviour of prey is the type and level of predation threat (Brown et al., 2005). When different types of predation (e.g. pursuit or ambush predation, ground or aerial predation) represent different levels of threat (along the low-high continuum), the prey has to be able to distinguish and categorise the threat and adjust its risk-taking behaviour accordingly (Palleroni et al., 2005; Courter and Ritchison, 2010; Strnad et al., 2012). In these situations, individuals that assess a given predation risk properly and subsequently adjust their reactions flexibly, rather than repeating the same behaviour, will have fitness advantages (Kleindorfer et al., 1996, 2005; Swaisgood et al., 1999), as they can save energy and time which, for example, could be spent later on foraging or parental care.

Most species face various forms of life-threatening situations during their lives induced by different predators. For hole-nesting passerines,

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one of the most vulnerable phases is the breeding season, when the parents are bound to the nest (Ricklefs, 1969; Martin, 1995). In altricial species, the nestlings are entirely dependent on their parents for provision and protection; thus, when exposed to a predator, the adults face a serious dilemma: either they defend their offspring or they ensure their own safety and future reproductive success. This situation describes a well-established trade-off between reproductive effort and survival (Trivers, 1972). Avian predators, in contrast to snakes and small mammals, usually impose risk only on the adults, as they cannot access the nestlings in the tree cavities. However, they have an indirect effect on the nestlings, because if the parents suspend their parental care in the suspected presence of a predator, it reduces the nestlings' chance of survival (Mutzel et al., 2019). Those individuals that can categorise the different types of threat and adjust their reactions, can save energy and time by choosing the proper anti-predator behaviour as compared to those individuals that show the same behavioural pattern towards different predator stimuli (Mahr et al., 2015). This topic was investigated in several bird species experimentally (e.g. Duré Ruiz et al., 2017; Dahl and Ritchinson, 2018), but the results were contradictory, as individuals either differed in their responses towards the different predator stimuli, or they showed the same risk-taking behaviour regardless of the type of threat.

Sexes could differ in their roles and investments during the breeding season, independently of the environmental factors (Hogstad, 2005). In some species, the role of each sex is similar (Massoni et al., 2012; Wojczulanis-Jakubas et al., 2016), while in other species, sexes allocate parental care in a different manner (Paredes et al., 2006; Peralta-Sanchez et al., 2020). In passerines, it is common that females invest more energy in the current brood as they form, lay and incubate the eggs (Reid et al., 2002; Tinbergen and Williams, 2002; Goulaud et al., 2018). The duty to feed the nestlings can also fall on females for the most part, as males have to defend their territories around the nest beside the provisioning of the offspring (Slack, 1976). Furthermore, unlike females, males cannot be absolutely sure about their parenthood, because there could be some nestlings within the brood that are fathered by other males due to extra-pair paternity (Lea, 1984). In addition, due to differences in feather colouration (Ekanayake et al., 2015; Møller et al., 2019), conspicuous motions or behaviours (e.g. singing behaviour, Ellison and Ydenberg, 2019), sexes might attract predators in different ways. Considering these potential sex-specific differences, the value of the current brood and the vulnerability against predation can differ between the sexes, which might actually create differences in risk-taking behaviour (Redondo, 1989; Fernández and Llambías, 2013).

The aim of the present study was to assess the risk-taking behaviour of the collared flycatcher (*Ficedula albicollis*) parents in different life-threatening contexts (as mimicked by the use of different predatory stimuli) during the breeding season. We predicted that the parents would generally react differently towards a predator and a non-predator model (i.e. individuals will take less risks when exposed to a predator than to a non-predator species). Based on the facts that nest defence behaviour differ between sexes in this species, as males are more aggressive than females (Krist, 2004); that males have elaborate feather colouration that has a higher potential to attract predators (Huhta et al., 1997); and that approximately 20–50 % of the broods contained extra-pair youngs, leaving males with uncertainty of their parenthood (Garamszegi and Møller, 2004; Rosivall et al., 2009), we hypothesised that sexes would differ in their observed responses towards the different models, because males would take less risk due to differences in the perceived value of the brood and threat level. We could repeat the behavioural tests at some nests by using two out of three different types of threat. Hence, we could statistically characterise the changes in individual behaviour among different contexts (i.e. when presenting different models), thus assessing individual plasticity in risk-taking un-

der the hypotheses that individual behaviour would vary between predator and non-predator stimuli, and between the two predator species due to differences in their hunting techniques and diet. For testing our predictions, we mimicked predatory threat by placing a stuffed model of the Eurasian sparrowhawk (*Accipiter nisus*) or the long-eared owl (*Asio otus*) near the flycatcher nests, while we used the song thrush (*Turdus philomelos*) as control. We varied these stimuli across tests in a random manner, and assessed risk-taking behaviour by measuring the latency to resume feeding activity.

## 2. Material and methods

### 2.1. Study area and model species

Our experiment was carried out in the Pilis Mountains, in Hungary (47°43'N, 19°01'E). The study area is a continuous, mainly oak-dominated woodland which was established in 1982 (Török and Tóth, 1988) to study hole-nesting passerines in the wild. The study area is managed and protected by the Duna-Ipoly National Park. There are approximately 800 nestboxes on the study plots, where our model species, the collared flycatcher breeds together with other small passerines, like the great tit (*Parus major*) and the blue tit (*Cyanistes caeruleus*). The collared flycatcher is a long-distance migratory bird, which arrives to the breeding site from Africa in the middle of April, and leaves in August for wintering (Cramp and Perrins, 1993). Usually, males arrive earlier to the breeding site and start singing to attract females in front of a few selected nestboxes. Females arrive later, and after the courtship period, they start building their nests by using dry leaves and grass. Females usually lay 4–8 (most frequently six) blue eggs and incubate them for 13–14 days (Török and Tóth, 1990), while males provide them food occasionally (Kötél et al., 2016). Both parents feed and take care of the nestlings equally (Szász et al., 2019) until the fledglings leave the nest at the age of 14–15 days. Males and females do not differ considerably in size, but they show sexual dichromatism in their feather colouration. During the breeding season, male flycatchers have black and white plumage that provides them with higher contrast against the green vegetation making easier for predators to detect them. In contrast, females with brown and white feather colouration might be less easily detected, but once detected females might be less able to escape a potential predator (Slagsvold et al., 1995).

### 2.2. Capturing and measuring procedures

In each experimental year, we aimed to capture all the breeding pairs in their nestboxes using spring traps during the nestling-rearing period, when the nestlings were 8–10 days old. Already in the capturing phase, based on certain criteria, we were able to choose the nestboxes where we would assess the risk-taking behaviour of the parents later on. We included a nestbox in the behavioural study, when we captured both parents, there were at least 5 nestlings, and no other experiment was conducted at the nestbox. And based on the experience during capturing phase, it was extremely rare that we caught two males at the same nestbox, thus we could be certain in the identity of the focal male. We did not include polygynous males in the tests, there was no overlap between the tested individuals in the two experimental years.

After capturing the parents, we measured various morphological traits to describe body size, condition and plumage characteristics. We measured in particular tarsus length reflecting body size using a calliper (with a precision of 0.1 mm), and body mass to estimate body condition using a Pesola spring balance (with a precision of 0.1 g). We could easily determine the age of males based on their feather colouration (Svensson, 1992; Török et al., 2003). The age of the females is hard to determine based on morphology, thus we were only able to determine the age of females (based on our long-term ringing records)

that already had rings. Before release, each individual received an individually numbered ring for long-term identification (if they were not ringed already).

### 2.3. Ethical note

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 (reference numbers: 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 (reference number: TTK/2203/3). No individual was harmed during our experiment, and the nestlings did not suffer any short-term consequences of the behavioural tests.

### 2.4. Behavioural assays

Two of us (KK and GM) performed the behavioural experiments during the nestling-feeding period in 2018 and 2019, when the nestlings were 10–12 days old. First tests representing the morning block were carried out between 8 and 12 AM, when we challenged the parents with a randomly assigned stimulus (that was also randomly varied between the observers). When the logistic constraints during the field season allowed, second tests were performed at certain nestboxes (see sample sizes in Table 1). In the afternoon block, the second tests started between 1 and 3 PM to collect repeated within-individual data from the same parents by using a different stimulus type. In these cases, minimum two hours were left between the two tests. In each test, we recorded data for both parents, because one individual's behaviour is not independent from its social mate's behaviour (Mänd et al., 2013). We always checked the chosen nests one day prior to the tests. Before presenting one of the stuffed model species to the parents, we ensured from a distance of 30 m (using binoculars) that they performed nestling-provisioning by repeatedly entering the nestbox with food items in their beaks. Then we set up the video camera 15–20 m from the nest, and we approached the nestbox to check the ratio of nestlings begging for food (i.e. the proportion of nestlings opening their gaps) informing us about the overall hunger level of the brood. When the hunger level was low in the brood (i.e. less than half of the nestlings were begging for food), we placed one of the stimuli on the top of the

**Table 1**

The three-column matrix shows sample sizes for the different pair-wise combinations of the stuffed model species that were used to obtain within-nest/individual repeats (29 nests).

		Number of pair-wise combinations in repeated tests		
		First test		
Stimulus		Song thrush	Long-eared owl	Eurasian sparrowhawk
	Second test			
Song thrush		0	4	5
Long-eared owl		3	4*	5
Eurasian sparrowhawk		3	5	0

\* Cases when we used the same stuffed model in the first and second tests, which were not included in the statistical models for within-individual analyses testing for responses towards different stimuli.

nestbox, and we left the surrounding area of the nestbox immediately. When the hunger level was high, we did not proceed with the experiment for ethical reasons. We did not include the hunger level in the models because the nestlings' hunger level was low with almost zero variance ( $V_{2018} = 0$ ;  $V_{2019} = 0.05$ ) in both experimental years.

After putting one of the stuffed model species on the top of the nestbox, we hid approximately 30 m from the nestbox, and estimated the occurrence of alarm calls and the closest approach distance of the parents to the stimulus by using rough approximate scales. These data were used only to verify that the treatment was effective in both sexes, but were judged unsuitable to test our main predictions given the limitations of these variables in terms of both quality and quantity. After being assured that both parents had seen the model species (which always occurred within 15 min), we removed the stimulus as fast as possible with the least disturbance. While retreating from the area, we started to video record the nestbox for at least 45 min. Based on our experience from a pilot study in 2017, this time interval is sufficient for the parents to return and enter the nestbox again. The average duration of the recordings was  $55.4 \pm 3.8$  min, and the variance above the 45-minute threshold was merely caused by field constraints. With this strict protocol, both experimenters followed the same standardised experimental steps and minimised the disturbance around the nestboxes (see more about potential observers' effect below). There were only nine tests out of 125 in which only one parent was present during the exposure to the stimulus, and these tests were excluded from the subsequent analysis. We assessed the risk-taking behaviour of the parents by measuring their latency to resume feeding activity, which is the time difference between the removal of the stuffed model and the moment when parents entered the nestbox. Risk-taking behaviour and latency are inversely related, as risk-taker individuals should enter the nestbox earlier. The parents usually landed on the nestbox hole many times before actually entering, and several of them were seen doing so with food items in their beaks. The latency to approach the nest (i.e. landing on the entrance of the nestbox) strongly and positively correlated with the latency to resume feeding activity in case of both sexes (males:  $r = 0.703$ ,  $N = 116$ ; females:  $r = 0.798$ ,  $N = 116$ ). Some of the parents entered within a few minutes, while others needed more than half an hour to resume nestling-feeding activity. Irrespective of the treatment, it was random which sex entered the nestbox first ( $P = 0.289$ ). After every test we checked the nestlings, and we did not find any short-term negative effect of the experiment on their condition as reflected by the hunger level in the brood.

### 2.5. Description of the stuffed models

We chose two avian species, the Eurasian sparrowhawk and the long-eared owl, as our predator models because they elicit greater risk-taking response than snakes or small mammals, as they pose a threat directly to the parents. The sparrowhawk and the owl differ in their hunting strategies resulting in different selection pressures on their preys. The sparrowhawk is a specialised daytime predator of small birds in Europe that captures its preys in the air (Zawadzka and Zawadzki, 2001; Bujoczek and Ciach, 2009). Several studies investigated risk-taking behaviour with a predator model by using this species as a stimulus (Listøen et al., 2000; Beránková et al., 2014; Królikowska et al., 2016), thus our results can be easily compared to these studies. Conversely, the long-eared owl is mostly active during the night and at dawn (Svensson et al., 2009), and its diet is mainly composed of different mammalian species (Tome, 2009). Furthermore, when owls hunt small birds, they typically capture them on the ground or from low vegetation, where the prey is roosting at night (Charter et al., 2018). Given these attributes, the owl is unlikely to be the main predator of the flycatchers during the breeding season, because fly-

catchers forage only during day-time and do not spend the night on the ground. However, the owl also bears the typical raptorial features, such as the eyes, curved beak and talons (Scaife, 1976; Beránková et al., 2014), in addition to the characteristic feather colouration and patterns (Veselý et al., 2016), and it is known that the pied flycatcher (*Ficedula hypoleuca*) is a part of its diet (Glue, 1972). Therefore, we assumed that the owl also imposes at least some threat to the collared flycatchers, while the sparrowhawk embodies a more important selective factor on our focal species. We used a stuffed song thrush as the control model, since it lives in the same habitat as the flycatchers, and eats a wide range of invertebrates (Török, 1985), and supposedly do not represent a true predatory threat for the flycatchers. We considered the possibility that flycatcher parents would not consider the song thrush as a threat due to its importantly smaller body size compared to the sparrowhawk or the owl (Palleroni et al., 2005). However, based on the results of Beránková et al. (2015), which highlighted that prey probably combines raptor-specific features (e.g. eyes, hooked beak and claws with talons) and species-specific characteristics (e.g. body size, feather colouration) in the process of predator recognition, we inferred that body size effects are unlikely to raise considerable bias in the results.

## 2.6. Details about sample sizes

All together, we tested the risk-taking behaviour of the flycatcher parents at 90 different, independent nestboxes with at least one of the three stuffed model species during the two experimental years. Along our initial aims to characterise within-individual changes in behaviour, we could repeat the behavioural assay only at 32 nestboxes with another stuffed model type on the same day (Table 1). Given the logistic constraints as well as ethical considerations, we did not aim to use all three stuffed model species at the same nestbox. The same constraints together with unsuitable weather conditions also forced us to shift the balance between sample sizes at different levels towards a higher number of nests/individuals tested at the costs of reducing the number of the within-nest/individual repetitions. Therefore, the sample size for the within-individual repeats was limited. Overall, after removing some recordings due to camera failure or disturbance by other birds, we successfully obtained data for the first tests at 87 nests ( $N_{\text{thrush}} = 25$ ,  $N_{\text{owl}} = 32$ ,  $N_{\text{sparrowhawk}} = 30$ ) and for the repeated tests at 29 nests, which could be used in our analyses.

## 2.7. Statistical analyses

### 2.7.1. Analysis of risk-taking behaviour in general

In our analyses, we focused on the general relationship between latency to resume feeding activity and the type of predatory stimulus (model species), and we used linear mixed-effect models (LMMs) with random intercepts. As all individuals entered the nestbox within 45 min of observation, the distribution of latency values was not truncated. We used the  $\log_{10}$ -transformed latency values (sec) as a response variable in all statistical analyses to achieve the normal distribution of model residuals (that was generally checked for all models). We also assumed that the biological effects are more likely to operate on the log-scale (i.e. one unit of difference on the log-scale has the same biological meaning in both sides of the distribution), thus we also provided the figures and based our interpretations on the log-scale (Houle et al., 2011). The main model fitted to the whole data included the model species, the sex of the focal bird and their interaction, the order of the tests, the year and the standardised date of the tests (i.e. the number of days from the start of the given year, which separates early and late breeders from each other), the standardised time of the test on the day of observation, the observer, the number and age of the nestlings, and the adults' body mass and tarsus length as fixed predictors. We nested

the ring number (as individual ID) within the nestbox ID as random intercepts, because we had hierarchically structured data from the same nestbox (i.e. we collected data from the male and female in the same nestbox, and we also collected repeats from the same individuals in some cases). Although we initially considered including the age of the parents in the model, we discarded this potential predictor due to the lack of information on the age of females in many cases. However, we verified that there was no relationship between the age and the risk-taking decision during the nestling-rearing period in males ( $P = 0.556$ ) and females ( $P = 0.927$ , based on the available data), suggesting that the omission of age effect is unlikely to alter our results (see also Jablonszky et al., 2017 showing weak age effect on another estimate of risk-taking behaviour). We standardised the time of the test based on the order of the tests (i.e. separately within the morning and the afternoon blocks of experiments), because these two variables were highly correlated (i.e. the first tests were carried out always earlier in time, during the morning hours, while second tests were conducted in the afternoon). We used standardised body mass and tarsus length, which we calculated separately for each sex, and each experimental year. This standardisation was important because we collected data from different individuals in different years, and we intended to control for the differences originated from either social (e.g. ratio of juveniles) and/or environmental factors (e.g. quality and quantity of food resources, climatic conditions). We used likelihood ratio tests (LRT) to determine the level of significance (P-values) for each predictor by comparing models including and lacking the respective predictor. We did not perform model selection for the fixed effects, because basically, we were interested in the effect of the treatment while controlling for confounders. However, we note that if we excluded the non-significant terms from our models, the main results of the study, as presented below, did not change. We used the Tukey Honest Significant Difference test, as the post hoc test to confirm which groups were different from one another for each sex and treatment. For the Tukey's HSD test, we used only the feeding latency values of the first tests, as the observations should be independent within and between groups. We calculated between-individual repeatability of risk-taking behaviour across stimuli by dividing the respective between-individual variance component with the total variance (Lesells and Boag, 1987).

### 2.7.2. Analyses of sex-specific risk-taking behaviour

We also fitted LMMs separately for each sex to compare how the considered predictors mediate sex-specific response in risk-taking behaviour. The response variable was the  $\log_{10}$ -transformed feeding latency of either males or females. The statistical models included the same set of predictors as in the above model except for the sex and the interaction between sex and treatment, while we added the feeding latency of the pair as a fixed predictor. We included the ring number (as individual ID) as random factor because certain individuals were tested two times (while the nestbox ID level was not relevant anymore because only one individual per nest was represented in the underlying set of data).

Before interpreting the model outputs, we performed a series of model diagnostic tests to check whether all the necessary model assumptions were fulfilled by inspecting the distribution of the model residuals with q-q plots, checking the normality of the fixed effects and inspecting multicollinearity by calculating VIF (O'Brien, 2007). We also used Levene's test to check the homogeneity of variances.

### 2.7.3. Analyses of within-individual changes in risk-taking behaviour

The above LMM combines both between-individual and within-individual effects (van de Pol and Wright, 2009). To investigate within-individual effects further, we created subsets of data based on the sets of repeated measurements, in which we considered a particular combination of the treatments (long-eared owl/Eurasian sparrowhawk,

long

eared owl/song thrush, and Eurasian sparrowhawk/song thrush). Using these subsets, we built Markov Chain Monte Carlo Bayesian generalized linear mixed models (MCMCglmm) with random intercepts and slopes to characterise individual reaction norms (Hadfield, 2010), describing patterns of plastic within-individual changes in risk-taking behaviour towards different stimuli. All together, we created three models, where the response variable was the  $\log_{10}$ -transformed feeding latency and the predictor variable was the stuffed model species. We included the nestbox ID as random factor in the models. As the approach for the individual behavioural reaction norm requires (Dingemanse and Dochtermann, 2013), the predictor variable of the model species was linearised and centred by setting one particular treatment to  $-1$  and the other particular treatment to  $1$ . For the random part of the model, we considered uncorrelated random intercepts (defining individual differences in mean behaviour) and random slopes (defining individual differences in plasticity) grouped separately for each sex in the models. We defined priors necessary for the Bayesian modelling for the residual and random variance structure with inverse Wishart distribution. The parameter of the degree of freedom for the priors was equal to the number of response variables (Hadfield, 2010). The models ran for 1,100,000 iterations, with 100,000 samples discarded at the beginning and with a thinning interval of 1,000. We ran each model three times to ensure stability. Due to the small sample sizes, we could not include more predictor variables to control for their effects, and for simplicity, we avoided including correlated random effects. We analysed 25 repeated measurements reflecting pair-wise cases with different models (see particular combinations in Table 1). The distribution of all variables were checked visually, and also autocorrelation between iterations. In addition, we checked mixing and convergence with Gelman-Rubin statistics (Gelman and Rubin, 1992). Limited samples sizes for this approach to characterise reaction norms precludes powerful inferences about the effect of the estimated parameters (Martin et al., 2011; van de Pol, 2012). However, we could use the outputs of these models to check if the main results (as summarised in Table 2) are mediated by within-individual effects.

All statistical analyses were carried out in R statistical environment (R Development Core Team, 2015) using 'lme4' (Bates et al., 2015), 'lmerTest' (Kuznetsova et al., 2017) and 'MCMCglmm' packages (Hadfield, 2010).

### 3. Results

#### 3.1. General patterns emerging from the whole data

The results of the statistical model exploring the relationship between the type of stimuli and risk-taking behaviour of collared flycatcher parents, are shown in Table 2.

The LMM relying on the whole data indicated that the type of the presented stuffed model had an effect on the risk-taking behaviour of the flycatcher parents (LRT:  $P < 0.001$ ,  $\chi^2 = 18.464$ ). The result of the Tukey Honest Significant Difference test comparing the feeding latency values of the sexes showed that males and females significantly differed in their risk-taking behaviour in case of the long-eared owl (Fig. 1). Furthermore, the post hoc analysis also revealed that males showed statistically differentiable responses to the long-eared owl and the Eurasian sparrowhawk as compared to the song thrush, while females did not react in a different manner towards the stuffed models statistically.

The results of the LMM also showed a significant relationship between latency and the date of the test (Table 2), as individuals that started their breeding relatively late had higher latency values than individuals that started earlier (Fig. 2). Furthermore, we found a significant effect of the year on the estimated latency (LRT:  $P < 0.001$ ,

**Table 2**

The results of the linear mixed-effect model (LMM) estimating the relationship between  $\log_{10}$ -transformed feeding latency (sec) and the examined predictor variables: the treatment (stimulus: song thrush, long-eared owl and Eurasian sparrowhawk), the sex of the individual, the order of the tests, the year and the date of the experiment, the time of the test on the day of observation, the observer, the number and the age of the nestlings, the adults' tarsus length and body mass, and the interaction between the treatment and sex. The random factors in this model included the nestbox ID and the ring of the individuals in a nested design. P-values for the coefficients are based on Satterthwaite approximations of the degrees of freedom (P-values reflecting the significance of each categorical predictor variable based on LRT tests are given in the text). P values for the random effects are based on LRT. The abbreviations mean the following: ST = song thrush; LEO = long-eared owl; ESH = Eurasian sparrowhawk; M = male.  $N_{\text{all}} = 232$ .

Fixed effects	$\beta$	95 % CI	SE	t-value	P
treatment (ST)	0.648	-3.535, 4.826	2.222	0.292	0.771
treatment (LEO)	0.813	-3.403, 5.020	2.237	0.363	0.717
treatment (ESH)	1.107	-3.093, 5.299	2.230	0.497	0.621
sex (M)	-0.068	-0.348, 0.213	0.145	-0.470	0.639
order (2nd)	-0.129	-0.328, 0.067	0.103	-1.256	0.212
year (2019)	-0.564	-0.814, -0.315	0.132	-4.260	<0.001
date	0.030	0.006, 0.055	0.013	2.346	0.021
time	0.026	-0.073, 0.126	0.053	0.494	0.623
observer (2)	-0.094	-0.276, 0.088	0.096	-0.973	0.332
number of the nestlings	0.035	-0.094, 0.163	0.068	0.513	0.604
age of the nestlings	0.084	-0.111, 0.279	0.104	0.806	0.422
tarsus	0.024	-0.075, 0.123	0.052	0.461	0.646
mass	0.029	-0.067, 0.122	0.049	0.594	0.554
treatment (LEO) : sex (M)	0.402	0.025, 0.775	0.194	2.069	0.040
treatment (ESH) : sex (M)	0.038	-0.353, 0.427	0.202	0.189	0.851
Random effects		Variance	P		
nestbox ID		0.076	0.039		
nestbox ID/ring		0.005	0.916		
residual		0.352			

$\chi^2 = 17.045$ ), as in 2019 the latency values were much lower independently of the stimulus than in 2018 (Fig. 2).

The random part of the model showed that the variance of latency across nestboxes was 0.076 on the logarithmic scale, which corresponded to the 17.6 % of total variance reflecting the repeatability at the within-nest level (Table 2). The associated significance showed that this variance component was statistically different from zero. On the contrary, the variance of feeding latency across individuals was more than 10-fold lower, and the within-individual repeatability of the focal variable, as could be calculated from this variance component was only 1.16 %.

The results of the sex-specific linear mixed-effect models are shown in the Supplementary material, but were generally provided very similar results than the above model. For males (Table S1), we found that there was a significant difference in latency among the different model species (LRT:  $P = 0.001$ ,  $\chi^2 = 13.537$ ), indicating that males reacted differently towards the predator and non-predator stimuli, while there was no difference between the reaction towards the two predator models (Fig. 1). In contrast to males, we found no significant relationship

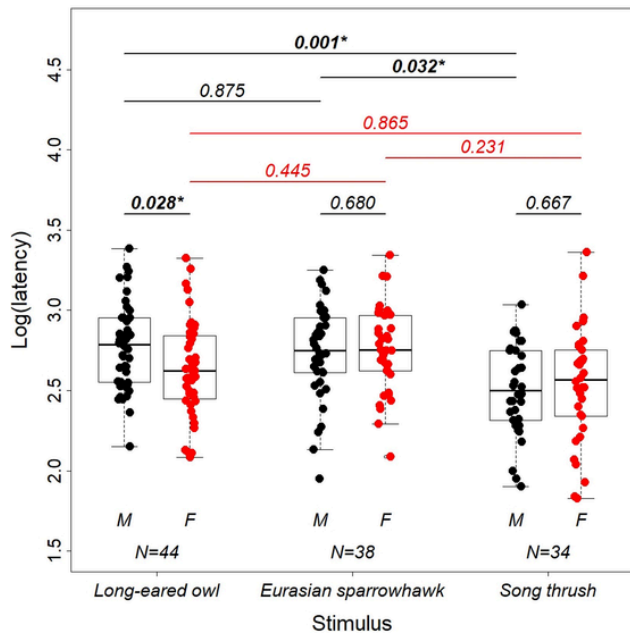


Fig. 1. The relationship between the  $\log_{10}$ -transformed feeding latency (sec) of flycatcher parents and the stuffed model species. The black and red points in addition to the label 'M' and 'F', represent the feeding latency of the males and females, respectively. P-values are shown based on the Tukey Honest Significant Difference test including the feeding latency only of the first tests. The number of tested nests with the given stimulus is shown under each box;  $N_{\text{all}} = 232$ .

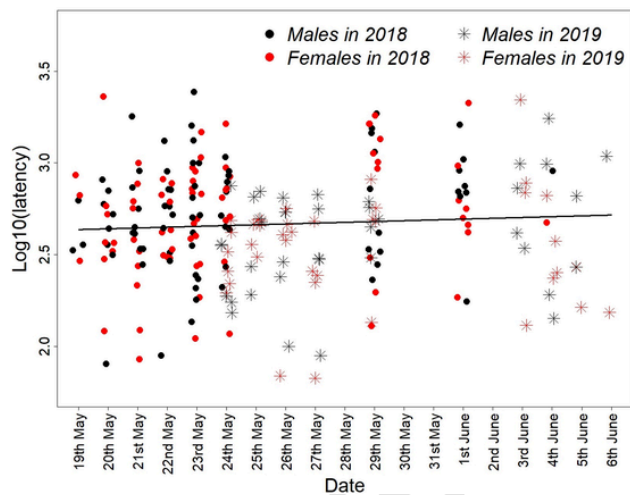


Fig. 2. The  $\log_{10}$ -transformed feeding latency (sec) of flycatcher parents in relation to the date of the tests separating early and late breeders. The colours represent the sexes, while the symbols represent the two experimental years (note that date was standardised across years for the analysis). The regression line is from the linear regression of the  $\log_{10}$ -transformed feeding latency on the date of the tests to help visualisation (see Table 2 for the appropriate statistical description of the relationship). Date is a discrete variable, the added noise to the data is only for preventing the points from overlapping.  $N_{\text{all}} = 232$ .

between latency to resume feeding activity and the identity of model species in females (Table S2, Fig. 1). In addition, the LMM of both sexes showed that the feeding latency of the parents were significantly related to each other within the nestbox, which explained the effect of the nestbox ID in the previous model. The random part of the models showed that the between-individual repeatability of risk-taking behaviour across stimuli was low in case of both sexes (i.e. repeatability of males and females were 0.220 and 0.195, respectively).

### 3.2. Within-individual reaction norms

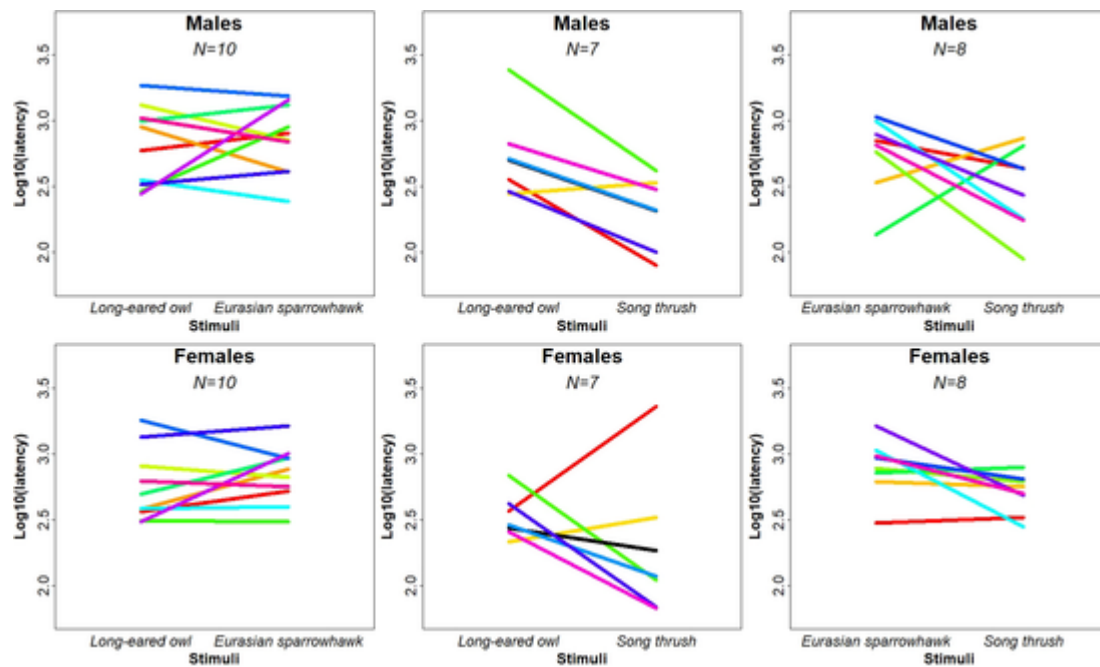
The patterns of change in individual responses towards the different stuffed stimuli, as could be characterised based on the available within-individual repeats, are illustrated on Fig. 3, while the underlying statistical description of the context-specific responses is provided in Table 3.

The within-individual modelling, which was constrained by a low sample size, recovered some of the context-specific patterns that were identified in the main model that relied on the whole sample and combined within- and between-individual effects (Table 2). First, as compared to the song thrush, parents provided in general stronger response to the predator stimuli. This was reflected by the generally steeper slope for the within-individual reaction norms, which even reached statistical significance in the contexts describing the long-eared owl/song thrush and the Eurasian sparrowhawk/song thrush environmental change. Second, there was no tendency for differential response towards the two predator stimuli, which also resembles the patterns found in the main model. The inspection of the random part of the model suggested that the 95 % credible intervals of the posterior distribution of variances of the intercepts did not differ considerably between sexes in either contexts, which suggested that the mean behaviour of the individuals showed similar variances in case of both sexes. However, in case of the long-eared owl/song thrush context, the posterior mean of the variance was four times higher in females, then males. This might suggest that risk-taking behaviour of females could be more plastic, which could give an explanation why there was no difference in latency to resume feeding activity between the three stuffed models. Moreover, in case of the Eurasian sparrowhawk/song thrush context, the posterior mean of the variance was six times higher in males, then females, which could be clearly seen on Fig. 3.

### 4. Discussion

Here, we investigated experimentally the risk-taking behaviour of the collared flycatcher in different life-threatening situations, during the nestling-rearing period. We exposed individuals to one or two out of the three different stuffed bird species, and assessed latency to resume feeding activity to estimate risk-taking behaviour. We found statistical evidence that sexes differed in their risk-taking behaviour in case of the long-eared owl. Males had different latencies when challenged with predatory and non-predatory stimuli, while for females, we did not find any significant association between risk-taking behaviour and the presented model species. We detected a considerable repeatability at the within-brood level, which also manifested in the significant correlation between the latency values of males and females attending the same nest. In addition, we found significant evidence for within-individual plasticity in risk-taking behaviour of the flycatchers in the long-eared owl/song thrush and Eurasian sparrowhawk/song thrush context. Finally, we found evidence for date and year effects on the risk-taking behaviour of the parents, as they took less risk when breeding relatively later, and they took generally more risk during the second experimental year.

When comparing risk-taking behaviour towards predator and non-predator stimuli, our results showed that flycatcher males react differently toward the predator than to the control stimuli, which fit well with previous findings in the literature (Burhans, 2000; Thomson et al., 2011; Strnad et al., 2012). However, females did not react in a different manner towards the predator and non-predator models. A plausible explanation can be that our approach was ineffective in case of females, as they might lack the ability to discriminate between different treatments, but we can discard this option as females also showed stress behaviour (e.g. occurrence of alarm calls, quickly chang-



**Fig. 3.** Within-individual changes in risk-taking behaviour of the collared flycatcher parents displayed in response to different combinations of two model species. The repeated measurements of responses of males are shown in the upper row, while the measurements of their pairs are presented in the lower row. Each column represents a particular context (i.e. particular combination of two stimuli). Colours reflect different nestboxes within a given context, thus individuals belonging to the same nestbox have the same colour between the two rows of the same column (while the colours are not comparable across columns). Note that the order of presentation of the stuffed models was random.

**Table 3**

The results of the MCMCglmm models investigating the within-individual responses of collared flycatcher parents in terms of risk-taking behaviour by the statistical characterisation of reaction norms, defined separately for each context (along the tabulation of Fig. 3). The models considered nestbox ID as a random effect, and the corresponding variance components were calculated separately for each sex (grouped random effects), whereby defining within-individual reaction norms, while controlling for nestbox-specific effects. The abbreviation means the following: p.mean = posterior mean; B = between-individual; W = within-individual; CrI = credible interval (i.e. the Bayesian 95 % confidence interval).

Contexts	Long-eared owl – Eurasian sparrowhawk			Long-eared owl – Song thrush			Eurasian sparrowhawk – Song thrush		
<b>Fixed effects</b>	<b>p.mean</b>	<b>95 % CrI</b>	<b>P</b>	<b>p.mean</b>	<b>95 % CrI</b>	<b>P</b>	<b>p.mean</b>	<b>95 % CrI</b>	<b>P</b>
(Intercept)	2.815	2.713, 2.904	<0.001	2.459	2.319, 2.606	<0.001	2.715	2.614, 2.823	<0.001
Treatment	0.039	-0.038, 0.107	0.278	-0.178	-0.302, -0.055	0.014	-0.110	-0.199, -0.015	0.018
<b>Random effects</b>	<b>p.mean</b>	<b>95 % CrI</b>		<b>p.mean</b>	<b>95 % CrI</b>		<b>p.mean</b>	<b>95 % CrI</b>	
<b>Males (B)</b>									
V(intercept)	0.042	0.0003, 0.107		0.060	0.0002, 0.180		0.029	0.0003, 0.082	
V(slope)	0.018	0.0002, 0.047		0.014	0.0002, 0.047		0.066	0.0003, 0.177	
<b>Females (B)</b>									
V(intercept)	0.035	0.0003, 0.089		0.059	0.0003, 0.185		0.021	0.0003, 0.068	
V(slope)	0.008	0.0002, 0.024		0.066	0.0003, 0.197		0.011	0.0002, 0.035	
Residual (W)	0.032	0.0004, 0.069		0.065	0.0003, 0.153		0.031	0.0005, 0.069	

ing position around the stimulus, raising wings in distress) in the presence of the predator models, while they entered the nestbox and rarely started alarm calls in the presence of the song thrush. Therefore, we believe that females recognised the risk, although, they did not respond equally compared to males. A possible explanation for the observed differences between the sexes is that females with their brown and white feather colouration can hide better in the environment, and due to such camouflage effects, their thresholds for making risk-taking decision might be different compared to males. In a field study, Møller et al. (2019) showed that in two pheasant species (common pheasants, *Phasianus colchicus* and golden pheasants, *Chrysolophus pictus*), adult males with brightly coloured plumage had longer and more variable flight initiation distance (FID) estimates (i.e. taking less risk against the human experimenter as a potential predator), while adult females with cryptically coloured plumage had shorter and more invariable FID estimates (i.e. taking more risk). Accordingly, flycatcher females with cryp-

tical feather colouration might experience weaker selection pressure from predators than male flycatchers making them less susceptible and responsive to a predatory threat, which might lead to that the detected latencies of females in the contexts of predators and song thrush do not differ considerably. A possible explanation for the similar response of females towards predator and non-predator models might be that females might have invested more time and energy into the current brood (e.g. forming and incubating the eggs, higher feeding rate) than males, and potential failure in the breeding attempt would have more costs for females. Therefore, it is plausible that flycatcher females resumed feeding activity independently of the level of threat to save their investment (Kokko and Jennions, 2008). Moreover, females could be absolutely sure about their parenthood of the nestlings, so the brood represents more value and gives more motivation to the female to resume feeding activity after a potential predator attack, to prevent the starvation of the nestlings. In contrast, males might hesitate to resume

feeding under the threat of predation due to the suspicion of extra-pair nestlings in the nest (Sheldon, 2002). Furthermore, we only assessed risk-taking behaviour of the parents at complete and intact nests, where the hunger level was generally low (with almost zero variance). It is plausible, that in case the nestlings would be more vulnerable, then the female would have different response towards the stuffed models.

We found no statistical evidence for either sex that individuals reacted differently towards the two predator models. Recent studies show contradictory results in this respect. For example, Dahl and Ritchison (2018) investigating the responses of blue jays to different avian predators at feeding stations during winter found that the tested group of birds apparently showed different responses towards certain predators (representing different levels of risk), while they reacted similarly to others within the same experiment. Duré Ruiz et al. (2017) testing the risk-taking behaviour of breeding southern house wrens when exposed to three different avian predators found similar patterns, as the tested birds considered one of the predator models more dangerous than the other two. Based on the numerous studies, it is obvious that birds react in a different manner towards different predator species (Curio et al., 1983; Suzuki, 2012), presumably because the cues are predator-specific, and thus trigger different risk-taking behaviour. Apparently, in case of the collared flycatcher, there is no strong selection for discriminating between the sparrowhawk and the owl, despite the fact that the former is a more important predator of the species. This might be explained by the fact that selection mainly affects individuals to recognise the major predator-specific cues, such as the colour and the pattern of the plumage. Another plausible explanation is that there is no considerable cost of reacting too shyly towards the owl, which makes the parents to delay their feeding activity a little bit longer than necessary in the presence of this predator during daytime. Note that most studies (that we are aware of) used only one predator species and one control species in their experiments to assess the risk-taking behaviour of their test subjects, while we used two predator species to be able to compare the risk-taking behaviour towards two types of threat.

We found that the sexes might differ in their general responses towards the different stuffed models (Fig. 1). The results of the LMM including all data revealed that the interaction between treatment and sex was not significant, but several patterns indicated sex-specific effects (e.g. sex-specific responses after the long-eared owl; or sex-specific evaluation of the predator and non-predator stuffed models, etc.). The comparison of the LMMs of each sex revealed that males reacted towards the stuffed models in a different manner than females. Moreover, the modelling of reaction norms also recovered some sex-specific patterns that were identified in the model that was fitted to the whole data (Fig. 3): parameter estimates for the reaction norm slopes indicated that compared to the song thrush, males provided generally stronger response to the predator stimuli than females. However, we note that our sample size was limited, especially for the within-individual context, which warns against making strong inferences about non-significant patterns (see further limitations emerging from the sample sizes in Martin et al., 2011; van de Pol, 2012). We could only find a few attempts in the literature that aimed to uncover sex-specific responses towards different predators. For example, Goullaud et al. (2018) found no evidence in horned lark (*Eremophila alpestris*) parents for a sex-specific response towards different stimuli (red fox, *Vulpes vulpes*; common raven, *Corvus corax*; savannah sparrow, *Passerculus sandwichensis*) during the nestling-rearing period. On the other hand, Expósito-Granados et al. (2016) found that European roller (*Coracias garrulus*) males had increased provisioning rate under experimental exposition to a ladder snake (*Zamenis scalaris*) model during the provisioning period of the breeding season, while females did not alter their rates, indicating that risk-taking behaviour is sex-specific in this bird species.

We found that the nestbox ID explained higher proportion of the variance in risk-taking behaviour than individual ID, and also that fe-

males and males attending the same nest had correlating latencies. These results can be mediated by brood-specific characteristics, as the value of the brood can define the risk-taking behaviour of both parents, raising similarity between their behaviour (Rytönen, 2002; Tilgar and Kikas, 2009). The value of the brood could depend on various nest- or parent-specific variables (e.g. number and age of the nestlings: Amat et al. (1996); health condition of the parents: Cantarero et al., 2016). We intended to characterise the value of the brood by using the number and age of the nestlings, but these variables did not affect the risk-taking behaviour of the parents. However, we cannot exclude that we left some important brood-specific traits uncharacterised (e.g. body mass and health condition of the nestlings, asynchrony in hatching) that do have an influence on risk-taking. Another possible explanation for the effect of the brood is that individuals might choose their pairs based on similarities in their behaviour (King et al., 2015), which could be even independent of the value of the brood. Our results showed that the feeding latency within the pair significantly correlated, but from these results, it is premature to conclude that the parents actually chose their partners assortatively for their behaviour. The correlation may also indicate that the parents behaved similarly because they were under the same constraints (e.g. they must have made allocations based on the same brood value), or independent of the brood value, the parent that restarted the feeding activity first, stimulated its pair to do the same.

The relationship between risk-taking behaviour and the actual timing of the flycatcher nests was significant, as latency to resume feeding activity increased along the date of the experiment, which separates early and late breeders. The flycatchers starting a nest later in the breeding season usually lay fewer eggs, and as the abundance of the food supply decreases, nestlings have lower survival prospects than at the beginning of the breeding season (Garamszegi et al., 2004; Rice et al., 2013). Due to the change in environmental conditions, the value of the nestlings and their chance of survival might be lower at later nests, thus it is plausible that parents take less risk when exposed to predation threat (Clermont et al., 2019). Another possible explanation for the observed increase in latency could be that individuals experienced more predatory threat later in the breeding season, as predators probably also have to meet increased energetic demands to provision and protect their own offspring (McNitt et al., 2020). And the flycatcher parents could become more risk sensitive and reduced provisioning rates more strongly due to the elevated predator activity (Ghalambor et al., 2013; Schneider and Griesser, 2014). Another alternative explanation for the observed increase in feeding latency is that birds arriving later to the breeding site might be younger and less experienced, that is, they might behave generally shyer. We can discard this option because we found no relationship between the age of males and their risk-taking behaviour during the nestling-rearing period, so it is unlikely that age effects mediate the relationship between the feeding latency and the date (see also Jablonszky et al., 2017 for another trait for risk-taking that is also unrelated to arrival date). Note that although the date of the tests had a significant effect on the risk-taking behaviour, the time of the tests within a given experimental days did not influence risk-taking (i.e. feeding latency did not differ between the morning and afternoon blocks). As the order of the tests on a given day was not a significant predictor of feeding latency, we can also exclude sensitisation or habituation effects in the risk-taking behaviour of the parents, at least in a within-day context.

Our study can be considered as a useful addition to a previous study, in which Michl et al. (2000) investigated the risk-taking behaviour in the same collared flycatcher population by also using a stuffed predator as stimulus to investigate danger-dependent parental care in three nestling stages. This previous study based on a single-measurement approach found that parents took greater risk after being exposed to the mistle thrush (*Turdus viscivorus*) model, while the risk-



taking behaviour of the parents depended on both sex and nestling stage. The current study provides novel findings because *i.*) we also assessed responses to other predator species; *ii.*) we exposed some pairs to two different stuffed models, which allowed us to observe within-individual responses as required for making inferences about context-dependent decision making.

In conclusion, we explored sex-specific differences in risk-taking behaviour of adult collared flycatchers during the nestling-rearing period by using one or two out of three different stuffed model species representing different types of threat. Our results indicated that males and females displayed different behavioural responses towards the model species suggesting that sexes could follow different decision-making strategy when resolving the trade-off between reproductive success and survival under predatory pressure. We also found some indications that the differences between sexes might be mediated by different within-individual plasticity of risk-taking. However, further repeated measurements are needed to demonstrate how sex- and stimulus-dependent behavioural responses are mediated by sex- and individual-specific patterns of plasticity.

### CRedit authorship contribution statement

**Katalin Krenhardt:** Formal analysis, Investigation, Data curation, Writing - original draft, Visualization. **Gábor Markó:** Investigation, Writing - review & editing. **Mónika Jablonszky:** Formal analysis, Writing - review & editing. **János Török:** Validation, Writing - review & editing. **László Zsolt Garamszegi:** Conceptualization, Methodology, Writing - review & editing, Project administration, Supervision.

### Declaration of Competing Interest

The authors declare that they have no conflict of interest

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### Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:<https://doi.org/10.1016/j.beproc.2021.104360>.

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