**Escape ability and risk-taking behaviour in a Hungarian population of the
collared flycatcher (*Ficedula albicollis*)**

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Abstract

Risk-taking decisions in front of a predator are crucial for the fitness of the animals. Risk-taking behaviour can be hypothesized to depend on escape ability, which is difficult to study in the wild. In this field study, we investigated whether escape ability (i) is a consistent individual-specific characteristic and (ii) whether it can explain between individual variation in risk-taking behaviour in male collared flycatchers (*Ficedula albicollis*). We estimated escape ability by the time that was needed to capture individuals by hand in an outdoor aviary during both the courtship and the nestling feeding phases. We estimated risk-taking by human-induced flight initiation distance (FID) and parental nest-defence behaviour. We also measured variables that reflect individual quality and condition to assess how these affect escape ability. Time to capture was weakly repeatable in the within- and between-season contexts, but was considerably repeatable within a day. We found that time to capture decreased between courtship and nestling feeding phases, probably due to parallel changes in body condition (as shown by the systematic decline of individual body mass between phases correlating with within-individual changes in time to capture). Overall, time to capture was not significantly related to risk taking behaviour, but we found a negative correlation between time to capture and FID in yearlings. In conclusion, escape ability in flycatchers seems to be a condition-dependent plastic trait, and it has the potential to affect immediate risk-taking decisions.

Keywords: antipredator behaviour, passerine, personality, plasticity, predation avoidance, repeatability

Significance Statement

We investigated the proximate determinants of escape ability in collared flycatcher males and whether this trait can be a potential driver of risk-taking behaviour, which is a rarely considered issue. We measured escape ability as time needed to capture birds in an outdoor aviary by hand. We found that escape ability was repeatable only in a short-term context, and differed between the courtship and chick-feeding periods, probably due to parallel changes in body condition. Furthermore, escape ability in yearlings (but not in adults) correlated with an estimate of risk-taking in the wild indicating that males with better ability to escape take higher risk. Our findings highlight that individual decisions about risk-taking might partially rely on how individuals assess their potential escape success.

Introduction

Risk-taking decisions of an animal reflect the trade-offs between predation avoidance and the benefits of continuing the present activity (Lima and Dill 1990). The main proximate factors determining risk-taking decisions are the assessment of the current level of risk and the ability to escape (Lima and Dill 1990). The latter may influence the former if animals can assess their own escape ability, and if they adjust their behavioural response to this knowledge. Accordingly, individuals with the same levels of observed risk-taking that have different ability to escape actually would take different amount of risk.

The former component of risk-taking decision, the assessment of the risk level, is based on the sensitivity of the animal's sensory organs and the speed of cognitive processes or capacity that help forming immediate judgements about the relative costs of the different responses (Sih and Del Giudice 2012). The distance at which an approaching predator is noticed is called alert distance (AD), and it is crucial for the risk-taking decision (Fernández-Juricic et al. 2001). AD varies between species, it is influenced by habitat structure and it is

usually associated with flight initiation distance (FID), which is the distance between the approaching predator and its prey at the moment the prey starts to flee (Fernández-Juricic et al. 2001; Blumstein 2010). Assessment of risk when providing the offspring usually depends on the value of the brood or the potential harm suffered by the offspring (Koskela et al. 2000; Boukhriss and Selmi 2010).

Escape ability, the other component of risk-taking, is also a complex trait that potentially includes both sensory and motor capacities that are needed for the active avoidance of being captured by a predator that is chasing the prey. In birds, flight performance is a fundamentally important component of escape ability (Veasey et al. 1998); being a composite trait, it includes aspects of speed, manoeuvrability and endurance. However, it is difficult to disentangle such components when measuring escape ability in the wild, and its biological relevance may vary across the different predators that prey upon the species (Witter and Cuthill 1993; van den Hout et al. 2010). For example, escape from ambush predators necessitates good reflexes and fast manoeuvring in the first moments of the attack (Metcalf and Ure 1995), whereas, in long chases by predators that rely on the exhaustion of the prey, endurance may become the most important factor (Schwilch et al. 1996).

Performance traits, similarly to behavioural traits (Réale et al. 2007), can be considered as being both plastic within and consistent across individuals. Flight performance can change within an individual for several reasons. For example, the nutrient and vitamin content of the food can alter the birds' flight capacity through their effect on body condition (Blount and Matheson 2006; Arnold et al. 2010). Other flight capacity influencing factors are age, mass, the condition of the feathers, and the characteristics of the habitat (Metcalf and Ure 1995; Merilä and Hemborg 2000; Burns and Ydenberg 2002; Kullberg et al. 2002; Labocha et al. 2015). On the other hand, the elements of flight performance may also be

individual-specific due to their genetic basis or differences in early experience and developmental conditions that raise consistent between-individual differences in the trait (Birkhead et al. 1998; Criscuolo et al. 2011; Møller et al. 2011; O'Hagan et al. 2015).

Animals are probably aware of their competencies to escape, thus they could incorporate such information into their immediate risk-taking decision leading to a relationship between observed risk-taking and the ability to escape. For instance, budgerigars (*Melopsittacus undulatus*) can reliably assess their ability to manoeuvre, as they were able to precisely assess the width of a gap (a vertical slit between two cloth panels) in relation to their wing span (Schiffner et al. 2014). To be able to do this, animals may inherently know their own characteristics (which can be genetically determined or condition-dependent) or are able to learn them from previous experiences. The evolutionary importance of this knowledge is that if individuals adjust their behaviours in the presence of predators according to their escape ability, the realized risk associated with the same behavioural response will be different for individuals with different abilities. Hence, stable between-individual differences in escape ability might lead to stable between-individual differences in risk-taking behaviour and thus escape-ability variation might be responsible for risk-taking personalities. Escape ability may influence risk-taking behaviour in a way that individuals that are better at escaping can flee earlier (Blumstein 2010). Alternatively, individuals that are hard to catch (and that are aware of it) may not have to flee immediately, as they can safely escape even when a predator is in their close proximity (Ydenberg and Dill 1986).

The aim of the current study was to explore in a wild collared flycatcher (*Ficedula albicollis*) population whether escape ability was an individual-specific trait and linked to risk-taking or other individual-specific characteristics. To this end, in a field study of eight years, we measured the time needed to capture a male bird by hand in an outdoor enclosure during both the courtship and chick-feeding period to assess escape ability, and FID during

the courtship period and the latency to resume the feeding activity after an exposition to a predatory threat during the chick-rearing period to characterise risk-taking. We also measured other individual traits reflecting body size and condition. To determine the biological relevance of escape ability, based on the careful analysis of video-recordings of the capturing events, we derived a trait that mirrors response to a single attack of an ambush predator and characterised its relationship with our estimate of escape ability. Based on this correlative data we could assess the between-individual consistency of escape ability on increasing time-scales (within-day, within season and between seasons), and link this trait to behavioural and phenotypic traits. We predicted that the time to capture would be repeatable, if it is an individually consistent trait. However, if it is plastic trait e.g. due to condition-dependence or experience both raising considerable within-individual variance, we expect to observe lower repeatability for the trait, and also that the trait is associated with age and/or other phenotypic traits reflecting immediate condition. We predicted a correlation between time to capture and risk-taking, if birds can reliably assess their escape ability and, based on such information, adjust their FID or time to resume feeding activity after seeing a predator.

Methods

Study site and species

The study was performed in a deciduous forest area in the Pilis Mountains, close to Budapest, Hungary (47°43'N, 19°01'E). The research area belonged to the Duna-Ipoly National Park, and consisted of about 800 artificial nest boxes with 3.2 cm entrance diameter and 24x11x11 cm cavity (Lambrechts et al. 2010). The breeding performance of collared flycatchers and other hole-nesting passerines, mainly great tits (*Parus major*) and blue tits

(*Cyanistes caeruleus*), have been monitored since 1981 (Török and Tóth 1988). In our study area, birds could be studied in their natural environment, with a minimal human disturbance.

The collared flycatcher is a small, hole-nesting migratory passerine. The males arrive earlier than females (Harnos et al. 2015) to establish their territories. Males prefer artificial nest boxes over natural nest-holes (Lundberg et al. 1981). During the reproduction period, males could be distinguished from females based on their black and white plumage traits (forehead and wing patch), which reflect individual quality and/or condition, and also has an important role in their behavioural display (Gustafsson et al. 1995; Török et al. 2003). Females incubate alone, but both parents take part in food provisioning (Cramp and Perrins 1994).

Unfortunately, there is relatively little information available on the natural predators of the study species, the collared flycatcher. The sister species, the pied flycatcher (*Ficedula hypoleuca*) is frequently depredated by the European sparrowhawk (*Accipiter nisus*) (Götmark and Post 1996; Slagsvold and Dale 1996). Documented nest predators of the flycatcher species are mainly species of Mustelidae and woodpeckers (Lundberg and Alatalo 1992; Stański et al. 2008). In the study area, the European sparrowhawk, the Northern goshawk (*Accipiter gentilis*), domestic cat (*Felis catus*), and Aesculapian snake (*Zamenis longissimus*) as well as Mustelidae and woodpecker species were observed as potential or real predators of collared flycatchers (LZG personal observations) during the breeding season. Concerning predators in the African wintering grounds we have no information. Given the broad array of predators to which the studied species is exposed to, we infer that both manoeuvring ability and endurance may play an important role in determining escape ability.

The data for the present study were collected in eight consecutive breeding seasons between 2009 and 2016. The measurements were taken between April 11 and May 10 in the courtship period and between May 17 and June 22 in the chick-feeding period. All behaviours

were measured between 6:30 and 15:45. Only data for males were used here (because behavioural assessments for the courtship period can be done only for this sex, as females cannot be captured in the nest box before the initiation of the nest). We used blinded methods in the sense that the identity and other information on the assayed birds were unknown to the person conducting the tests. We measured overall 380 male collared flycatchers (246 adults and 134 yearlings) for escape ability (see details below), of which 80 birds were measured more than once, either within a season or in different years. In 2016, birds were tested for escape ability two times in a day. Hence, we could calculate repeatability of escape ability on three levels: between years, within years (between the courtship and chick-feeding periods) and within day (only in 2016).

Risk-taking behaviour

In the courtship period, we assessed FID as a component of risk-taking. FID by definition is distance at which an individual flee when a potential predator, typically a human observer is approaching (Blumstein 2003; Garamszegi et al. 2008). Previous studies at both the within-species and between-species level found that FID is an important component of risk-taking that influences fitness and life-history (Møller and Garamszegi 2012; de Jong et al. 2013; Díaz et al. 2013; Møller and Tryjanowski 2014). In our population of collared flycatcher FID seems to be an individual-specific characteristic as it is repeatable at both the within- and between-year contexts (but it also varies at the within-individual level) (Garamszegi et al. 2015a), and between-individual variation in this phenotype relates to the between-individual variation in the genotype of two functional gene complexes (Garamszegi et al. 2014, 2015b).

In our measurements of FID, we first localized a male displaying at his naturally occupied nest box. Then the experimenter began to walk approximately from 30m from the

193 next-box when the focal bird was observed to be engaged in territorial defence with a caged
194 decoy bird (we established this situation in order to standardise the basic activity of the focal
195 birds), and proceeded at normal walking speed and stopped when the birds took flight. We
196 waited maximum 1 minute for the focal bird to return, if so, we continued the approach until
197 the next fleeing event. Allowing the birds to return to fight and measuring the distance
198 between the cage and the person when the bird did not return anymore to the cage, we
199 ascertained that individuals had an opportunity to notice the threat. The measurement of FID
200 was carried out by six persons, partly coinciding with the experimenters in the time to capture
201 measurement, and we controlled for potential between-observer effects in the statistical
202 models (see below). The experimenters wore camouflage clothing.

203 In the chick-feeding period, when a predator appears close to the nest, parents are
204 faced with an important trade-off between avoiding predation and providing the young.
205 Therefore, risk-taking was also assessed as latency to resume chick-feeding activity after a
206 predator threat when nestlings were 7-13 days old. The threat was represented by a stuffed
207 long-eared owl (*Asio otus*), which was placed on the top of the nest box for 5 minutes. After
208 the removal of the dummy, we measured the time that elapsed until the parents resumed their
209 feeding activity. We waited maximum 20 minutes for the birds to return. An earlier study in
210 our population showed that the behavioural response to the presence of an aerial predator
211 dummy depends on the relative value of the brood (Michl et al. 2000), while in pied
212 flycatchers it was shown that clutch-size manipulation, chick condition and predator type
213 were important factors in determining risk-taking levels (Listoen et al. 2000; Tilgar and Kikas
214 2009; Tilgar et al. 2011). Therefore, as control variables, we recorded brood size, and scored
215 the begging activity of the chicks and the intensity of alarm calls of the parents, each on a
216 scale of 0-2. For begging, a score of 0 meant when chicks did not move after the nest box had
217 been opened, a score of 1 when less than half of the chicks showed at least moderate begging

activity (only positioning), and a score of 2 when more than the half of the chicks displayed intensive begging (positioning and vocalisation). Score of 0 for alarm call indicates when there was no alarm call, score of 1 when one parent called, and score of 2 when both parents alarmed. If both parents called we supposed that both parents were exposed to the model predator, so we included the alarm call score to the subsequent analyses.

Escape ability

Time to capture was measured in a 5×5×2 m outdoor aviary mounted in the study area. Within the enclosure, we provided three perching trees, each with two horizontal branches. The experimental area, where the enclosure was set up, was remote and independent from the territory of the assayed individuals enabling us to control for the confounding effect of territory quality on behaviour (Pärt 1994). Furthermore, during the chick-feeding period, the parents could be measured independently of each other (van Oers et al. 2005).

We measured time to capture as follows. After catching the birds at their nest boxes in either the courtship or/and the chick-feeding period after behavioural tests with a conventional nest box trap, we transferred them to the aviary in a standard bird bag and released them therein. We left the area for six minutes, during which we video-recorded the individuals remotely to derive behavioural traits (not used in this study) that suggested that they recovered from the stress caused by the trapping and human handling. After this recovery period, the experimenter came out from his/her hiding position, entered the aviary and attempted to catch the focal bird by hand. The person continuously followed the escape manoeuvres of the focal birds with the same running speed without stopping and used the same technique for catching. The time needed for capturing the bird was used as an estimate of escape ability. Four persons who had been carefully trained to perform this assay carried

out the tests. We statistically controlled for any potential variance posed by observers' effect (see our statistical models below).

We appreciate that predatory attacks and chases in the wild rarely occur in small and closed areas like our test aviary, and thus one may question the biological relevance of our estimate of escape ability. Therefore, we performed some validation tests based on video-taping the observers' capturing efforts. In 2016, we recorded the human chasing events for 22 birds (some individuals were recorded twice, thus we used 39 videos in total) in the aviary during the chick-feeding period. From the subsequent slow-motion analysis of the movements of the birds, we estimated the closest distance at which the observer could approach the subject upon the first capture attempt. We were confident that all birds noticed the human entering the aviary, because at this point the bird could be localized in one corner of the aviary showing intentions to fly away. We infer that the birds' reaction to the first capturing effort has a biological relevance, because the underlying situation resembles to an attack of a predator that applies an ambush strategy. Escape strategy by the prey in this predatory event is less likely confounded by endurance and rather reflects the animal's quick decisions on how to avoid an immediate attack by a predator that is already detected in the close proximity. Accordingly, we can assume that the distance measured at the first approach indicates how birds react in a similar situation that can also occur in the wild. The difference between our estimate of FID and the first approach distance in the validation test of escape ability is that the former corresponds to a trade-off situation in which individuals balance between the benefits of continuing a current activity (i.e. territorial defence) and risk of being captured. On the other hand, the latter does not include such risk assessments, as it reflects escape strategies and behaviours that are relevant when the prey needs to avoid the direct attacks of a predator. There was a highly significant, positive relationship between the first approach distance and the time needed to capture individuals ($N=39$, $\beta \pm SE = 0.508 \pm 0.126$, $t = 4.047$, $P < 0.001$, as

given by a model in which we controlled for effects arising from the identity of birds and observers). This finding indicates that those birds that were generally hard to catch in the aviary also reacted relatively fast (i.e. at higher distance) to the observer's first approach. The link between these two variables suggests that we can consider that time to capture may be a good proxy of escape ability in general. We performed further analyses to validate this consideration, which are presented in the supplementary material.

Other variables

The following phenotypic traits were measured after the aviary test of escape ability. Body mass was measured using a Pesola spring balance (with a precision of 0.1 g), tarsus length, size of the wing and forehead patches were measured with a digital calliper (with a precision of 0.01 mm) and wing length was measured with a ruler (with a precision of 1 mm). Wing patch size was calculated as the sum of the length of the white area on the 4-8th primaries. Forehead patch size was calculated as the product of the maximum length and width of the white region on the forehead (Hegyi et al. 2002; Török et al. 2003). Age of males was determined based on the colour of the remiges (brown of the yearlings and black of the adults) (Mullarney et al. 1999). We recorded the date of the first day of observation at the breeding sites and assumed that it reflects arrival date, because we intensively monitor the study area for newly arrived males. The arrival at the breeding site in this species is very important, because being long-distance migratory birds, they face a considerable time constraint on reproduction (Wiggins et al. 1994).

Statistical analyses

For most of the analyses we used Linear Mixed Models (LMM) to control for the non-independence in the data caused by the identity of the focal birds, year effects, the identities

of the decoy bird and the experimenters. During model building, we did not considered interactions due to the large number of variables we wanted to test. The models were fitted using Maximum Likelihood instead of Restricted Maximum Likelihood method (Bolker et al. 2009). Prior to the analyses and the interpretation of model outputs, the distribution of the variables, as well as model residuals was checked visually by inspecting histograms and q-q plots. Based on these diagnostics we decided to $\log_{10}$ transform time to capture, FID and latency to resume feeding activity to achieve criteria for normal distribution. Furthermore, homogeneity and homoscedascity of the residuals, the stability of models against influential data points, as well as presence of collinearity with Variance Inflation Factor (VIF) (O'Brien 2007; Freckleton 2011) were also verified before the interpretation of the model outputs. We extracted results from the full models. Random factors were excluded only when their explained variance was close to 0 and the sample size for the model was low. P-values for fixed predictors were calculated with Likelihood Ratio test (LRT) comparing models with and without the focal predictor. We did not derive significance estimates for random factors, but we provide the variance explained by them.

Repeatability of escape ability was calculated by dividing its between-individual variance with the total variance (Lessells and Boag 1987). Variance components were derived from the appropriate LMMs (Nakagawa and Schielzeth 2010) including time to capture as the response variable, and individual, the identity of the experimenter and year as random factors. Period was also added to the model (see also below), but we avoided to include other variables because of the limited sample size that was available in the repeated measurement design. Repeatability was calculated for three intervals, i.e. for the within-day, within-year and between-year scenarios. In the within-day and between-year scenarios, we assessed repeatability also for the two periods (courtship and chick-feeding) separately. P-values and confidence intervals were computed with randomization and parametric bootstrap approaches,

respectively, according to Nakagawa and Schielzeth (2010). Within-day repeatability were computed from a slightly different model, including age and condition of the birds, order of the time to capture measurement, time elapsed between capture at the nest box and release into the aviary, with the same random structure as above, excluding year.

To investigate whether time to capture was predicted by phenotypic traits, we constructed a model that included the following predictors. Mass, tarsus length and wing length were representing the birds' size, and white wing patch size, and forehead patch size were used as a proxy for male quality. The former patch size is related to age and body condition (Török et al. 2003), while the latter is not in the Hungarian population in contrast to Swedish data (Hegyi et al. 2002). Thus, wing patch size was standardised for age, and body mass was standardised for tarsus length, using the residuals from the appropriate linear regressions. Age, date, time of the experiment, and period were also included in the model. Date of observation was standardised across years by re-coding it relatively to the encounter with the first male displaying the typical territorial behaviour in the given year. Learning or habituation can affect the behaviour in repeated measurements design. Thus, in an alternative model we included also the experience of the focal bird with time to capture measurement, i.e. whether the bird was or was not subjected previously to the assay in the aviary, to control for these confounding effects. The random effects were the same as in the repeatability model.

To further analyse the relationship between time to capture, mass and period, the potential shift in the expression of behaviour and mass between years or periods was checked with paired t-test. In these analyses, we used the original measure of mass without controlling for body size, because we focused on the changes in the birds' condition that are not confounded by skeletal size (i.e. it can be assumed to be stable within the observation period). We also built a LMM with time to capture as the response variable and within-individual centered body mass as predictor variable to model whether individuals differed in how they

changed their escape ability when their condition changed. At the hierarchical level of individuals, we considered both random intercept and random slopes, and investigated whether individuals display different responses in their behaviour as their body mass changes. We included also the identity of the experimenter as random factor. In another model, we tested for the relationship between escape ability change and mass change between periods controlling for the original time to capture and using year as a random effect.

The association between FID and time to capture was also analysed with a LMM, in which the response variable was FID and the predictor variables were standardised mass, age, date and time to capture (all assessed during the courtship period). Year, the identity of the subject, of the male decoy and of the observer of the FID test were entered as random factors. Control variables were included in the model, because FID depends on physiological and morphological traits, like body mass (Blumstein 2006; Møller et al. 2013) and we aimed to control for the potentially confounding effects of unknown environmental factors (Javurkova et al. 2012; Møller 2014) by including also year and date. After the post hoc inspection of the results of the model and the visual inspection of the data, we performed separate LMMs for yearlings and adults, with explanatory variables and random structures as defined above (excluding age). To be able to make at least an indirect inference about the separation of age and experience effects, the separate model for the adult birds included also the experience with FID measurement (whether there was a previous FID measurement from the focal bird or not) as control variable.

Latency from the risk-taking experiment during chick-feeding was controlled for the response of the female and brood size using residuals from a linear regression model containing the above-mentioned predictor variables on latency as the response (statistics for the overall model: $F_{2,109} = 39.060$, adjusted $R^2 = 0.407$, $P < 0.001$). From this model, we calculated the residuals and used these as a measure of male risk-taking during chick-feeding.

The relationship between this residual latency and time to capture during the chick-feeding period was investigated in a model in which age, standardised mass, date and year were used as control variables. In this case, we used general linear models, because the availability of the corresponding data was not hierarchically structured by any confounding variables.

All statistical analyses were conducted and the figures were drawn in the R statistical environment (R Development Core Team 2015). LMMs relied on the “lme4” package (Bates et al. 2011). Variation Influence Factor was calculated by a function from the „car” package (Fox and Weisberg 2011).

Results

Repeatability

The time to capture ranged from 2 to 150s (N = 380, mean = 27.040, median = 20, standard deviation = 24.790). Within-day repeatability was considerable and significant in the overall dataset (N = 45, R = 0.236, P = 0.022) and during courtship (N = 39, R = 0.378, P = 0.010; Fig. 1a), and was of similar magnitude, but not significant (probably due to smaller sample size) during chick-feeding (N = 13, R = 0.416, P = 0.111; Fig. 1a). However, repeatability could not be discriminated statistically from zero between periods (N = 52, R = 0.041, P = 0.356; Fig. 1b) and between years (N = 34, R < 0.001, P = 0.758), even when the latter was analysed separately for the periods (courtship: N = 21, R = 0.030, P = 0.386; chick-feeding: N = 13, R = 0, P = 0.886; Fig. 1c).

Proximate determination of time to capture

When we assessed the relationship between time to capture and proximal predictor variables, we found that escape ability was significantly lower in the chick-feeding season

than during courtship ($N = 350$, $\beta \pm SE = 0.526 \pm 0.110$, $t = 4.781$, $P < 0.001$). However, given that there was a strong negative association between period and standardised body mass (t-test: $N = 368$, $t_{269,22} = -5.404$, $P < 0.001$), we cannot separate clear period effects from the effects of the parallel condition change with our correlative design. When we dropped the period from the model, the relationship between time to capture and standardised mass became significant (Table 1). Including experience with the time to capture assay in the model did not alter our results, the variable itself being nonsignificant ($N = 349$, $\beta \pm SE = -0.031 \pm 0.118$, $t = -0.267$, $P = 0.790$).

With the multiple measurements from different phases of the breeding season, we investigated the relationship between body mass, time to capture and period based on a longitudinal approach. We detected that the time to capture showed a significant decline within individuals from the courtship towards the chick-feeding period (paired-t test: $N = 52$, $t = 2.596$, $P = 0.012$, Fig. 2a). Similarly, body mass also depicted a consistent within-individual decrease between the periods (paired-t test: $N = 50$, $t = 5.790$, $P < 0.001$, Fig. 2b). The first- and second-year capture records of the same birds did not differ significantly when we compared them pairwise (paired-t test: $N = 31$, $t = -0.276$, $P = 0.785$).

Relying on a simplified model containing only mass and the considered random effects, we found that a model that only included random intercepts offered the best fit to the data, when compared to the model considering random slopes ($N = 173$, LRT test: $\chi^2 = 0.137$, $P = 0.711$) or a correlation between random slopes and intercepts (LRT test: $\chi^2 = 0.345$, $P = 0.842$). The connection with mass was significant in the final model (LRT test: $\chi^2 = 13.443$, $P = 0.001$) indicating that individuals are generally easier to capture when they have lower body mass. The model, in which the change in time to capture between the two periods was the response variable, revealed that the original time to capture had a significant negative ($N = 50$,

$\beta \pm \text{SE} = -0.900 \pm 0.140$, $t = -6.423$, $P < 0.001$) and the change in body mass had a significant positive ($\beta \pm \text{SE} = 0.518 \pm 0.215$, $t = 2.409$, $P = 0.027$) relationship with the response variable.

Risk-taking and time to capture

In the model analysing the correlation between time to capture, age and mass and FID, only age had a significant impact, as older males took less risk than younger males (Table 2, Fig. 3). The final model contained only the first measures, because there were relatively few repeated measures in this analysis ($N = 18$) and the random factor of identity explained negligible variance. The visual inspection of the data revealed that there might be an age-dependent relationship between the focal variables (Fig. 3). When yearlings were analysed separately the negative relationship between time to capture and FID was significant (Table 3). In the model with adult birds including experience with FID measurement this variable was not significant ($N=119$, $\beta \pm \text{SE} = 0.115 \pm 0.119$, $t = 0.97$, $P = 0.360$).

When analysing the residual response of males to an owl decoy as a response variable, none of the considered variables (time to capture, date, year, age, and standardised mass) were significant predictor of risk-taking during the chick-rearing period (Table 4).

Discussion

The most salient findings of this study are the followings. First, time to capture that can be used as a proxy for escape ability in general was only repeatable within day but not within or among years. Second, time to capture was higher during courtship than in the chick-feeding period. Third, within-individual change in time to capture was accompanied by within-individual changes in body condition (i.e. those individuals that became easier to catch also lost more body weight). Fourth, time to capture and FID were only linked (negatively) in yearlings during courtship. Our results suggest that (i) time to capture is a labile but non-

random trait that characterized by the actual state of an individual and (ii) it does have the potential to influence risk taking decisions in young, less experienced flycatchers where escape success might depend on locomotor performance (speed, endurance, manoeuvrability) more directly than in older, experienced birds.

We observed that time to capture had repeatability close to zero between years and also between the different periods of the breeding season, but has a considerable repeatability within a day, comparable with that of behavioural traits (see Bell et al. 2009). In other species (e.g. in the zebra finch, *Taeniopygia guttata*) capture order (the order in the birds are captured by an experimenter) was repeatable in 5 weeks ($R = 0.39$), but in captive birds (Birkhead et al. 1998). In any case, the repeatability near to 0 of the trait observed in our study species between longer periods and its association with changes in body mass indicate that time to capture is a rather labile trait. Importantly, time to capture was considerably repeatable within a day, suggesting the existence of individual strategies in escaping at least within a short time window, which is connected to individual state.

Breeding period had a clear effect on the time to capture, and it was in fact a significant determinant of the within-individual variance of the trait. Individuals were harder to catch during the courtship than in the chick-feeding phase of the breeding season. We inferred that such changes across different periods are associated with changes in body condition, as it is also changed between periods and we showed that the within-individual decline in time to capture occurred in parallel with within-individual declines in body mass. The decreased body mass during the chick-feeding period is likely to be a consequence of higher workload required for the intense provisioning of the nestlings. Lower mass can indicate worse body condition leading to decreased performance, but can also be adaptive during such a period with an intense workload, because it decreases the cost of flight (Norberg 1981; Hillström 1995; Schmidt-Wellenburg et al. 2007). Because our study is

correlative, we cannot draw conclusions about the causality of the relationship between body mass and escape ability. However, according to our results birds in bad condition has impaired escape ability. It is likely that lower body mass indicate deteriorated physiological state or oxidative status, or birds in better condition can endure further the metabolic cost of an effective escape from a predator due to both better manoeuvring or endurance (Schwilch et al. 1996). A possible confounding effect due to experience (Ydenberg and Dill 1986; Walker et al. 2006) may arise due to the fact that birds have already experienced capture by humans before the chick-feeding period and learnt that there is no risk associated with this. However, getting used to being handled by humans just after one occasion is unlikely. Furthermore, there were no differences between the first and second year, and experience with the measurement did not explain significant amount of variance in time to capture.

Phenotypic traits, like age, wing length, body size and the size of two sexually-selected plumage ornaments were not significant predictors of escape ability. This finding is in contrast with other studies on capture order in house sparrows (*Passer domesticus*) (Moreno-Rueda 2003; De Neve et al. 2010), which showed that this trait can indeed depend on age and morphological characteristics. Because in these models we assessed repeatability over a relatively long time period (after about a months or between years), it is possible that other individual characteristics that change on a smaller scale (as suggested by our low repeatability estimates between years and periods, but relatively high repeatability within a day), similarly to mass, may influence also the escape ability. For example, escape ability may differ in terms of stress responsiveness (van Oers and Carere 2007) or parasite load, and such differences were left uncontrolled in our statistical models that used morphological traits and age only.

Although we failed to detect a significant relationship between risk-taking and time to capture using the full data, among yearlings we found statistical support for that individuals

allowing a potential predator at a closer distance were those that were also more difficult to catch in the aviary. This result may indicate that birds with better escape ability do not flee until the threat is really close, probably because they are aware of their superior abilities, which allows them to avoid the cost of fleeing longer than their inferior conspecifics (Lima and Dill 1990). Accordingly, it is known that birds can assess their own ability to flee at least in some species. For example, in western sandpipers (*Calidris mauri*) individuals with higher wing loading, which signifies lower escape ability occur in less dangerous sites during winter (Nebel and Ydenberg 2005). In a series of experiments on European starlings (*Sturnus vulgaris*), it was found that heavier birds, which are worse at manoeuvring, lower the angle of ascent in favour of velocity during escape and leave the cover more reluctantly (Witter et al. 1994). In studies with lizards, researchers also found some evidence for the relationship between risk-taking and escape performance (Vanhooydonck and Van Damme 2003; Qi et al. 2014). However, the generally weak association between FID and time to capture in our data warrants careful interpretations and further investigations, in which more individuals are included and additional potential confounding variables are also taken into account.

FID was significantly associated with age, as yearling flycatchers had lower FID than adults, and such patterns can help understand the age-specific relationship between FID and escape ability. In crickets (*Gryllus campestris*), boldness is increasing with age (Fisher et al. 2015), while two studies on wandering albatrosses (*Diomedea exulans*) and chinstrap penguins (*Pygoscelis antarctica*) found greater risk-taking level in juveniles (Martín et al. 2006; Patrick et al. 2013). In our population of collared flycatchers, attack latency during territorial aggression is also shorter in yearlings, which could be another form of risk-taking (Garamszegi et al. 2006). Experience may play a role in this phenomenon, as it is known to alter the behaviour in a wide range of taxa (Bell and Stamps 2004; DiRienzo et al. 2012; Zimmer et al. 2013). However, in our data there was no difference between adult birds that

are experienced or not experienced with the procedures involved in the measurement of FID in the field. Another possible explanation is that the different residual reproductive value of the age categories may influence the level of risk-taking behaviour (Wolf et al. 2007). An important implication of the age-specific risk-taking is that the decreased level of risk-taking in adults may lead to the loss of relationship between time to capture and FID in older birds (Fig. 3). Adults likely have so long FID that their escape ability has no importance in the higher range of trait variation. It implies that they can safely escape without exerting their maximal fleeing potential when a predator is farther. However escape ability become important in yearlings that let the predators approach them systematically closer.

We have not found a significant relationship between escape ability and risk-taking during chick-feeding assessed as response to a dummy aerial predator, which can be explained by the difference in the type of predator (Ellis-Felege et al. 2013) and the different context. However, due to our limited sample size this pattern also requires further investigation.

In conclusion, we found remarkable within-individual variance in time to capture that likely reflects a biologically relevant escape ability of male collared flycatchers, which is probably the consequence of condition-dependence. Furthermore, considerable repeatability in the within-day context supports the hypothesis that the time that a potential predator takes to capture its victim can be an individual-specific characteristic of the prey at a given time point (i.e. it is non-random). Our data suggest that escape ability might have a role in determining risk-taking strategies in young, inexperienced birds that generally take higher risks. Further research is needed to understand the evolutionary ecology of how individuals avoid incidences of captures when a predator chases them, and how it affects realized risk-taking behaviour.

Compliance with ethical standards

All applicable international, national, and/or institutional guidelines for the care and use of animals were followed. Permissions for the fieldwork have been provided by the Middle-Danube-Valley Inspectorate for Environmental Protection, Nature Conservation and Water Management, ref. no's: KTVF 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) and was approved by the ethical committee of the Eötvös Loránd University (ref. no. TTK/2203/3).

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Conflict of interest

The authors declare that they have no conflict of interest.

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Tables

Table 1 Results from the linear mixed model investigating the relationship between escape ability and the considered predictor variables in male collared flycatchers. The random factors were individual and experimenter identity and year. Period was excluded from the variables in order to investigate the effect of body mass that vary to a great extent between periods (see text for further details). P-values were calculated with likelihood ratio test (LRT). N=350

Predictor variables	β (SE)	t	LRT χ^2	P
standardised mass	0.252 (0.080)	3.134	9.094	0.003
wing length	0.006 (0.028)	0.230	0.053	0.818
tarsus length	-0.025 (0.094)	-0.262	0.068	0.794
age	0.124 (0.117)	1.067	1.072	0.301
standardised wing patch size	<-0.001 (0.001)	-0.432	0.185	0.667
forehead patch size	<0.001 (<0.001)	1.151	1.294	0.255
date	0.018 (0.009)	1.902	3.489	0.062
time	-0.071 (0.034)	-2.055	3.502	0.061
Random effects	Variance	Standard Deviation		
year	0.021	0.144		
identity	0.063	0.252		
experimenter	0.019	0.137		
residual	0.631	0.794		

Table 2 The results of the linear mixed model investigating the relationship between flight initiation distance (FID) and escape ability and the considered control variables in male collared flycatchers. The random factors taken into account in this model are identity of the

763 observer, year and the identity of the male decoy. P-values were calculated with likelihood
764 ratio test (LRT). N=192

Predictor variables	β (SE)	t	LRT χ^2	P
time to capture	-0.082 (0.046)	-1.77	3.01	0.083
age	-0.326 (0.088)	-3.70	12.7	<0.001
standardised mass	-0.131 (0.072)	-1.82	3.21	0.073
date	0.011 (0.009)	-1.26	1.37	0.240
Random effects	Variance	Standard Deviation		
year	0.012	0.111		
observer	0.046	0.214		
male decoy	0.011	0.105		
residual	0.273	0.522		

765
766 **Table 3** Results from the linear mixed model investigating the relationship between flight
767 initiation distance (FID) and escape ability with control variables in yearling male collared
768 flycatchers. The random factor for this model is year (we left out the identity of the decoy bird
769 in this model, because of the limited sample size and because it accounted for zero variance).
770 P-values were calculated with likelihood ratio test (LRT). N=91

Predictor variables	β (SE)	t	LRT χ^2	P
time to capture	-0.155 (0.077)	-2.02	3.98	0.046
standardised mass	-0.159 (0.119)	-1.34	1.78	0.180
date	<0.001 (0.014)	0.02	0	0.980
Random effects	Variance	Standard Deviation		

year	-0.018	0.136
residual	0.364	0.603

771

772 **Table 4** Results from the multiple linear regression investigating the relationship between
773 residual owl latency and escape ability with control variables in male collared flycatchers. P-
774 value for the year factor was calculated with likelihood ratio test (LRT), other P-values were
775 extracted directly from the model outputs. N=46

Predictor variables	β (SE)	t	LRT χ^2	P
time to capture	<0.001 (0.139)	0.005		0.996
standardised mass	-0.081 (0.215)	-0.379		0.707
age	0.095 (0.344)	0.277		0.783
date	-0.038 (0.027)	-1.436		0.159
year			2.877	0.245

776

Figure legends

Fig. 1 Repeatability of escape ability (estimated as time to capture in sec) within day (a), within years (b) and between years (c) shown as the relationship of behavioural scores between the two measurements within a day, between the two periods and years, respectively. The lines represent linear regression lines. In a) and c) data from the courtship (filled circle, solid line) and chick-feeding period (open circle, dashed line) are displayed separately

Fig. 2 The change in escape ability (estimated as time to capture in sec) (a), and body mass (b) between the courtship and the nestling periods. Values originating from the same individuals are connected

Fig. 3 The relationship between FID (m) and escape ability (estimated as time to capture in sec) in adults (filled circle) and yearlings (open circle) with regression lines (solid and dashed, respectively) given separately for the two groups

log (time to capture (s)),
second in a day

log (time to capture (s)), first in a day

log (time to capture (s)),
chick-feeding

log (time to capture (s)), courtship

log (time to capture (s)),
year 2

log (time to capture (s)), year 1

Figure

log (time to capture (s))

body mass (g)

Figure