Journal of Evolutionary Biology, 2024, **37**, 566–576
https://doi.org/10.1093/jeb/voae046
Advance access publication 16 April 2024
Research Article

JOURNAL OF
Evolutionary Biology
eseb
European Society for Evolutionary Biology

The effect of environmental variation on the relationship between survival and risk-taking behaviour in a migratory songbird

Katalin Krenhardt[1,2], Jesús Martínez-Padilla[3], David Canal[4], Mónika Jablonszky[1,2], Gergely Hegyi[2], Márton Herényi[2,5], Miklós Laczi[2,6,7], Gábor Markó[8], Gergely Nagy[1,2], Balázs Rosivall[2], Eszter Szász[2], Eszter Szöllősi[2], János Török[2,9], Éva Vaskuti[2], Sándor Zsebők[1,2], László Zsolt Garamszegi[1]

[1]Evolutionary Ecology Research Group, Institute of Ecology and Botany, HUN-REN Centre for Ecological Research, Vácrátót, Hungary
[2]Behavioural Ecology Group, Department of Systematic Zoology and Ecology, ELTE Eötvös Loránd University, Budapest, Hungary
[3]Department of Biological Conservation and Ecosystem Restoration, Pyrenean Institute of Ecology (IPE-CSIC), Huesca, Spain
[4]Department of Evolutionary Ecology, National Museum of Natural Sciences (MNCN-CSIC), Madrid, Spain
[5]Department of Zoology and Ecology, Hungarian University of Agriculture and Life Sciences, Gödöllő, Hungary
[6]HUN-REN-ELTE-MTM Integrative Ecology Research Group, Budapest, Hungary
[7]The Barn Owl Foundation, Orosztony, Hungary
[8]Department of Plant Pathology, Institute of Plant Protection, Hungarian University of Agriculture and Life Sciences, Budapest, Hungary
[9]MTA-ELTE-MTM Ecology Research Group, Budapest, Hungary

Corresponding author: Katalin Krenhardt, Evolutionary Ecology Research Group, Institute of Ecology and Botany, HUN-REN Centre for Ecological Research, Alkotmány utca 2-4, 2163 Vácrátót, Hungary. Email: krenhardt.katalin@ecolres.hu

Abstract

Temporal changes in environmental conditions may play a major role in the year-to-year variation in fitness consequences of behaviours. Identifying environmental drivers of such variation is crucial to understand the evolutionary trajectories of behaviours in natural contexts. However, our understanding of how environmental variation influences behaviours in the wild remains limited. Using data collected over 14 breeding seasons from a collared flycatcher (*Ficedula albicollis*) population, we examined the effect of environmental variation on the relationship between survival and risk-taking behaviour, a highly variable behavioural trait with great evolutionary and ecological significance. Specifically, using annual recapture probability as a proxy of survival, we evaluated the specific effect of predation pressure, food availability, and mean temperature on the relationship between annual recapture probability and risk-taking behaviour (measured as flight initiation distance [FID]). We found a negative trend, as the relationship between annual recapture probability and FID decreased over the study years and changed from positive to negative. Specifically, in the early years of the study, risk-avoiding individuals exhibited a higher annual recapture probability, whereas in the later years, risk-avoiders had a lower annual recapture probability. However, we did not find evidence that any of the considered environmental factors mediated the variation in the relationship between survival and risk-taking behaviour.

Keywords: environmental variation, risk-taking behaviour, flight initiation distance, survival, annual recapture probability, passerine

Introduction

The observation that a phenotypic trait in a population exhibits covariation with certain environmental factors is a core concept of evolutionary ecology (Michel et al., 2014). When analyzing the evolution of a phenotypic trait, the focus is usually on the association between the trait and individual fitness, assuming that individuals express similar phenotypes when exposed to similar environmental selective pressures, which is often false (Bolnick et al., 2003). Variation in phenotypic expression is most likely to evolve in spatially and temporally variable environments where there might not be a single optimal strategy (Coates et al., 2019). Therefore, identifying those environmental factors that shape the covariation between phenotypic traits and proxies of fitness is fundamental for understanding how environmental variation influences the evolution of animals' phenotypes in wild populations (Grant & Grant, 2003).

Previous research on phenotypic selection has primarily concentrated on abiotic (i.e., climatic) factors (Charmantier & Gienapp, 2014; Evans & Gustafsson, 2017; Gienapp et al., 2008; Merilä & Hendry, 2014), and our understanding of the influence of biotic factors on phenotypic selection is still imperfect (e.g., Morales-Mata et al., 2022). However, climatic factors may not necessarily be the direct drivers of selection but rather mediate the impact of biotic factors acting as true environmental determinants of the evolution of phenotypic traits (e.g., climatic factors mediate the prevalence and load of ectoparasites; Moyer et al., 2002; Pollock et al., 2015). Furthermore, most papers on phenotypic selection have concentrated on morphological and life-history traits (Kingsolver et al., 2001, 2012), with only a few studies focussing on ornamentation (Cuervo & Møller, 1999, 2001) and even fewer on behaviour (Dhellemmes et al., 2021; Garant, 2020; Lapiedra

Received September 1, 2023; revised March 26, 2024; accepted April 15, 2024

et al., 2018; Réale & Festa-Bianchet, 2003). Undoubtedly, it is challenging to quantify the relative influence of behaviour on fitness due to the complexity and multifaceted nature of the behaviour, compounded by the difficulty of directly measuring and manipulating environmental factors in natural settings and the challenges associated with gathering long-term data.

Animal behaviour involves a wide range of activities and strategies that animals use to interact with their environment, trying to increase their survival and reproduction (Réale et al., 2007; Wolf & Weissing, 2012). One remarkable feature of animal behaviour is its ability to adjust to rapid environmental changes (Wong & Candolin, 2015). Animals exhibit behavioural plasticity, which allows them to react promptly to new challenges and exploit available resources more effectively by adjusting their responses in the face of changing environmental conditions (Van Buskirk, 2012). Understanding how animal behaviour adjusts to these rapid environmental changes is crucial, as it provides insights into the evolutionary processes that shape species persistence in dynamic environments (Sih, 2013). This understanding aids in identifying traits that enable animals to cope with and thrive in the face of environmental variability. Such knowledge contributes to our broader understanding of how animal behaviour could evolutionarily adapt to new environmental conditions and how this adaptation influences the persistence of traits within a population.

Risk-taking is an important behavioural trait that defines how individuals respond to various risky situations, including encounters with predators (Quinn & Cresswell, 2005), potential exposure to parasites (Møller et al., 2013), or competition for resources (Behney et al., 2019). Risk-taking may confer advantages, such as reducing negative consequences for survival and increasing potential benefits (e.g., gaining access to resources or higher-quality territories, Ydenberg & Dill, 1986). Risk-taking is considered highly plastic because individuals can adjust it to environmental conditions and contextual factors (Heynen et al., 2016; Jolles et al., 2019; Krenhardt et al., 2021). For example, animals may exhibit bolder behaviours in resource-limited environments with low predation pressure, thus taking greater risks to access valuable resources (Borcherding & Magnhagen, 2008). In contrast, in resource-limited environments with high predation pressure, individuals may adopt more cautious behaviours to decrease risks and increase their chances of survival (Smith & Blumstein, 2008). The plasticity of risk-taking behaviour may allow animals to adjust to varying ecological conditions and optimize their trade-offs between potential rewards and costs. However, it is important to note that while this behavioural change is often attributed to plasticity, it could also be achieved without plasticity if animals that consistently differ in their behaviour are favoured by selection in these different predation scenarios. This nuanced understanding of risk-taking behaviour is crucial when considering its evolutionary significance. Risk-taking is not only a heritable behaviour (Carrete et al., 2016) with considerable fitness consequences, particularly through its relation to survival (Smith & Blumstein, 2008), but it also exhibits substantial variation among individuals.

Predation pressure is an important biotic agent of selection for risk-taking behaviour, as exposure to predators can strongly and directly affect the risk-taking behaviour of prey while simultaneously affecting their survival (D'Anna et al., 2012; Møller, 2014). Individuals under elevated risk of predation have to make an immediate decision whether to continue their current activity (e.g., foraging, singing, defending territory) with an elevated risk of mortality (Kortet et al., 2010) or avoid predation by escaping (Verdolin, 2006). Thus, individuals have to face a trade-off between the costs of predation and their intrinsic necessities (e.g., energetic demands) to optimize their chances of survival (Brown & Kotler, 2004). The balance between costs and benefits is expected to be context dependent (Lima & Bednekoff, 1999), with individuals adjusting the balance between current activity and future survival in response to the actual predation risk. We know from the study of Lapiedra et al. (2018) on brown anoles (*Anolis sagrei*) and the study of Dhellemmes et al. (2021) on lemon sharks (*Negaprion brevirostris*) that predation pressure can influence the relationship between risk-taking behaviour and survival. Both studies found that bolder individuals have a lower survival chance in case of higher predation pressure. However, we still know little about how temporally fluctuating selection works on risk-taking behaviour in the case of bird species.

Besides predation pressure, another biotic environmental factor potentially mediating the relationship between survival and individual risk-taking behaviour is the relative abundance of food resources, which continuously changes over the years (Le Cœur et al., 2015; Santicchia et al., 2018). Foraging (or acquiring other valuable resources) typically comes with associated costs, and a growing body of evidence suggests that animals weigh these costs and benefits strategically (Caraco, 1980; Hurly & Healy, 2018). Food availability directly impacts the benefits an animal can obtain compared to the costs it incurs. Consequently, an animal's ideal level of risk-taking (or foraging effort) ought to be influenced by food availability (Abrams, 1991). Theoretically, bolder individuals could acquire resources more efficiently in years of low food availability. A higher food intake could translate into better body condition and, subsequently, a higher survival chance. In contrast, bolder individuals could have a lower survival chance in years with high food availability, as being bold is costly for animals, and when the benefit does not offset this cost (as it does under low food availability), bold animals are worse off than shy ones (Biro & Stamps, 2010).

Furthermore, changes in abiotic environmental factors could also directly affect the relationship between survival and risk-taking behaviour. Temperature is one of the most studied abiotic factors shaping phenotypic selection (Charmantier et al., 2008; Kingsolver et al., 2015; Le Vaillant et al., 2021; Marrot et al., 2018). Temperature affects the energy requirements of animals, and in cold environments, animals may need to allocate more energy towards thermoregulation, leaving fewer resources available for risky activities and vice versa (Smith et al., 2019). Moreover, temperature can influence biotic environmental factors, such as predator–prey dynamics and food availability. For example, warmer temperatures may increase the activity levels of predators, making foraging riskier for prey (Johnson & Buller, 2016). This could result in prey exhibiting more cautious behaviour and reducing risk-taking to mitigate predation risk and increase the chance of survival. Temperature can also affect food availability, as extreme temperatures change the abundance, distribution, and accessibility of food resources, forcing animals to modify their risk-taking behaviour accordingly (Mathot et al., 2014).

Here, we empirically examined the effect of environmental variation on the relationship between survival and risk-taking behaviour using data collected over 14 breeding seasons from a wild population of collared flycatchers (*Ficedula albicollis*). Specifically, using annual recapture probability as a proxy of survival, we evaluated the effect of predation pressure, food availability, and mean temperature on the relationship between survival and risk-taking behaviour (measured as flight initiation distance [FID]; Blumstein, 2006; Møller, 2008). We predicted that risk-averse individuals would have a higher survival chance in years of higher predation pressure and/or favourable environmental conditions (i.e., abundant food and higher mean temperature).

Materials and methods

Study area and model species

Data were obtained from a population of collared flycatchers breeding in the Pilis Mountains (47° 43′N, 19° 01′E), Hungary. The study population is located in a continuous, mainly oak-dominated woodland within the protected and managed area of the Duna-Ipoly National Park and the Pilisi Parkerdő Zrt. The study area is approximately 45 ha, and it contains 550 nest boxes, mainly occupied by collared flycatchers. In each breeding season (April–June), the reproductive performance of collared flycatchers has been intensively monitored as part of a long-term study initiated in 1982 (Török & Tóth, 1988). Intensive monitoring also allowed us to estimate annual recapture probability.

The collared flycatcher is a small, relatively short-lived (4–5 years on average), long-distance migratory bird that breeds in deciduous forests in Central Europe (Cramp & Perrins, 1993). After spring migration from their winter quarters in Africa (arriving by mid-April), males establish territories around a nest hole, defend it by aggressive interactions against intruding individuals (Garamszegi et al., 2006), and try to attract prospecting females to the nesting site by singing close to it. The species nests in tree cavities but prefers artificial nest boxes (if available) over natural holes (Lundberg et al., 1981). The collared flycatcher is a highly philopatric species. In our population, males bred on average only 128 m and females 358 m away from the nest box occupied in the previous year (Könczey et al., 1992).

Fieldwork

We used field data on the risk-taking behaviour of male collared flycatchers from 2007 to 2020 and data on annual recapture probability from 2008 to 2021 (see Table 1 for annual sample sizes and Figure 1 for summary statistics). We assayed individual risk-taking behaviour in a standardized way by measuring FID during the courtship period (Garamszegi et al., 2008). FID quantifies the distance at which a focal individual flees from an approaching experimenter (Blumstein, 2003; Ydenberg & Dill, 1986). Therefore, it is an inverse measure of risk-taking behaviour, as risk-taking individuals allow the experimenter to approach closer, while risk-averse individuals flee when the experimenter is at a greater distance. The critique of FID is that it primarily reflects responses to humans rather than natural predators, and our results thus should be considered in this light. However, several studies have demonstrated that FID is related to antipredator behaviour in natural settings (Díaz et al., 2013; Møller & Tryjanowski, 2014; Møller et al., 2010). Thus, it is reasonable to assume that FID measured in the presence of an approaching human reflects the overall risk-taking behaviour of the tested individual. FID is a reliable measure of variation in risk-taking behaviour in our collared flycatcher population, as the adjusted repeatability of FID is moderate and significant in the within-day ($R = 0.461$, CI (95%) = 0.049–0.951, $p = 0.002$) and within-year ($R = 0.524$, CI (95%) = 0.395–0.624, $p < 0.001$) context, while the adjusted repeatability of FID is low in the among-year context ($R = 0.004$, CI (95%) = 0.000–0.335, $p = 0.955$; Krenhardt, 2022).

Table 1. Total number of collared flycatcher males (N_{ind}) assayed annually for their risk-taking behaviour (by estimating flight initiation distance [FID]) during the courtship period upon arrival to the breeding ground.

Year	*Nind*	Annual recapture		Recapture probability
		Not recaptured	Recaptured	
2007	15	7	8	0.53
2008	5	4	1	0.20
2009	35	21	14	0.40
2010	21	11	10	0.48
2011	29	23	6	0.21
2012	8	7	1	0.13
2013	39	25	14	0.36
2014	35	24	11	0.31
2015	37	16	21	0.57
2016	36	19	17	0.47
2017	9	7	2	0.22
2018	43	25	18	0.42
2019	31	21	10	0.32
2020	11	9	2	0.18
Σ	354			0.34

Note. The focal males were also categorized based on whether they were recaptured in the following breeding season. Recapture probability indicates the proportion of focal males recaptured in the next breeding seasons.

We could only gather FID data for males because their behaviour can be assessed around the defended nest boxes during courtship, while a similar procedure cannot be established for females. To assess FID, we first located singing and displaying males in their occupied territories just after their arrival from their winter quarters. Then, we simulated territorial aggression against the focal male by presenting a live male flycatcher (Garamszegi et al., 2006). The experimenter placed the decoy male—representing an intruder—1 m from the front of the focal male's nestbox inside a small cage. By doing so, we ensured that each focal bird was engaged in the same behavioural situation before assessing FID. When the focal male was observed displaying typical territorial behaviour (involving calls and excited flights) around the nest box or on the cage of the decoy male with a clear intention to fight, the experimenter started to approach the focal male from a distance of about 30 m at normal walking speed. The approach continued until the focal male flew away from the surroundings of the nest box. When this happened, the experimenter stopped and stood still, waiting. If the focal male returned to the surroundings within 2 min to continue its original activity, the experimenter started to approach the male again. This process was continued until the focal male did not return for

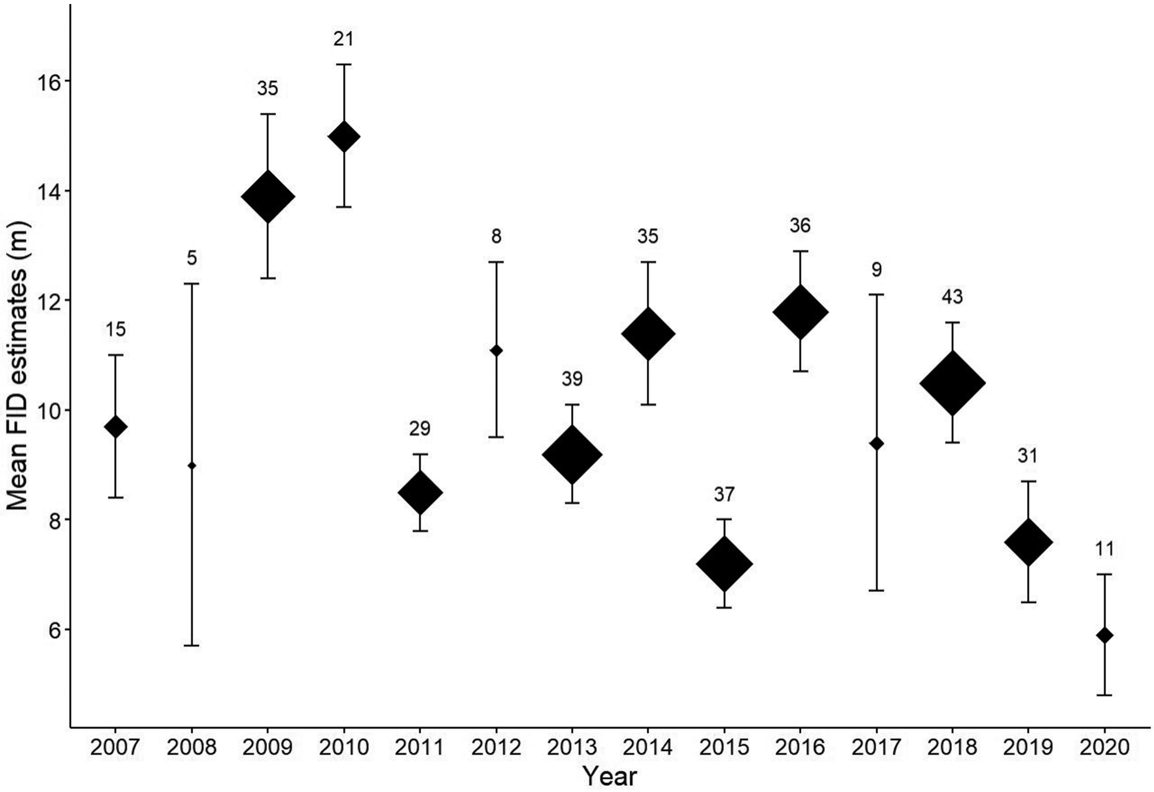

Figure 1. The annual mean of flight initiation distance (FID) characterizing the risk-taking behaviour of collared flycatcher males during the courtship season. The error bars show the ±SE, and the size of each diamond represents the sample size in the given year (also given above the error bars). There is no relationship between the annual mean FID and the study year (β (SE) = −0.280 (0.153), $z = -1.836$, $p = 0.091$).

at least 1 min. FID was measured as the distance between the cage of the decoy male and the last position of the experimenter that caused the focal male to flee and stay away from the stimulus cage for more than 1 min. FID measurements were carried out by 6 trained experimenters. Previous studies showed that the among-experimenter effect was negligible, so we did not consider this a potentially confounding factor here (Jablonszky et al., 2017).

We approximated individual survival with annual recapture probability, a binary variable describing whether or not a focal male was recaptured in the following breeding season. Individuals not recaptured in the following years were treated as dead. It is important to note that individuals in the study population show a strong breeding fidelity. Most individuals (95%) showed no gaps during their breeding history. Furthermore, instances of breeding outside the study plots were infrequent (personal observation), whether in the surrounding areas or in more distant locations (including other study populations of flycatchers, as indicated by ring recoveries). The above evidence suggests that most surviving individuals bred in the study population and that the fraction of surviving individuals broadly represented all surviving individuals. Thus, akin to similar long-term studies (Pärn et al., 2009), we assumed that local recruitment estimates were unbiased and reliably estimated survival.

Environmental factors

We characterized each breeding season with three different environmental factors at the population level: yearly estimates of nest predation pressure, food availability, and mean temperature during the courtship period. Nest predation pressure was calculated as the proportion of nests that were partially or fully predated from the egg-laying to the nestling-feeding period (breeding efforts were monitored in each nest box by regular checks) to the total number of nests (including all breeding bird species) in each year. This measure aimed to quantify the perceived risk of predation. The most common nest predators in our study area were the European pine marten (*Martes martes*) and the beech marten (*Martes foina*) during the investigated time period. Both are opportunistic predators and have a diverse diet (Bakaloudis et al., 2012; Twining et al., 2019). While they primarily feed on small mammals and birds, both species are skilled tree climbers and can opportunistically target the nests of various birds in tree cavities. They also targeted the artificial nest boxes in our study area, and they left clear signs of their activity at the nest boxes, including heavily disturbed nest material, nestling remains, or parts of the parents around or on the top of the nest box. The female martens give birth to their offspring in the first half of April, and their offspring live on their mother's milk for about 6 weeks (Mead, 1994). Therefore, during this period, females have elevated energy demands. As this intensive offspring care in martens overlaps with the egg-laying period of the two tit species (*Parus major* and *Cyanistes caeruleus*) in our study area, we relied on the assumption that predation pressure measured from the egg-laying of the tit species (from the beginning of April) reflected predation pressure when we perform the behavioural tests of collared flycatcher males from mid-April to early May. Predation pressure varied from negligible to 50% over the study years.

Food availability was estimated by the peak of the caterpillar biomass in each breeding season (we had data between

2007 and 2018). Given that foliage-eating caterpillars are one of the main items in the flycatchers' diet (Löhrl, 1976), we could reasonably assume that caterpillar biomass is a good predictor of the overall annual food supply. Each year, we collected caterpillar frass about every 5 days (the range was between 4 and 6 days) during the breeding season using five standard collectors (0.25 m^2 each) at two standard locations (ten in total). The mean annual frass masses were similar in the two locations (two-sample Welch's t-test; $p = 0.73$), suggesting that the spatial variation of caterpillar biomass is low in our study area and, therefore, that the collectors used are sufficient to characterize it. We weighed the collected frass samples to the nearest 0.001 g. After calculating the daily mean of the collected frass mass for each collection interval, we could determine the date of the peak of caterpillar biomass (see also Laczi et al., 2019). In most cases (8 of 12 study years), the date of the peak of the caterpillar biomass overlapped with the period of the behavioural tests, while in the rest of the years, the peak date was later. Moreover, the frass mass measured at the peak of the caterpillar biomass predicted the frass mass earlier in the season (Spearman's rank correlation: $\rho = 0.846$, $p < 0.001$). Therefore, we could reasonably assume that the measured frass mass at the peak of the caterpillar biomass reflected the food supply when the behavioural tests were performed. Two of the 12 study years were gradation years, when the population of caterpillars reached extremely high densities, resulting in almost 4 times higher food supply than the average food availability in other years. Therefore, we binarized our data based on whether the given study year was an ordinary or a graduation year. Although binarization caused information loss, we chose to binarise frass mass as other transformations could not handle its unusual distribution, and the values clearly fell into two categories.

Finally, we calculated the average value of the mean daily temperatures for each day between the first and last behavioural tests conducted within a given study year (i.e., one temperature estimate per year), using measurements from a nearby meteorological station supplied to the NOAA's National Climatic Data Centre (ftp://ftp.ncdc.noaa.gov/pub/data/gsod). This calculation provided a summary measure of the temperature conditions experienced by the collared flycatcher males throughout the behavioural testing period within a particular study year. By considering the average value of the mean daily temperatures, we obtained an overall representation of the temperature environment during the study period, capturing the central tendency of temperature values experienced by the animals over that time frame.

Statistical analyses

We built generalized linear mixed models (binomial distribution) using our 14-year-long dataset to examine whether the among-year variation in the annual predation pressure, food availability, and the average value of the mean daily mean temperatures during the courtship season was related to the among-year variation in the relationship between annual recapture probability and FID. Since the number of measured males in several study years was moderate (see Table 1), the effect of the three environmental factors was analyzed independently in separate models to avoid over-parametrization. Each model contained annual recapture probability (proxy of fitness) as the binary response variable, FID, z-transformed year (as a continuous variable to estimate trend effects), and one of the environmental factors as predictor variables. We also included the interaction between FID and z-transformed year (as a continuous variable) to test whether there was a temporal trend in the relationship between risk-taking behaviour and annual recapture probability and the interaction between FID and the environmental factor to test the effect of the environmental factor on the relationship between annual recapture probability and FID. The random part of the models contained the random intercept and random slope of FID for the year. Individual risk-taking behaviour might change along the repeated tests, as the individuals, based on their experiences during the tests, may become either bolder by getting accustomed to the test conditions (habituation) or shyer due to increased caution (sensitization). Therefore, we only considered the males' first tests in our current study; thus, neither habituation nor sensitization could have influenced their behaviour.

Previous studies revealed that the age of the individual, the date of the behavioural test, and the year of the test significantly affect the risk-taking behaviour of male flycatchers in our population (Krenhardt et al., 2016, 2021). Thus, the model above used relative FIDs, which were estimated as residuals from a linear model that contained the square root of (FID + 1) as a continuous response variable, and the age of the individual (two-level class variable: first-year old and older), the standardized date of the behavioural test (the number of days from the first day in the given year), and the year of the behavioural test as predictor variables.

To calculate and visualize the yearly slopes of the relationship between annual recapture probability and FID (Figure 2), we run a Bayesian regression model using Stan. This contained recapture probability as response variable (with Bernoulli distribution) and log10-transformed (FID + 1), age of the focal individual, and date of the behavioural test as fixed variables, a random intercept for the year and random slope of FID for the year. All continuous variables were z-transformed. The model was built with the "brms" package (Bürkner, 2017).

All analyses were carried out in the R statistical environment (version 4.1.2, R Core Team 2023). GLMM were fitted using the "glmmTMB" function from the "*glmmTMB*" package (version: 1.1.3, Brooks et al., 2017). This frequentist framework and the use of "*glmmTMB*" package allowed us to fit more complex models, as this package was specifically designed to deal with convergence issues common to complex generalized linear mixed models by working in the model template builder.

Ethical approval

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 and the Inspectorate for Environmental Protection, Nature Conservation and Waste Management of the Government Office of Pest County, Hungary (reference numbers: KTVF 16360-2/2007, KTVF 30871-1/2008, KTVF 43355-1/2008, KTVF 10949-8/2013, PE/KTF/11978-5/2015, PE-06/KTF/8550-4/2018, PE-06/KTF/8550-5/2018, PE-06/KTF/3331-4/2018), and the experimental procedure was approved by the ethical committee of the Eötvös Loránd University (reference number: TTK/2203/3). No individual

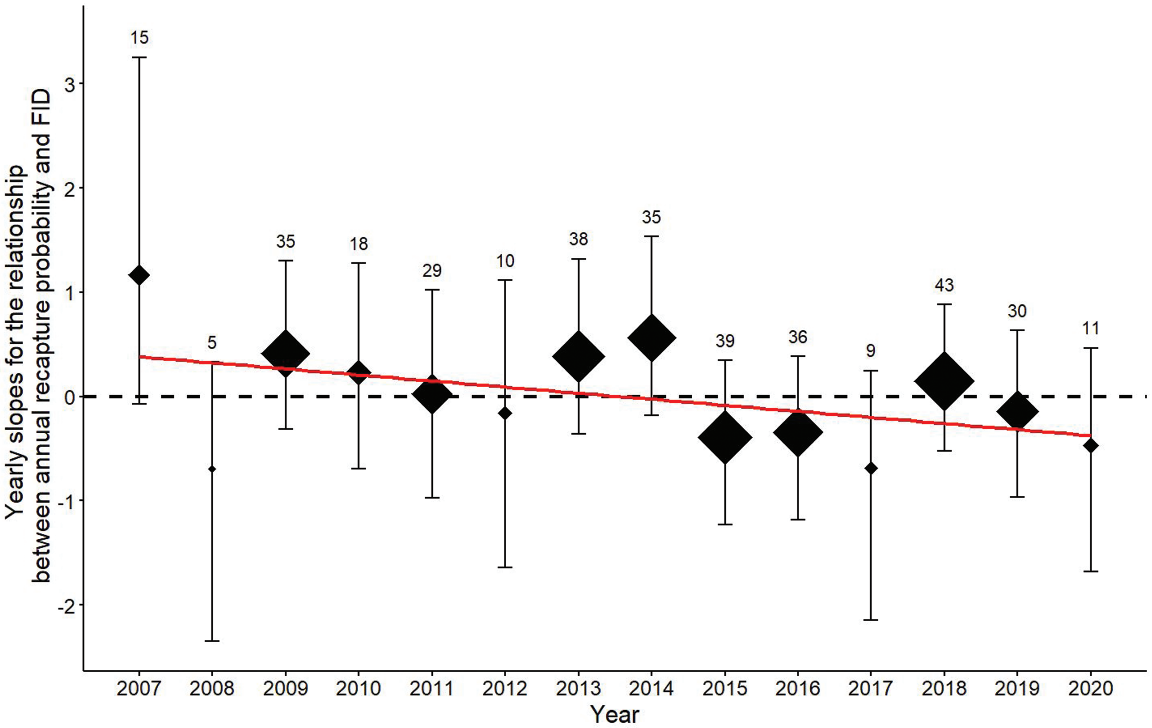

Figure 2. The effect of temporal trend on the relationship between annual recapture probability and FID in collared flycatcher males over the study period (solid line). The error bars represent the credible intervals around the estimates of year-specific random slopes from a statistically appropriate Bayesian regression model using Stan. Each diamond represents a relationship between annual recapture probability and FID observed in the designated year with a size proportional to the underlying sample size (also given above the error bars). The dashed grey line represents $r = 0$ correlation and is shown for guidance.

was harmed during our experiments, and none suffered any short-term consequences of the behavioural tests. To assess FID during the courtship period, we used live decoys that we captured on a remote study plot to ensure that the focal males were not familiar with the decoys. During the behavioural tests, we presented the decoys to the focal males in small cages (15 cm × 20 cm × 15 cm), which protected the decoys from any harmful encounters with the focal males. After the behavioural tests, we placed the decoys in larger cages (40 cm × 24 cm × 40 cm) covered with cotton sheets to minimize the level of stress and provided them with food (i.e., mealworms) and freshwater ad libitum. The decoys were held in captivity for as shortly as possible, and they were released at the site of capture after we ensured they were in good condition (i.e., proper body mass, active, and vivid behaviour). The time spent in captivity did not have any long-term effects on the decoys, as their reproductive success and survival in the given year did not differ from other flycatchers in the population (Garamszegi et al., 2009).

Results

We measured risk-taking behaviour in 354 individuals, on average 25 individuals (range 5–43) per season (see Table 1 for annual sample sizes). Mean risk-taking behaviour varied markedly over the years (Figure 1).

We found that the relationship between annual recapture probability and FID varied along a temporal trend over the study years, which was indicated by the statistically significant interaction between FID and year in the models (Table 2). Specifically, we found that the relationship between annual recapture probability and FID decreased over the study years and changed from positive to negative (Figure 2). The negative trend in the relationship between annual recapture probability and FID was also confirmed by our base model (β (SE) = −0.255 (0.128), $z = -1.991$, $p = 0.046$), in which none of the three environmental variables were included. However, none of the environmental factors considered independently or iteratively with FID affected annual recapture probability. Overall, these results suggest that these environmental factors did not mediate the temporal variation in the relationship between annual recapture probability and FID.

Discussion

During 14 breeding seasons, we investigated the mediating effects of three environmental factors (i.e., predation pressure, food availability, and mean temperature) on the relationship between survival and risk-taking behaviour in a free-living population of collared flycatchers. We found significant variation in the relationship between annual recapture probability and FID across the study years, as indicated by the interaction between FID and year in our models, revealing a negative linear trend. Specifically, we found that the relationship between annual recapture probability and FID decreased over the study years. However, none of the three considered environmental factors, independently or iteratively with FID, affected annual recapture probability.

Understanding the nuances of risk-taking behaviour is crucial for interpreting the observed patterns. Flight initiation distance is a critical component of an individual's antipredatory strategy, reflecting its ability to assess and respond to

Table 2. Results from generalized linear mixed models investigating the effect of environmental factors on the relationship between annual recapture probability and flight initiation distance (FID).

	Predation pressure			Food availability			Mean temperature		
Predictors	β (SE)	z	p	β (SE)	z	p	β (SE)	z	p
FID	0.206 (0.127)	1.618	0.106	0.144 (0.149)	0.966	0.334	0.199 (0.125)	1.595	0.111
Year	−0.081 (0.163)	−0.500	0.617	0.078 (0.127)	0.613	0.54	0.042 (0.147)	0.289	0.773
Env. factor*	−0.043 (0.167)	−0.257	0.797	−0.406 (0.311)	−1.304	0.192	−0.217 (0.150)	−1.448	0.148
FID: Year	−0.280 (0.182)	−1.539	0.124	**−0.283 (0.126)**	**−2.249**	**0.025**	**−0.338 (0.154)**	**−2.196**	**0.028**
FID: Env. factor*	−0.025 (0.166)	−0.153	0.878	0.310 (0.298)	1.042	0.297	0.162 (0.154)	1.053	0.293
Random effects	Variance			Variance			Variance		
Year	0.07			0.018			0.048		
FID | year	0.008			0.003			0.002		

Note. All models had the same structure except for the environmental factor (Env. factor*) considered. Three environmental factors were analyzed independently, and the statistics for each of those models are shown in each vertical section of the table for predation pressure (left), food availability (centre), and mean temperature (right). See the main text for further details. The significant results are shown in bold. $N = 354$.

potential environmental threats. Thus, a few metres of reduction in FID could suggest a nuanced but critical adjustment in the risk-taking behaviour of the population. One plausible interpretation is that individuals exhibiting a shorter FID may be more tolerant of proximity to potential threats in general and predators in particular. This behavioural change could be driven by various factors, including a perceived decrease in predation pressure, increased familiarity with the environment, or alterations in resource distribution. Such changes in anti-predatory responses could influence the survival and reproductive success of individuals within the population, thus population structure, predator–prey dynamics, and community interactions.

One possible explanation for the linear trend observed for the relationship between annual recapture probability and FID might be the adaptation to climate change. Climate change via elevated temperatures and unpredictable climatic variations has drastically altered the environmental conditions in the last few decades, to which migrant birds are particularly sensitive (Romano et al., 2023). European flycatchers have demonstrated considerable phenological responses to climate change, advancing the onset of breeding through early arrival from their winter quarters and early clutch initiation as springs get warmer (Both & Visser, 2001; Both et al., 2005). In the studied population, we have also observed a remarkable shift in breeding dates (i.e., the laying date of the first egg in a particular breeding season has shifted significantly (approximately 1 week) earlier between 2000 and 2020: β (SE) $= -0.336$ (0.127), $z = -2.645$, $p = 0.016$, unpublished data). Selection for breeding earlier also selects for early arrival, resulting in individuals exposing themselves to the more unpredictable weather conditions of early spring (Brown & Brown, 2000). Individuals that leave their winter quarters early are likely to find favourable environmental conditions at the breeding areas, but in some years, they may also meet very harsh conditions upon arrival (Bêty et al., 2004). Furthermore, climate change can also cause increased fluctuations in the local weather; thus, early arriving birds may put themselves at a higher risk as investments into early arrival can incur costs if breeding is delayed due to local conditions (Shipley et al., 2020). Therefore, adaptation to climate change via the advancement of laying date requires the selection of more risk-taker individuals that cope with unpredictable environmental conditions during early arrival. We might have captured this selection process via the observed temporal trend in the relationship between annual recapture probability and FID over the study period.

Other environmental factors, not inherently connected to climate change, could also be responsible for the temporal variation in the relationship between survival and risk-taking behaviour, resulting in linear changes over time (e.g., population density, Nicolaus et al., 2016). In our statistical models, the effects of the year may be assumed to reflect the effects of climate change, but they may also reflect other environmental factors that linearly changed over the years independently of climate change. Moreover, selection for higher risk-taking may occur during the winter quarters or during migration; thus, the linear trend in our study area may not necessarily reflect changes in the environment at the breeding areas (Remisiewicz & Underhill, 2022). Note that our models included mean temperature, but always as an additional covariate to the linear trend; thus, this variable can be interpreted to reflect temperature variations that are independent of climate change.

We found no evidence that the analyzed environmental factors (i.e., predation pressure, food availability, and mean temperature) mediated the temporal variation in the relationship between survival and risk-taking behaviour, which could be due to several reasons. First, it is plausible that other unevaluated environmental factors, such as habitat complexity, may have a greater impact on shaping selection for this trait than those considered here (Boon et al., 2008) or elsewhere (le Vaillant et al., 2021), especially if these factors act outside the breeding season. Unfortunately, as occurs with other migratory taxa, our current understanding of the numerous environmental factors affecting collared flycatcher males during their annual cycle is very limited (Briedis et al., 2017). Second, it is also possible that we have considered the right environmental factors as predictors, but we relied on unjustified assumptions. For example, we assessed predation pressure from the egg-laying to the nestling-feeding period, and we assumed that the predation pressure of the two marten species was stable during the whole breeding season (Mead, 1994). Third, it is possible that we did not have adequate statistical power.

Although we were able to incorporate data from 14 study years, it is important to note that in a few instances, particularly in 3 or 4 years, our sample sizes were relatively small. This variability in sample sizes may introduce difficulties in making robust inferences and could potentially impact the reliability of our interpretations. We may have also needed a longer time period to detect the effects of the measured environmental factors, given that the environmental factors may operate through weak or intermediate effects (Li et al., 2019). Fourth, within-individual variation in risk-taking behaviour could have also been a confounding, unaccounted factor in our study, which may introduce an error in the year-specific estimates of fitness costs associated with risk-taking behaviour. Birds may plastically adjust their risk-taking behaviour to the changing environment across years, which is corroborated by the low among-year repeatability of FID. Finally, it is possible that individuals with different behavioural phenotypes might have different chances to disperse beyond the study area, and therefore, they remain undetected, thereby introducing noise in our data (Duckworth et al., 2015).

In conclusion, we found temporal variation in the relationship between survival and risk-taking behaviour over our 14-year-long study period. We found that the relationship between annual recapture probability and FID decreased over the study years. Specifically, in the early years of the study, risk-avoiding individuals exhibited a higher annual recapture probability, whereas in the later years, risk-avoiders had a lower annual recapture probability. However, the specific factors driving this apparent selective pattern remained elusive, as none of the three assessed biotic and abiotic factors mediated this relationship. Further research is needed to delve into the intricate interplay of behaviours and environmental factors in wild populations. Comprehending the evolutionary dynamics of risk-taking along with those of other behavioural characteristics within a population is essential to gain insights into the adaptive nature of these traits and their role in shaping the survival and persistence of animal populations over time.

Data availability

The data underlying this article are available in Dryad at https://doi.org/10.5061/dryad.jdfn2z3ht.

Author contributions

Katalin Krenhardt (Conceptualization [Equal], Data curation [Lead], Formal analysis [Equal], Investigation [Equal], Methodology [Equal], Project administration [Equal], Visualization [Lead], Writing—original draft [Lead], Writing—review & editing [Lead]), Jesus Martinez-Padilla (Formal analysis [Equal], Methodology [Equal], Writing—review & editing [Equal]), David Canal (Methodology [Equal], Writing—review & editing [Equal]), Mónika Jablonszky (Formal analysis [Equal], Investigation [Equal], Methodology [Equal], Visualization [Supporting], Writing—review & editing [Equal]), Gergely Hegyi (Investigation [Equal], Writing—review & editing [Equal]), Márton Herényi (Investigation [Equal], Writing—review & editing [Supporting]), Miklós Laczi (Investigation [Equal], Writing—review & editing [Equal]), Gábor Markó (Investigation [Equal], Writing—review & editing [Supporting]), Gergely Nagy (Investigation [Equal], Writing—review & editing [Supporting]), Balázs Rosivall (Investigation [Equal], Writing—review & editing [Supporting]), Eszter Szász (Investigation [Equal]), Eszter Szöllősi (Investigation [Equal], Writing—review & editing [Supporting]), János Török (Investigation [Equal]), Éva Vaskuti (Investigation [Equal]), Sándor Zsebők (Investigation [Equal], Writing—review & editing [Supporting]), and László Garamszegi (Conceptualization [Lead], Funding acquisition [Lead], Investigation [Equal], Methodology [Equal], Project administration [Equal], Supervision [Lead], Writing—review & editing [Equal])

Funding

This study was supported by the Hungarian National Research, Development and Innovation Office (K-115970, K-124443, K-139992, FK-127917, PD-121276, FK-146466) and the Ministry of Economy and Competitiveness in Spain (CGL2015-70639-P). KK was supported by a PhD scholarship awarded by the Eötvös Loránd University, Budapest, Hungary. JM-P was funded by ARAID Foundation and the Ministry of Science and Innovation (PID2019-104835GB-I00). DC was supported by the Hungarian Academy of Sciences (MTA Premium Postdoctoral Research Program; Ref: 2019-353), a Talent Attraction fellowship from the Autonomous Community of Madrid (CAM), Spain (2022-T1/AMB-24025), and the project PID2022-141763NA-I00 funded by MCIN/AEI. GM was supported by the Hungarian Ministry for Innovation and Technology within the framework of the Thematic Excellence Programme 2020 (TKP2020-IKA-12, TKP2020-NKA-16). ESzö was supported by the János Bolyai research scholarship from the Hungarian Academy of Sciences (BO/00163/22).

Acknowledgments

We are grateful to the Pilis Park Forestry for their cooperation and support.

Conflicts of interest

None declared.

References

Abrams, P. A. (1991). Life history and the relationship between food availability and foraging effort. *Ecology*, *72*(4), 1242–1252. https://doi.org/10.2307/1941098

Bakaloudis, D. E., Vlachos, C. G., Papakosta, M. A., … Chatzinikos, E. N. (2012). Diet composition and feeding strategies of the stone marten (*Martes foina*) in a typical Mediterranean ecosystem. *Scientific World Journal*, *2012*, 163920.

Behney, A. C., O'Shaughnessy, R., Eichholz, M. W., & Stafford, J. D. (2019). Worth the reward? An experimental assessment of risk-taking behavior along a life history gradient. *Journal of Avian Biology*, *50*(6), e02068.

Bêty, J., Giroux, J. -F., & Gauthier, G. (2004). Individual variation in timing of migration: Causes and reproductive consequences in greater snow geese (*Anser caerulescens atlanticus*). *Behavioral Ecology and Sociobiology*, *57*, 1–8.

Biro, P. A., & Stamps, J. A. (2010). Do consistent individual differences in metabolic rate promote consistent individual differences in behavior? *Trends in Ecology and Evolution*, *25*(11), 653–659. https://doi.org/10.1016/j.tree.2010.08.003

Blumstein, D. T. (2003). Flight-initiation distance in birds is dependent on intruder starting distance. *Journal of Wildlife Management*, *67*(4), 852–857. https://doi.org/10.2307/3802692

Blumstein, D. T. (2006). Developing an evolutionary ecology of fear: How life history and natural history traits affect disturbance tolerance in birds. *Animal Behaviour*, *71*(2), 389–399. https://doi.org/10.1016/j.anbehav.2005.05.010

Bolnick, D. I., Svänback, R., Fordyce, J. A., … Forister, M. L. (2003). The ecology of individuals: Incidence and implications of individual specialization. *The American Naturalist*, *161*(1), 1–28. https://doi.org/10.1086/343878

Boon, A. K., Réale, D., & Boutin, S. (2008). Personality, habitat use, and their consequences for survival in North American red squirrels *Tamiasciurus hudsonicus*. *Oikos*, *117*(9), 1321–1328. https://doi.org/10.1111/j.0030-1299.2008.16567.x

Borcherding, J., & Magnhagen, C. (2008). Food abundance affects both morphology and behaviour of juvenile perch. *Ecology of Freshwater Fish*, *17*(2), 207–218. https://doi.org/10.1111/j.1600-0633.2007.00272.x

Both, C., Bijlsma, R. G., & Visser, M. E. (2005). Climatic effects on timing of spring migration and breeding in a long-distance migrant, the pied flycatcher *Ficedula hypoleuca*. *Journal of Avian Biology*, *36*, 368–373.

Both, C., & Visser, M. E. (2001). Adjustment to climate change is constrained by arrival date in a long-distance migrant bird. *Nature*, *411*(6835), 296–298.

Briedis, M., Hahn, S., & Adamík, P. (2017). Cold spell en route delays spring arrival and decreases apparent survival in a long-distance migratory songbird. *BMC Ecology*, *17*(1), 11. https://doi.org/10.1186/s12898-017-0121-4

Brooks, M. E., Kristensen, K., van Benthem, K. J., … Bolker, B. M. (2017). glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. *R Journal*, *9*, 378–400.

Brown, C. R., & Brown, M. B. (2000). Weather-mediated natural selection on arrival time in cliff swallows (*Petrochelidon pyrrhonota*). *Behavioral Ecology and Sociobiology*, *47*, 339–345.

Brown, J. S., & Kotler, B. P. (2004). Hazardous duty pay and the foraging cost of predation. *Ecology Letters*, *7*(10), 999–1014. https://doi.org/10.1111/j.1461-0248.2004.00661.x

Bürkner, P. C. (2017). brms: An R package for Bayesian multilevel models using Stan. *Journal of Statistical Software*, *80*(1), 1–28.

Caraco, T. (1980). On foraging time allocation in a stochastic environment. *Ecology*, *61*(1), 119–128. https://doi.org/10.2307/1937162

Carrete, M., Martínez-Padilla, J., Rodríguez-Martínez, S., … Tella, J. L. (2016). Heritability of fear of humans in urban and rural populations of a bird species. *Scientific Reports*, *6*, 31060. https://doi.org/10.1038/srep31060

Charmantier, A., & Gienapp, P. (2014). Climate change and timing of avian breeding and migration: Evolutionary versus plastic changes. *Evolutionary Applications*, *7*(1), 15–28. https://doi.org/10.1111/eva.12126

Charmantier, A., McCleery, R. H., Cole, L. R., … Sheldon, B. C. (2008). Adaptive phenotypic plasticity in response to climate change in a wild bird population. *Science*, *320*(5877), 800–803. https://doi.org/10.1126/science.1157174

Coates, W. D., Hale, R., & Morrongiello, J. R. (2019). Dispersal decisions and personality in a freshwater fish. *Animal Behaviour*, *157*, 209–218. https://doi.org/10.1016/j.anbehav.2019.07.012

Cramp, S. & Perrins, C. M. (1993). *Handbook of the birds of Europe, the Middle East and North Africa: The birds of the Western Palearctic*. Oxford University Press.

Cuervo, J. J., & Møller, A. P. (1999). Phenotypic variation and fluctuating asymmetry in sexually dimorphic feather ornaments in relation to sex and mating system. *Biological Journal of the Linnean Society*, *68*(4), 505–529. https://doi.org/10.1111/j.1095-8312.1999.tb01186.x

Cuervo, J. J., & Møller, A. P. (2001). Components of phenotypic variation in avian ornamental and non-ornamental feathers. *Evolutionary Ecology*, *15*(1), 53–72. https://doi.org/10.1023/a:1011913804309

D'Anna, G., Giacalone, V. M., Fernández, T. V., … Badalamenti, F. (2012). Effects of predator and shelter conditioning on hatchery-reared white seabream *Diplodus sargus* (L., 1758) released at sea. *Aquaculture*, *356*, 91–97.

Dhellemmes, F., Finger, J. S., Smukall, M. J., … Krause, J. (2021). Personality-driven life history trade-offs differ in two subpopulations of free-ranging predators. *The Journal of Animal Ecology*, *90*(1), 260–272. https://doi.org/10.1111/1365-2656.13283

Díaz, M., Møller, A. P., Flensted-Jensen, E., … Tryjanowski, P. (2013). The geography of fear: a latitudinal gradient in anti-predator escape distances of birds across Europe. *PLoS One*, *8*(5), e64634. https://doi.org/10.1371/journal.pone.0064634

Duckworth, R. A., Belloni, V., & Anderson, S. R. (2015). Cycles of species replacement emerge from locally induced maternal effects on offspring behavior in a passerine bird. *Science*, *347*(6224), 875–877. https://doi.org/10.1126/science.1260154

Evans, S. R., & Gustafsson, L. (2017). Climate change upends selection on ornamentation in a wild bird. *Nature Ecology & Evolution*, *1*(2), 39. https://doi.org/10.1038/s41559-016-0039

Garamszegi, L. Z., Eens, M., & Török, J. (2008). Birds reveal their personality when singing. *PLoS One*, *3*(7), e2647. https://doi.org/10.1371/journal.pone.0002647

Garamszegi, L. Z., Eens, M., & Török, J. (2009). Behavioural syndromes and trappability in free-living collared flycatchers, *Ficedula albicollis*. *Animal Behaviour*, *77*(4), 803–812. https://doi.org/10.1016/j.anbehav.2008.12.012

Garamszegi, L. Z., Rosivall, B., Hegyi, G., … Eens, M. (2006). Determinants of male territorial behavior in a Hungarian collared flycatcher population: Plumage traits of residents and challengers. *Behavioral Ecology and Sociobiology*, *60*(5), 663–671. https://doi.org/10.1007/s00265-006-0210-4

Garant, D. (2020). Natural and human-induced environmental changes and their effects on adaptive potential of wild animal populations. *Evolutionary Applications*, *13*(6), 1117–1127. https://doi.org/10.1111/eva.12928

Gienapp, P., Teplitsky, C., Alho, J. S., … Merilä, J. (2008). Climate change and evolution: Disentangling environmental and genetic responses. *Molecular Ecology*, *17*(1), 167–178. https://doi.org/10.1111/j.1365-294X.2007.03413.x

Grant, R. B., & Grant, P. R. (2003). What Darwin's finches can teach us about the evolutionary origin and regulation of biodiversity. *BioScience*, *53*, 965–975.

Heynen, M., Borcherding, J., Bunnefeld, N., & Magnhagen, C. (2016). Plasticity and consistency of behavioural responses to predation risk in laboratory environments. *Journal of Zoology*, *300*(3), 228–235. https://doi.org/10.1111/jzo.12375

Hurly, T. A., & Healy, S. D. (2018). How variance and risk affect foraging behavior. In B. D. Roitberg (Ed.), *Reference module in life sciences*. Elsevier

Jablonszky, M., Szász, E., Markó, G., … Garamszegi, L. Z. (2017). Escape ability and risk-taking behaviour in a Hungarian population of the collared flycatcher (*Ficedula albicollis*). *Behavioral Ecology and Sociobiology*, *71*(3), 54.

Johnson, P. T. J., & Buller, I. D. (2016). Temperature-dependent effects of predator exposure on prey foraging behavior and growth. *Oecologia*, *182*, 449–458.

Jolles, J. W., Briggs, H. D., Araya-Ajoy, Y. G., & Boogert, N. J. (2019). Personality, plasticity and predictability in sticklebacks: Bold fish are less plastic and more predictable than shy fish. *Animal Behaviour*, *154*, 193–202. https://doi.org/10.1016/j.anbehav.2019.06.022

Kingsolver, J. G., Diamond, S. E., Siepielski, A. M., & Carlson, S. M. (2012). Synthetic analyses of phenotypic selection in natural populations: Lessons, limitations and future directions. *Evolutionary Ecology*, *26*(5), 1101–1118. https://doi.org/10.1007/s10682-012-9563-5

Kingsolver, J. G., Higgins, J. K., & Augustine, K. E. (2015). Fluctuating temperatures and ectotherm growth: Distinguishing non-linear and time-dependent effects. *The Journal of Experimental Biology*, *218*(Pt 14), 2218–2225. https://doi.org/10.1242/jeb.120733

Kingsolver, J. G., Hoekstra, H. E., Hoekstra, J. M., … Beerli, P. (2001). The strength of phenotypic selection in natural populations. *The American Naturalist*, *157*(3), 245–261. https://doi.org/10.1086/319193

Könczey, R., Török, J., & Tóth, L. (1992). Breeding success and breeding territory fiedelity in the Collared flycatcher (*Ficedula albicollis*). *Állattani Közlemények*, *78*, 69–76. (in Hungarian)

Kortet, R., Hedrick, A. V., & Vainikka, A. (2010). Parasitism, predation and the evolution of animal personalities. *Ecology Letters*, *13*(12), 1449–1458. https://doi.org/10.1111/j.1461-0248.2010.01536.x

Krenhardt, K. (2022). *The evolutionary ecology of animal personality—Unravelling individual-specific and environmental effects that shape consistency and plasticity in risk-taking behaviour in a passerine bird* [Doctoral dissertation]. https://doi.org/10.15476/ELTE.2022.141

Krenhardt, K., Markó, G., Jablonszky, M., … Garamszegi, L. Z. (2021). Sex-dependent risk-taking behaviour towards different predatory stimuli in the collared flycatcher. *Behavioural Processes*, *186*, 104360. https://doi.org/10.1016/j.beproc.2021.104360

Krenhardt, K., Markó, G., Szász, E., … Garamszegi, L. Z. (2016). A test on within-individual changes in risk-taking behaviour due to experience to predation in the collared flycatcher (*Ficedula albicollis*). *Ornis Hungarica*, *24*(1), 115–127. https://doi.org/10.1515/orhu-2016-0007

Laczi, M., Garamszegi, L. Z., Hegyi, G., … Török, J. (2019). Teleconnections and local weather orchestrate the reproduction of tit species in the Carpathian Basin. *Journal of Avian Biology*, *50*(12), e02179.

Lapiedra, O., Schoener, T. W., Leal, M., … Kolbe, J. J. (2018). Predator-driven natural selection on risk-taking behavior in anole lizards. *Science*, *360*(6392), 1017–1020. https://doi.org/10.1126/science.aap9289

Le Cœur, C., Thibault, M., Pisanu, B., … Baudry, E. (2015). Temporally fluctuating selection on a personality trait in a wild rodent population. *Behavioral Ecology*, *26*(5), 1285–1291. https://doi.org/10.1093/beheco/arv074

Le Vaillant, J., Potti, J., Camacho, C., … Martínez-Padilla, J. (2021). Fluctuating selection driven by global and local climatic conditions leads to stasis in breeding time in a migratory bird. *Journal of Evolutionary Biology*, *34*(10), 1541–1553. https://doi.org/10.1111/jeb.13916

Li, C., Zheng, X. -D., Feng, T. -J., … Tao, Y. (2019). Weak selection can filter environmental noise in the evolution of animal behavior. *Physical Review E*, *100*(5), 052411.

Lima, S. L., & Bednekoff, P. A. (1999). Temporal variation in danger drives antipredator behavior: The predation risk allocation hypothesis. *The American Naturalist*, *153*(6), 649–659. https://doi.org/10.1086/303202

Löhrl, H. (1976). Studies of less familiar birds. 179. Collared flycatcher. *British Birds*, *69*, 20–26.

Lundberg, A., Alatalo, R. V., Carlson, A., & Ulfstrand, S. (1981). Biometry, habitat distribution and breeding success in the pied flycatcher *Ficedula hypoleuca*. *Ornis Scandinavica*, *12*(1), 68–79. https://doi.org/10.2307/3675907

Marrot, P., Charmantier, A., Blondel, J., & Garant, D. (2018). Current spring warming as a driver of selection on reproductive timing in a wild passerine. *Journal of Animal Ecology*, *87*(3), 754–764. https://doi.org/10.1111/1365-2656.12794

Mathot, K. J., Nicolaus, M., Araya-Ajoy, Y. G., … Kempenaers, B. (2014). Does metabolic rate predict risk-taking behaviour? A field experiment in a wild passerine bird. *Functional Ecology*, *29*, 239–249.

Mead, R. (1994). Reproduction in *Martes*. In S. Buskirk, A. Harestad, M. Raphael, & R. Powell (Eds.), *Martens, sables, and fishers: Biology and conservation*. Cornell University Press.

Merilä, J., & Hendry, A. P. (2014). Climate change, adaptation, and phenotypic plasticity: the problem and the evidence. *Evolutionary Applications*, *7*(1), 1–14. https://doi.org/10.1111/eva.12137

Michel, M. J., Chevin, L. M., & Knouft, J. H. (2014). Evolution of phenotype-environment associations by genetic responses to selection and phenotypic plasticity in a temporally autocorrelated environment. *Evolution*, *68*(5), 1374–1384. https://doi.org/10.1111/evo.12371

Møller, A. P. (2008). Flight distance of urban birds, predation, and selection for urban life. *Behavioral Ecology and Sociobiology*, *63*(1), 63–75. https://doi.org/10.1007/s00265-008-0636-y

Møller, A. P. (2014). Life history, predation and flight initiation distance in a migratory bird. *Journal of Evolutionary Biology*, *27*(6), 1105–1113. https://doi.org/10.1111/jeb.12399

Møller, A. P., Erritzøe, J., & Nielsen, J. T. (2010). Causes of interspecific variation in susceptibility to cat predation on birds. *Chinese Birds*, *1*(2), 97–111. https://doi.org/10.5122/cbirds.2010.0001

Møller, A. P., Grim, T., Ibáñez-Álamo, J. D., … Tryjanowski, P. (2013). Change in flight initiation distance between urban and rural habitats following a cold winter. *Behavioral Ecology*, *24*, 1211–1217.

Møller, A. P., & Tryjanowski, P. (2014). Direction of approach by predators and flight initiation distance of urban and rural populations of birds. *Behavioral Ecology*, *25*(4), 960–966. https://doi.org/10.1093/beheco/aru073

Morales-Mata, J. I., Potti, J., Camacho, C., … Canal, D. (2022). Phenotypic selection on an ornamental trait is not modulated by breeding density in a pied flycatcher population. *Journal of Evolutionary Biology*, *35*(4), 610–620. https://doi.org/10.1111/jeb.13993

Moyer, B. R., Drown, D. M., & Clayton, D. H. (2002). Low humidity reduces ectoparasite pressure: Implications for host life history evolution. *Oikos*, *97*(2), 223–228. https://doi.org/10.1034/j.1600-0706.2002.970208.x

Nicolaus, M., Tinbergen, J. M., Ubels, R., … Dingemanse, N. J. (2016). Density fluctuations represent a key process maintaining personality variation in a wild passerine bird. *Ecology Letters*, *19*(4), 478–486. https://doi.org/10.1111/ele.12584

Pärn, H., Jensen, H., Ringsby, T. H., & Sæther, B. (2009). Sex-specific fitness correlates of dispersal in a house sparrow metapopulation. *Journal of Animal Ecology*, *78*(6), 1216–1225. https://doi.org/10.1111/j.1365-2656.2009.01597.x

Pollock, N. B., Gawne, E., & Taylor, E. N. (2015). Effects of temperature on feeding duration, success, and efficiency of larval western black-legged ticks (*Acari: Ixodidae*) on western fence lizards. *Experimental and Applied Acarology*, *67*(2), 299–307. https://doi.org/10.1007/s10493-015-9950-z

Quinn, J. L., & Cresswell, W. (2005). Personality, anti-predation behaviour and behavioural plasticity in the chaffinch *Fringilla coelebs*. *Behaviour*, *142*(9-10), 1377–1402. https://doi.org/10.1163/156853905774539391

R Core Team. (2023). R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/

Réale, D., & Festa-Bianchet, M. (2003). Predator-induced natural selection on temperament in bighorn ewes. *Animal Behaviour*, *65*(3), 463–470. https://doi.org/10.1006/anbe.2003.2100

Réale, D., Reader, S. M., Sol, D., … Dingemanse, N. J. (2007). Integrating animal temperament within ecology and evolution. *Biological Reviews of the Cambridge Philosophical Society*, *82*(2), 291–318. https://doi.org/10.1111/j.1469-185X.2007.00010.x

Remisiewicz, M., & Underhill, L. G. (2022). Large-scale climatic patterns have stronger carry-over effects than local temperatures on spring phenology of long-distance passerine migrants between Europe and Africa. *Animals*, *12*(13), 1732. https://doi.org/10.3390/ani12131732

Romano, A., Garamszegi, L. Z., Rubolini, D., & Ambrosini, R. (2023). Temporal shifts in avian phenology across the circannual cycle in a rapidly changing climate: A global meta-analysis. *Ecological Monographs*, *93*(1), e1552.

Santicchia, F., Gagnaison, C., Bisi, F., … Wauters, L. A. (2018). Habitat-dependent effects of personality on survival and reproduction in red squirrels. *Behavioral Ecology and Sociobiology*, *72*(8), 1–13.

Shipley, R., Twining, C. W., Taff, C. C., … Winkler, D. W. (2020). Birds advancing lay dates with warming springs face greater risk of chick mortality. *Proceedings of the National Academy of Sciences of the United States of America*, *117*, 25590–25594.

Sih, A. (2013). Understanding variation in behavioural responses to human-induced rapid environmental change: A conceptual overview. *Animal Behaviour*, *85*(5), 1077–1088. https://doi.org/10.1016/j.anbehav.2013.02.017

Smith, B. R., & Blumstein, D. T. (2008). Fitness consequences of personality: A meta-analysis. *Behavioral Ecology*, *19*(2), 448–455. https://doi.org/10.1093/beheco/arm144

Smith, D., Riley, J., & Wolf, B. (2019). Effects of temperature on energetic trade-offs and risk-taking behavior in lizards. *Journal of Animal Ecology*, *88*, 757–767.

Török, J., & Tóth, L. (1988). Density dependence in reproduction of the collared flycatcher (*Ficedula albicollis*) at high population levels. *Journal of Animal Ecology*, *57*, 251–258.

Twining, J. P., Montgomery, I., Fitzpatrick, V., … Tosh, D. G. (2019). Seasonal, geographical, and habitat effects on the diet of a recovering predator population: The European pine marten (*Martes martes*) in Ireland. *European Journal of Wildlife Research*, *65*(3), 51.

Van Buskirk J. (2012). Behavioural plasticity and environmental change. In U. Candolin & B. B. M. Wong (Eds.), *Behavioural responses to a changing world: Mechanisms and consequences* (pp. 145–158). Oxford University Press.

Verdolin, J. L. (2006). Meta-analysis of foraging and predation risk trade-offs in terrestrial systems. *Behavioral Ecology and Sociobiology*, *60*(4), 457–464. https://doi.org/10.1007/s00265-006-0172-6

Wolf, M., & Weissing, F. J. (2012). Animal personalities: Consequences for ecology and evolution. *Trends in Ecology & Evolution*, *27*(8), 452–461. https://doi.org/10.1016/j.tree.2012.05.001

Wong, B. B. M., & Candolin, U. (2015). Behavioral responses to changing environments. *Behavioral Ecology*, *26*(3), 665–673. https://doi.org/10.1093/beheco/aru183

Ydenberg, R. C., & Dill, L. M. (1986). The economics of fleeing from predators. *Advances in the Study of Behavior*, *16*, 229–249.